

The influence of socio-biological cues on saccadic orienting

Submitted by Nicola Jean Gregory

to the University of Exeter as a thesis for the degree of

Doctor of Philosophy in Psychology, June 2011.

This thesis is available for Library use on the understanding that it is copyright material and that no quotation from the thesis may be published without acknowledgement.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University

Signature:

Abstract

Previous research has suggested that viewing of another's averted eye gaze causes automatic orienting of attention and eye movements in observers due to the importance of eye gaze for effective social interaction. Other types of visual cues with no social or biological relevance, such as arrows, are claimed not to produce such a direct effect on orienting behaviour. The finding that processing of eye gaze is reduced in individuals with Autistic Spectrum Disorders as well as following damage to the orbitofrontal cortex of the brain, suggests that gaze processing is indeed critical for effective social behaviour and therefore eye gaze may constitute a "special" directional cue. This thesis tested these ideas by examining the influence of socio-biological (eye gaze and finger pointing) and non-social cues (arrows and words) on eye movement responses in both healthy control participants and those with damage to the frontal lobes of the brain. It further investigated the relationship between orienting to gaze and arrow cues and autistic traits in a healthy population. Important differences between the effects of socio-biological and non-social cues were found on saccadic eye movements. Although in the pro-saccade tasks, arrow cues caused a similar facilitation of responses in the cued direction as eye gaze and pointing cues, in the anti-saccade tasks (in which participants have to respond away from the location of a peripheral onset), arrows had a greatly reduced effect on oculomotor programming relative to the biologically relevant cues. Importantly, although the socio-biological cues continued to influence saccadic responses, the facilitation was in the *opposite* direction to the cues. This finding suggests that the cues were being processed within the same "anti-response" task set (i.e. "go opposite") as the target stimulus. Word cues had almost no effects on saccadic orienting in either pro- or anti-saccade tasks.

Schematicised eye gaze cues had a smaller magnitude effect than photographic gaze cues suggesting that ecological validity ("biological-ness") is an important factor in influencing oculomotor responses to social cues. No relationship was found between autistic traits and orienting to gaze or arrow cues in a large sample of males. However, findings from the neurological patients point to a possible double-dissociation between the neural mechanisms subserving processing of socio-biological and non-social cues, with the former reliant on the orbitofrontal cortex, and the latter on lateral frontal cortex. Taken together, these results suggest that biologically relevant cues have privileged access to the oculomotor system. The findings are interpreted in terms of a neurocognitive model of saccadic orienting to socio-biological and non-social cues, and an extension to an existing model of saccade generation is proposed. Finally, limitations of the research, its wider impact and directions for future work are discussed.

Contents

Abstract.....	2
Contents.....	4
Figures	8
Tables	12
Acknowledgements	14
Chapter 1: <i>Literature review and thesis overview</i>	17
1.1 Introduction.....	17
1.2 Eye movements and visual attention	18
1.3 Cognitive studies of gaze and other symbolic cues	29
1.4 The control of eye movements in relation to social and symbolic cues	49
1.5 Developmental issues	53
1.6 Neural bases of processing of gaze and other symbolic cues.....	60
1.7 Thesis overview	68
Chapter 2: <i>The effect of real-world eye gaze and arrow cues on performance in pro- and anti-saccade tasks</i>	71
Experiment 1: Pro-saccades.....	71
2.1 Introduction.....	71
2.2 Method	73
2.3 Results.....	80
2.4 Discussion.....	83
Experiment 2: Anti-saccades	85

	5
2.5 Introduction.....	85
2.6 Method.....	88
2.7 Results.....	91
2.8 General Discussion.....	96
2.9 Conclusions.....	103
Chapter 3: <i>An investigation into the gap effect in pro-and anti-saccade tasks with gaze and arrow cues</i>	105
Experiment 3: Pro-saccades.....	105
3.1 Introduction.....	105
3.2 Method.....	109
3.3 Results.....	112
3.4 Discussion.....	120
Experiment 4: Anti-saccades.....	130
3.5 Introduction.....	130
3.6 Method.....	132
3.7 Results.....	134
3.8 General Discussion.....	141
3.9 Conclusions.....	148
Chapter 4: <i>Influence of directional word and finger pointing cues on performance in pro-and anti-saccade tasks</i>	149
4.1 Introduction.....	149
Experiment 5a: Word cues and pro-saccades.....	151
4.2 Method.....	151
4.3 Results.....	153

Experiment 5b: Word cues and anti-saccades	158
4.4 Methods	158
4.5 Results.....	159
4.6 Discussion.....	162
Experiment 6a: Pointing cues and pro-saccades.....	167
4.7 Method	167
4.8 Results.....	169
Experiment 6b: Pointing cues and anti-saccades.....	175
4.9 Methods	175
4.10 Results.....	176
4.11 General Discussion	181
4.12 Conclusions.....	185
<i>Chapter 5: The role of ecological validity of gaze and arrow cues on automatic orienting</i>	
<i>in the anti-saccade task</i>	<i>186</i>
Experiment 7.....	186
5.1 Introduction.....	186
5.2 Method	188
5.3 Results.....	192
5.4 Discussion.....	200
5.5 Conclusions.....	203
<i>Chapter 6: The relationship between autistic traits and influence of gaze and arrow cues in</i>	
<i>males.....</i>	<i>204</i>
Experiment 8.....	204
6.1 Introduction.....	204

6.2	Method	207
6.3	Results	210
6.4	Discussion	215
6.5	Conclusions	218
Chapter 7: <i>Orienting to gaze and arrow cues in patients with frontal cortical damage</i>		219
7.1	Introduction	219
7.2	Patient case descriptions	221
Experiment 9a: Pro-saccades		229
7.3	Method	229
7.4	Results	231
Experiment 9b: Anti-saccades		242
7.5	Method	242
7.6	Results	242
7.7	General discussion	254
7.8	Conclusions	261
Chapter 8: <i>Towards a neurocognitive model of saccadic orienting to socio-biological cues</i>		262
8.1	Aims of the thesis	262
8.2	Overview of the chapter	262
8.3	The influence of social and non-social cues on saccadic eye movements	263
8.4	Limitations of research, past and present	291
8.5	Further work	292
8.6	Wider impact of research	295
8.7	Conclusions	296
References		298

Appendix A.....	332
-----------------	-----

The Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, et al., 2001).....	332
---	-----

Figures

<i>Figure 2.1:</i> Eyelink II eye tracker. Adapted from SR Research Ltd. (2008).....	75
--	----

<i>Figure 2.2:</i> Stimuli used for eye gaze and arrow cues.....	77
--	----

<i>Figure 2.3:</i> a) Procedure for a congruent trial with eye gaze cues.	78
--	----

<i>Figure 2.4:</i> Screenshot of Dataviewer software..	79
---	----

<i>Figure 2.5:</i> Mean correct SRTs in ms for congruent (C), neutral (N) and incongruent (I) gaze and arrow cues at the 3 SOAs..	81
--	----

<i>Figure 2.6:</i> a) A congruent trial with gaze cues and b) an incongruent trial with arrow cues..	89
---	----

<i>Figure 2.7:</i> Mean correct SRTs in ms for congruent (C), neutral (N) and incongruent (I) gaze and arrow cues at the 3 SOAs..	92
--	----

<i>Figure 2.8:</i> Mean correct SRT for congruent and incongruent arrow and gaze cues, collapsed over SOA..	94
--	----

<i>Figure 2.9:</i> Mean percentage error rates per participant for congruent, neutral and incongruent arrow and gaze cues over the 3 SOAs.	95
---	----

<i>Figure 3.1:</i> Procedures for gap, simultaneous and overlap Fixation conditions with gaze cues..	111
---	-----

<i>Figure 3.2:</i> Mean SRTs for congruent (C), neutral (N) and incongruent (I) gaze and arrow cues over the three Fixation conditions.	113
--	-----

<i>Figure 3.3:</i> Mean frequencies of large anticipatory saccades, made per participant, in the same and opposite directions to the arrow and gaze cues, over the three fixation conditions..	117
---	-----

Figure 3.4: Frequency of small anticipatory saccades per participant in the same and opposite direction as gaze and arrow cues.....	118
Figure 3.5: The peaks in the hypothesised salience map of Findlay and Walker's (1998) model on congruent and incongruent overlap trials.	125
Figure 3.6: Mean SRTs for congruent and incongruent gaze and arrow cues over the three fixation offset conditions.....	135
Figure 3.7: The mean percentage of error rates per participant, for congruent and incongruent gaze and arrow cues over the three Fixation conditions.....	137
Figure 3.8: Mean frequencies of large anticipatory saccades per participant, made in the same and opposite directions to the cues over the three fixation conditions.....	138
Figure 4.1: Directional word cue stimuli used in Experiment 5a and b.....	152
Figure 4.2: Frequency of large anticipatory saccades in the same and the opposite direction to the word cues over the 3 SOAs.	156
Figure 4.3: Finger pointing cue stimuli used in Experiment 6a and b.	168
Figure 4.4: The frequency of large anticipatory saccades made in the same and opposite directions to the pointing cues over the 3 SOAs, (pro-saccades)..	171
Figure 4.5: Mean fixation positions on the X axis with left and right pointing cues prior to trials entered into the SRT analysis..	173
Figure 4.6: Mean fixation positions on the X axis with left and right pointing cues prior to all trials	174
Figure 4.7: Mean correct SRT for congruent and incongruent pointing cues over the 3 SOAs for pro-saccades (Experiment 6a) and anti-saccades (Experiment 6b).....	178
Figure 5.1: Schematic gaze and arrow cues used in Experiment 8, based on Kuhn & Kingstone, 2009.....	190

Figure 5.2: Mean correct SRT for congruent and incongruent schematic gaze and arrow cues over the 3 SOAs.	193
Figure 5.3: Mean error rate per condition, per participant with congruent and incongruent schematic gaze and arrow cues over the 3 SOAs.	195
Figure 5.4: Frequency of large anticipatory saccades per participant, in the same and opposite direction to the cues, over the 3 SOAs.	197
Figure 5.5: Mean fixation position for all trials, with left and rightward cues over the 3 SOAs.	199
Figure 6.1: Mean correct SRTs for congruent and incongruent gaze and arrow cues used in Experiment 8.	211
Figure 6.2: Scatterplots of a) gaze cue congruency advantage and b) arrow cue congruency advantage against AQ score.	213
Figure 7.1: Example of a page from the Reading the Mind in the Eyes task (revised).	223
Figure 7.2: Multi-slice axial views of normalised T1 MRI structural scans for the 3 patients.	228
Figure 7.3: Mean correct SRTs in the pro-saccade task for a) the control group and (b – c) the patients for congruent and incongruent gaze and arrow cues over the two SOAs.	239
Figure 7.4: Mean frequency of anticipatory saccades in the pro-saccade task made in the same and opposite direction of gaze and arrow cues at both 300ms and 800ms SOA for a) controls and b) JW.	240
Figure 7.5: Trials in the pro-saccade task where patient BE’s first saccade began on the left or right of the screen and the percentages of those trials that started on the same or opposite side to the target in the preceding trial.	241

Figure 7.6: Mean correct SRT in the anti-saccade task with congruent and incongruent gaze and arrow cues at 300 and 800ms SOA for a) the control group, b) patient LG and c) patient JW.....	251
Figure 7.9: Trials in the anti-saccade task where patient BE’s first saccade began on the left or right of the screen and the percentages of those trials that started on the same or opposite side to the target in the preceding trial.....	254
Figure 8.1: A model of “anti-responding” to social and non-social cues in the anti-saccade task.....	279
Figure 8.2: a) Replica of fingerpost designed by Joseph Izod, 1669, Chipping Campden, Gloucestershire, UK. (Copyright John V. Nicholls and licensed for reuse under this Creative Commons Licence). b) Contemporary fingerpost, Monxton, Hampshire, UK (Copyright Department of Transport, 2005).....	286
Figure 8.3: Adaptation of Findlay and Walker’s model of saccade generation (1999)	290

Tables

Table 2.1: Mean SRTs and standard errors for correct saccades in the congruent, neutral and incongruent cue-target conditions in Experiment 1.....	82
Table 3.1: Mean congruency advantage, <i>t</i> values and significance values in gap, simultaneous and overlap conditions, collapsed over Cue type.....	114
Table 4.1: Mean SRT for congruent, neutral and incongruent word cues over the 3 SOAs. Figures in parentheses are standard errors of the mean.....	154
Table 4.2: Mean congruency advantage, <i>t</i> values and significance values at the 3 SOAs for pointing cues in the anti-saccade task of Experiment 6a.....	170
Table 4.3: Mean congruency advantage, <i>t</i> values and significance values at the 3 SOAs for pointing cues in the anti-saccade task of Experiment 6b.....	177
Table 5.1: Mean congruency advantages, <i>t</i> and significance values for schematic gaze and arrow cues over the 3 SOAs.....	194
Table 6.1: Correlation statistics and significance values of correlations between mean congruent and incongruent gaze and arrow SRTs and AQ score.....	214
Table 7.7.1: Mean correct SRTs, standard errors and 95% confidence intervals for congruent and incongruent arrow and gaze cues at both SOAs for the control group.....	233
Table 7.7.2: Mean congruency effects and 95% confidence intervals for gaze and arrow cues at 300 and 800ms SOA for the control group.....	233
Table 7.3: Mean frequency of anticipatory saccades per participant and 95% confidence intervals for gaze and arrow cues made in the same and opposite directions as the cue for the control group.....	235

Table 7.4: Mean congruency effects for gaze and arrow cues in the pro-saccade task at 300ms and 800ms SOA for the patients. * indicates effect which is outside of the 95% confidence intervals for the control group, presented in Table 7.1	236
Table 7.5: Mean correct SRTs, standard errors and 95% confidence intervals for congruent and incongruent arrow and gaze cues at both SOAs for the control group.	244
Table 7.6: Mean congruency effects and 95% confidence intervals for gaze and arrow cues at 300 and 800ms SOA for the control group.....	244
Table 7.7: Mean percentage of errors per condition per participant, as well as standard errors and 95% confidence intervals for congruent and incongruent arrow and gaze cues at both SOAs for the control group.	246
Table 7.8: Mean congruency effects for gaze and arrow cues in the anti-saccade task at 300ms and 800ms SOA for the three patients. * indicates effect which is outside of the 95% confidence intervals for the control group, presented in Table 7.6.	248

Acknowledgements

I would like to thank my supervisors Professor Tim Hodgson and Dr Huw Williams for their insight and expert guidance throughout the course of my PhD as well as Dr Cath Haslam for her part in giving me the opportunity to begin a PhD. I am also very grateful to my parents and friends for their continued support and patience as this work has been produced. I would also like to thank Adam Lloyd for providing the inspiration for this work and for allowing me to use his eyes as stimuli throughout my thesis. Finally, as this work was partially conducted under an Exeter Graduate Fellowship studentship, I express my sincere gratitude to Psychology at the University of Exeter for allowing me the opportunity to continue with and complete my PhD.

To
Molly Broughton



'Le Tricheur' ('The Card Sharp')

Oil on canvas, by Georges de la Tour (1593 – 1652)

Chapter 1: *Literature review and thesis overview*

1.1 Introduction

It is said that the eyes are the window to the soul. Our eyes certainly convey a remarkable wealth of information to others. Our emotions, our thoughts and intentions are portrayed in our eyes, whether we like it or not. In turn, the same mental processes of the people we are interacting with are influenced by this understanding of our mental state. Usually, this all happens effortlessly, without the need for words or conscious consideration. But this incredible ability is not indestructible. And when it fails it can have far reaching deleterious consequences.

This thesis addresses the extent to which eye gaze and other cues that are used to direct attention can directly activate eye movement programming mechanisms. It further looks at how processing of social, biologically relevant cues relate to *social intelligence* and how such mechanisms are affected in neurological damage.

The field of *social attention* research had emerged from converging disciplines of cognitive and developmental psychology by studying social behaviour in the experimental psychology framework. This thesis continues in this vein, addressing questions which are still unanswered since the conception of social attention research in the late 1990s.

Furthermore it ultimately attempts to move above the level of laboratory paradigms to contextualise the findings to speak of social intelligence in the real world.

The remainder of Chapter 1 will present an overview of the literature on attention and eye movement orienting, followed by the research into eye gaze and cueing by other

symbolic cues. Thereafter the influence of social and non-social cues on eye movements will be considered in terms of current models of saccade generation. It will then present evidence relating to the development of gaze processing and discuss the Autistic Spectrum Disorders which are characterised by social and communicative impairments, including reduced processing of eye gaze. The neural substrates of gaze processing will be considered and shared neural mechanisms between social behaviour more generally and eye gaze will be discussed. Finally, the aims of the thesis will be presented together with an overview of the chapters to follow.

1.2 Eye movements and visual attention

1.2.1 Attentional orienting

Our eyes move around three times per second in fast, jerky movements called saccades. In between saccades, fixations occur where the eyes are stationary and it is during fixations that visual information is extracted from the scene and processed via the retina, by the brain. The guiding influence behind these alternating saccades and fixations is *attention*.

We are continually bombarded with visual information whilst our eyes are open. It is essential that we are able to selectively focus on currently relevant information for further processing whilst rejecting the majority. Visual attention is the mechanism by which this aim is achieved. As our goals and environment change from second to second it is also imperative that we are able to change the focus of our attention at will to match our current situation, allowing only the most relevant information to be processed at any one time. Moving attention from one location or object to another is called *attentional orienting*.

Attention has traditionally been considered to take two forms (e.g. Jonides, 1981; Posner, 1980). The first is described by various terms such as bottom-up, stimulus-driven,

reflexive, involuntary, exogenous whilst the second is known as top-down, goal-driven, voluntary, volitional and endogenous. Regardless of the precise nomenclature, the distinction is fundamentally between external and internal influences on the movement or orienting of attention. External features of the environment, such as sudden onsets of light will cause a rapid reorienting of visual attention which would be considered to be reflexive (sometimes referred to as the Visual Grasp Reflex: (Hess, Brugli, & Bucher, 1946; Machado & Rafal, 2000a, 2004) and in the former category, whilst internal motivations such as searching for a particular object amongst others would cause a somewhat slower orienting of attention that would be considered voluntary or endogenous, and would fall in the latter category.

In most naturally occurring situations, this orienting will be achieved through the saccade and fixate movements of the eyes. However, attention can be shifted whilst the eyes are stationary and occurs when you “pay attention” to something “out of the corner of your eye”, whilst keeping your eyes fixed on another location. Posner (1980) differentiated these two modes of orienting by referring to them as *overt* (with eye and sometimes head movements), and *covert* (without eye movements).

1.2.2 The relationship between covert and overt attention

The realisation that attention could be allocated to one location whilst the eyes remain fixated on another encouraged a raft of research which aimed to identify the precise relationship between covert attention and the eye movement or *oculomotor* system. Broadly, there are three schools of thought on the matter ranging from accounts which consider covert and overt attention to be different processes (Klein, 1980; Klein & Pontefract, 1994; Remington, 1980) to those which regard covert attention to be a by-

product of the saccadic system and therefore inextricably linked to it (Rizzolatti, Riggio, & Sheliga, 1994; Rizzolatti, Riggio, Dascola, & Umiltà, 1987; Sheliga, Craighero, Riggio, & Rizzolatti, 1997; Sheliga, Riggio, & Rizzolatti, 1994) whilst others regard the two processes as related although able to operate independently of each other (Henderson, 1992; Shepherd, Findlay, & Hockey, 1986). The pre-motor theory of attention, put forward by Rizzolatti and colleagues (1987; 1994; 1994; 1997) is possibly the most parsimonious of the view points as it states rather than being separate mechanisms, the facilitation of processing of a location via covert attention occurs as a result of activity in the saccadic system as it prepares to execute a saccade to that location. Without motor preparation in the saccadic system, there can be no covert attentional allocation, the theory proposes. The evidence in favour of this theory includes findings that the trajectories of saccades made to a target deviate away from a concurrently covertly attended stimulus, suggesting interference between the two instructions within the same system (Kustov & Robinson, 1996; Rizzolatti et al., 1994; Sheliga, Riggio, & Rizzolatti, 1995; Van der Stigchel & Theeuwes, 2005; Van der Stigchel, Meeter, & Theeuwes, 2006). Other studies have demonstrated that if covert attention is allocated to one of four imaginary quadrants on a computer screen, it takes longer to shift from one quadrant to another than it does to reorient attention within the same quadrant, a phenomenon termed the “meridian effect”. This observation can be explained if the reorienting of covert attention is actually the product of a reprogramming of an eye movement, which when moving from one quadrant to another requires both a reprogramming of saccade direction and amplitude, as opposed to just saccade direction when within the same quadrant (Reuter-Lorenz & Fendrich, 1992; Rizzolatti et al., 1987). In further support of the premotor theory is the case of patient AI who was unable to make saccadic eye movements due to a disorder of the ocular muscles,

who was also impaired in covert spatial attention (Smith, Rorden, & Jackson, 2004). The findings from this study suggest that in order to shift covert attention, the ocular muscles must be functional. However, other work with this patient suggests otherwise. AI appeared to compensate by making saccade-like whole head movements, which although were larger and slower than ocular saccades, qualitatively resembled saccadic eye movements throughout a series of oculomotor (Gilchrist, Brown, Findlay, & Clarke, 1998) and real world tasks (Land, Furneaux, & Gilchrist, 2002). It was therefore suggested that the eye movement control system was likely to underpin AI's saccadic head movement strategy (Gilchrist et al., 1998) which, according to the pre-motor theory of attention, implies that covert attention must also be operating. Indeed, the midbrain structures the superior colliculi (SC) which are involved in saccadic eye movements (as will be discussed in the following section) have also been shown to be involved in gaze orienting of the head in primates (Freedman, Stanford, & Sparks, 1996; Klier, Wang, & Crawford, 2001). The case of AI indicates that the interrelatedness of overt and covert attention extends beyond attention with and without eye movements to encompass gaze orienting which also includes movements of the head.

In support of a common mechanism underlying saccadic eye movements and covert attention, neuroimaging and neurophysiological studies have found a great deal of overlap in the neural structures involved in both orienting with and without eye movements (Corbetta, 1998; Corbetta et al., 1998; Grosbras, Laird, & Paus, 2005; Ignashchenkova, Dicke, Haarmeier, & Thier, 2004; Kustov & Robinson, 1996). The following section will describe some of the critical structures of the saccadic eye movement system.

1.2.3 Neural basis of the saccadic eye movements

The saccadic system is subserved by a distributed neural network which involves both cortical and subcortical structures. Within this network are several structures which appear to have particularly critical roles in saccade generation. The superior colliculi (SC) are located in the midbrain, in what is considered in evolutionary terms, the older part of the visual system. Neurons of the SC are responsible for generating orienting movements of not only the eyes but also the head and body. They receive neural projections from both retina and cortex and therefore act as a site of “sensorimotor integration”, where sensory (visual, auditory and somatosensory) input is converted to motor commands (Sparks, 1999). Neurons in the SC which respond to the onset of a stimulus at a location in space also discharge during the gaze orienting movement which brings the fovea in line with that location (Quaia, Aizawa, Optican, & Wurtz, 1998). Furthermore, the neurons of the SC are organised topographically, in that the direction and size of gaze orienting movements (including head and body movements) depends on the site of neural activation in the SC, with adjacent populations of neurons representing adjacent locations of visual space. This organisation of motor neurons is referred to as a “motor-map” (Goldberg & Wurtz, 1972a; Schneider & Kastner, 2005), which converges with the “sensory maps” of visual, auditory and somatosensory space, to produce coordinated movements of head, body and eyes towards locations of sensory activation (Sparks, 1986, 1999). However, it is important to note that the gaze reorienting decision is not determined solely by isolated events in the environment; internal goals integrate with sensory activation to determine the size and direction of each saccade. In the visual environment, at any one time, many locations in the scene are likely to “compete” to be selected within a “saliency map”, with the one with greatest saliency (e.g. a distinct colour, shape size) becoming the target of the next saccade.

However, top-down, motivational factors, such as searching for an object with a particular feature amongst distracters in a visual search task, will compete with the visual salience of objects in the scene. This integration of bottom-up (salience) and top-down (relevance) attentional selection has been conceptualised as “priority”, with the site of this amalgamation being the SC. In this account, attentional selection occurs within a “priority map”, which extends the salience map to also account for top-down influences (Fecteau & Munoz, 2006).

The activity in the SC as measured by functional Magnetic Resonance Imaging (fMRI) has been shown to be negatively correlated with saccadic latency (the greater activity, the faster the saccades) (Neggers, Raemaekers, Lampmann, Postma, & Ramsey, 2005) whilst behavioural and neurophysiological studies have suggested that competition between different populations of neurons, activated by multiple potential saccade targets in the visual field is responsible for determining the metrics of saccades (McPeck & Keller, 2002a, 2002b; McPeck, Han, & Keller, 2003; Port & Wurtz, 2003). However, the SC does not act alone in the production of saccades as it receives direct and indirect projections from many cortical structures. The frontal eye fields (FEF) in the prefrontal cortex, which project to the SC, share some characteristics with the SC in that they too are organised topographically and damage to this area increases the rate of reflexive saccades towards to be ignored visual stimuli (Machado & Rafal, 2004). Like the SC, activity in the FEF is correlated with saccade latency (Connolly, Goodale, Goltz, & Munoz, 2005) and the FEF appear to have a particular role in the voluntary control of saccades (Everling & Munoz, 2000; Gaymard, Ploner, Rivaud-Péchoux, & Pierrot-Deseilligny, 1999; Rivaud, Muri, Gaymard, Vermesch, & Pierrot-Deseilligny, 1994). The intraparietal sulcus (IPS) of the parietal cortex also projects directly to the SC and includes an area with similar spatiotopic

organisation to the SC and FEF. Some parts of the IPS are thought to be involved in triggering saccades and others in determining their spatial properties, with evidence suggesting a particular role in voluntary saccade generation (Ford, Goltz, Brown, & Everling, 2005; Zhang & Barash, 2000, 2004). The dorsolateral prefrontal cortex (DLFC) is a further cortical area involved in the control of saccade generation. It is thought to have a critical role in the voluntary elements of saccade generation, particularly decisional processes and suppression of unwanted saccades (Guitton, Bachtel, & Douglas, 1985; McDowell et al., 2005; Pierrot-Deseilligny et al., 2003; Pierrot-Deseilligny, Rivaud, Gaymard, & Agid, 1991). However, other studies have attributed the role of inhibitory control of saccades to the ventrolateral prefrontal cortex (Hodgson et al., 2007; Walker, Husain, Hodgson, Harrison, & Kennard, 1998).

1.2.4 The study of eye movements

Although covert attentional paradigms have been extensively utilised in the field of attention research, there are distinct advantages to studying eye movement responses over covert attention. Firstly, in everyday life, unrestricted, natural attentional orienting occurs with the eyes and in this sense the study of oculomotor behaviour provides a more ecologically valid measure of attentional orienting. Secondly, it is possible to analyse a range of eye movement parameters, such as saccade amplitude, spontaneous movements, microsaccades, fixation position and saccade trajectories, which is clearly not possible in a covert attentional paradigm, where the eyes remain stationary.

In the following section, three commonly utilised oculomotor paradigms for the study of eye movements and attention will be described and discussed.

The pro-saccade task

In the pro-saccade task, the participant is required to maintain fixation on a central point displayed on a computer screen, until a peripheral stimulus appears at one or other side of the screen. At the onset of the peripheral stimulus, the participant is required to make a saccade to the target as quickly and accurately as possible. The most fundamental of dependent measures in the study of overt orienting of attention is saccadic reaction time (SRT). This is calculated as the time in milliseconds (ms) between the onset of an instruction to make a saccade and the initiation of the eye movement. The presence of other stimuli on the screen during a pro-saccade task can influence the saccadic system as is evident by variations in SRT to the saccade target. For example, if a task-irrelevant stimuli or *cue* is flashed briefly to one of the potential target locations before the target actually appears, correct SRTs are usually faster if the cue appeared at the target location (when the cue and target are *congruent*) than when the cue appeared at the opposite location to the target (i.e. when the cue and target are *incongruent*) (Cavegn, 1996; Crawford & Muller, 1992). This facilitation of SRT at the cued location over the uncued location is thought to occur because the onset of the cue initiates the generation of a saccade towards it in a reflexive manner. When the subsequent target appears at the same location, the saccade to the correct location has already partially been programmed. When the subsequent target appears at the other location, the saccade has to be reprogrammed in the opposite direction which takes time, resulting in a longer SRT (i.e. the *meridian effect*, described earlier). Directional cues presented centrally, rather than peripherally at the potential target locations can influence SRTs in a similar manner as in the pro-saccade task. Cueing by such *symbolic cues* will be discussed in detail in a later section.

The covert attentional homologue of the pro-saccade task is often credited to its first proponent, being referred to as a *Posner cueing paradigm* or alternatively as the *covert spatial cueing paradigm* (Posner, 1978, 1980). The task is basically the same as the pro-saccade task with the exception that eye movements are withheld, with participants maintaining fixation on a central point throughout, and giving their responses manually by pressing a button on a joystick. The application of the covert spatial cueing paradigm and the pro-saccade task will be discussed in detail in a later section.

The anti-saccade task

The anti-saccade task was first used by Hallett (Hallett, 1978; Hallett & Adams, 1980). In this task participants are required to make a saccade to a location opposite to where the peripheral “target” is displayed, as quickly and as accurately as possible. Although at first sight, the anti-saccade task might appear to simply be the opposite of the pro-saccade task, its successful completion requires considerably more cognitive effort on the part of the participant, thought to be subserved by additional cognitive processes. For example, participants must first try to inhibit the tendency to make a reflexive saccade to the target stimulus. Failure to achieve this is common, resulting in an erroneous pro-saccade to the target, with the average rate of such errors around 20% in healthy adults (Hutton, 2008). However, when first performing the task, error rates can be as much as 80%, but quickly reduce with practice, often to less than 10% (Hallett, 1978; Hallett & Adams, 1980). Secondly, they must voluntarily initiate a saccade to the mirror opposite location to the target (Everling & Fischer, 1998; Guitton et al., 1985; Munoz & Everling, 2004). The suppression of the reflexive saccade is achieved by increasing the activity of fixation mechanisms, whilst the later process of voluntarily generating the anti-saccade to

the correct location requires increased activation of saccade generating mechanisms, with both mechanisms reliant on neuronal activity in SC and FEF (Everling & Munoz, 2000; Everling, Dorris, Klein, & Munoz, 1999). Like in the pro-saccade task, reaction times are of importance in the anti-saccade task, but a further dependent measure of interest is the proportion of errors made (where participants incorrectly look towards the target). The SRTs of correct saccades in the anti-saccade task are considerably longer than those in the pro-saccade task which reflects the shift from reflexive to voluntary saccadic responses in the two tasks respectively (Fischer & Weber, 1992) but also the increased involvement of inhibitory mechanisms required to complete the anti-saccade task (Olk & Kingstone, 2003). However, saccades erroneously executed towards the peripheral stimulus have latencies more akin to those seen in the pro-saccade task (Evdokimidis et al., 2002), and are considered to be failures to inhibit the visual grasp reflex (Everling, Dorris, & Munoz, 1998). Damage to the dorsolateral (Guitton et al., 1985; Pierrot-Deseilligny et al., 2003, 1991) and ventrolateral cortex (Hodgson et al., 2007; Walker et al., 1998) is known to increase the rate of error saccades to the target in the anti-saccade task due to reduced inhibitory control over the prepotent reflexive pro-saccade response.

The influence of peripheral and symbolic cues has been little examined in the anti-saccade task. From the evidence that does exist there appears to be a less predictable pattern of responses than in the pro-saccade task, with saccades appearing to be facilitated in the direction opposite to both peripheral and symbolic cues (Koval, Thomas, & Everling, 2005; Weber, Durr, & Fischer, 1998). The effect of competing influences in the form of cues in the successful completion of the anti-saccade task is an avenue of research that warrants further investigation, as it may shed light on the degree to which different directional stimuli are processed by the brain under increased cognitive demands.

The gap paradigm

Saslow (1967) was the first to note that the introduction of a temporal gap between the offset of a central fixation point and the onset of a target in a pro-saccade task leads to reduced saccade latencies. In addition, increased rates of errors are usually observed, some of which are anticipatory in nature (i.e. occurring before the appearance of a target) (e.g. Fischer, Gezeck, & Hartnegg, 2000). The effect is highly robust, with the maximal reduction in SRT and increase in errors occurring with a gap of 200ms (Fischer & Weber, 1997). This phenomenon has become known as the *gap effect*.

The phenomenon of the gap effect has been shown to be due to neural activity in the superior colliculus (SC), which is modulated by the removal of the fixation stimulus. Fixation neurons of the rostral pole of the SC, which are active during fixation, decrease in activity during the gap at the same time as the inhibition of saccade-related cells decreases (Dorris & Munoz, 1995; Dorris, Pare, & Munoz, 1997). This results in a period of disengagement of the saccadic system, where other stimuli can be engaged (i.e. fixated) more quickly.

Although the gap effect has been reported in the anti-saccade task (Fischer & Weber, 1992, 1997; Weber et al., 1998) the effect is less universal (Forbes & Klein, 1996; Reuter-Lorenz et al., 1991; Van Koningsbruggen & Rafal, 2009). This is thought to be because the increased activity in fixation mechanisms which are needed to suppress the occurrence of a reflexive saccade to the target (Everling, Dorris, Klein, & Munoz, 1999; Munoz & Wurtz, 1992) counteracts the disengagement caused by the offset of the fixation stimulus.

In summary, the pro- and anti-saccade tasks are useful paradigms for investigating the control of the oculomotor system in the laboratory. Whereas the pro-saccade task measures the effects of manipulations of target and distractor presentations on saccadic reaction time, the anti-saccade task investigates the interplay between bottom-up and top-down factors on saccade generation. Both can be manipulated to produce “gap” versions, to enable the study of oculomotor engagement mechanisms in addition to reflexive and voluntary control of eye movements.

Having presented an overview of attentional and saccadic orienting and the tasks used to study these mechanisms, the following section will examine the effect that introducing visual stimuli with inherent visual meaning (or spatial *cues*) into covert spatial cueing paradigms and equivalent oculomotor tasks, has on the activation of attentional and saccadic eye movement systems.

1.3 Cognitive studies of gaze and other symbolic cues

1.3.1 Covert attentional orienting

In the spatial cueing paradigm, participants sit in front of a computer screen whilst keeping their eyes fixated on the centre of the screen. With a keyboard or joypad in front of them, participants indicate the precise moment they detect that a target stimulus has appeared on the left or the right of the screen by making the relevant key press whilst maintaining fixation in the centre of the screen. Presenting a directional stimulus such as an arrow at fixation whilst this task is performed has the effect of causing reaction times to be

reduced for responses made in the cued direction in comparison to the uncued direction. However, for many years, within the field of attention research a view predominated that symbolic cues such as arrows were only capable of orienting observer's attention when they were task-relevant, in other words, when they correctly predicted the correct direction of the target most of the time. They were not considered to be able to cause such attentional orienting when they were uninformative, i.e. if they were just as likely to predict the wrong location for the target, as the correct one.

The idea that arrow cues could not cause automatic orienting of attention when task-irrelevant resulted largely from the work by Jonides in 1981. Jonides very briefly (25ms) presented arrow cues to participants, who were told that the direction of the cue was not an indication of the location of an upcoming target and that consequently they should ignore them. The target appeared after a period of 50ms, whereupon participants had to identify a letter (L or R) at one of eight locations on an imaginary circle which may or may not have been indicated by the preceding centrally presented arrow cue. Jonides found that participants were no quicker to correctly identify the target when the arrow had indicated the correct location than when it had pointed towards one of the other locations. It was concluded from this work, and subsequently assumed for many years, that arrows which did not predict the location of a target could not automatically orient attention to that location.

In the late 1990s human eye gaze began to receive interest from attention researchers. Evidence emerged which suggested this type of cue exerted an automatic or reflexive effect on observers' attention, akin to the way exogenous cues, such as a brief flash of light, automatically captures attention, leading some to propose that eye gaze cues might represent a unique class of directional symbol based on their social and biological

importance. The first reported study of averted eye gaze causing such effects was conducted by Friesen and Kingstone (1998). These authors conducted a series of experiments based around the spatial cueing paradigm, including target detection, localisation and detection tasks. The gaze cues in these tasks were comprised on schematic faces with eyes represented as black circles within larger white circles, with the inner circles placed off centre to give the appearance of pupils looking left or right. The cues were presented in the centre of a computer screen and were nonpredictive of target location. After a time period (or *stimulus onset asynchrony (SOA)*) ranging between 105ms and 1005ms, a target would appear and the participants responded appropriately for the current task by pressing the relevant button on the keyboard. Friesen & Kingstone found that when the cue “looked” towards the correct location for the target (congruent trials), participants were quicker to correctly respond than when the cues were pointing towards the incorrect target location. This effect was observed at all the tested SOAs with the exception of the longest. These authors were the first to suggest that eye gaze cues exhibited some of the characteristics more usually associated with peripheral exogenous cues and for this reason they appeared to be acting to reflexively shift attention in observers. They based their conclusion on several aspects of the orienting which occurred: a) rapidly; as little as 105ms after the cue had been visible, too short a period for participants to voluntarily shift their attention in the direction of the cue, but absent at the longest SOA and b) when the cues were task irrelevant, in that they did not predict the likely location of the target and that the participants were instructed to ignore the cues. Unlike with peripheral cues however, Friesen & Kingstone noted that the congruency advantage did not reverse at longer SOAs. This reversal of the congruency advantage is an effect seen with peripheral cues which is attributed to an inhibition of return (IOR) mechanism and had been considered a

characteristic of true reflexive orienting (for a review of IOR see Klein, 2000). The fact that this was not observed with gaze cues but that so many other characteristics of reflexive orienting were apparent, lead the authors to conclude that the direction of eye gaze of another individual might represent a unique category of cue. Although not directly specifying an exact spatial location by appearing there, these centrally presented and uninformative gaze cues appeared to be automatically shifting the attention of the participants in a manner that had hitherto not been seen with other symbolic cues such as arrows.

Friesen and Kingstone's (1998) finding found support from other laboratories. Driver et al. (1999) used photographs of a female face with eyes looking left and right and showed that even though the direction that the eyes were looking in did not give any indication of where the target was going to be presented, participants were faster to detect or identify targets which were congruent with the cue direction. However Driver et al. went one step further: They showed that even when the eyes gazed in the most *unlikely* location of the target 80% of the time, a probability which the participants were made aware of, they were still quicker to correctly respond on congruent trials. This finding was extremely significant as it demonstrated that even when the participants expected the target to appear in one location most of the time they could not stop their attention being oriented by the cue to the least likely location of the target. This obligatory shift of attention diminished however when the SOA was increased to 700ms, which the authors attributed to the increased development of voluntary control within the longer period preceding the response.

As further data supporting the findings of Friesen & Kingstone (1998) and Driver et al. (1999) with nonpredictive gaze cues became evident (Ristic, Friesen, & Kingstone,

2002) some researchers began to question whether the effects seen with eye gaze were unique or whether other types of cue could cause apparently reflexive shifts in attention. Hommel, Pratt, Colzato, & Godijn (2001) demonstrated in a series of experiments that centrally presented non-predictive arrow cues caused enhanced target detection and identification at the cued location. Further, even when the target was four times more likely to appear on one side of fixation, the non-predictive arrow cues still caused a congruency advantage.

A study by Tipples (2002) supported Hommel et al.'s findings of automatic orienting effects with non-predictive arrows. Using a target identification task, Tipples showed that even with a very short interval between the cue's presentation and the target's onset (100ms SOA), participants were quicker to correctly identify congruent targets (where the arrow pointed to target) than to identify incongruent targets (where the arrow pointed away from the eventual target location). The fact that the congruency effect occurred at such a short SOA was a strong indication that the arrow cues were eliciting an automatic or reflexive effect on the observers' attention, as 100ms was thought not to be long enough for participants to volitionally influence their response based on the cue's direction. Tipples used two centrally presented arrows, which to some extent resembled a pair of eyes, but Ristic, Friesen, & Kingstone (2002) showed that even with a single centrally presented task-irrelevant arrow, congruency effects still emerged at an SOA of 195ms and persisted until 1005ms SOA.

In light of these findings which challenged traditional assumptions about the influence of arrow cues on attention, Gibson & Bryant (2005) attempted to replicate Jonides' (1981) original findings using the same target identification paradigm. However, unlike Jonides, these authors found congruency effects at the shortest SOA of 50ms, so

long as the cue remained on screen for 200ms (i.e. the cue remained onscreen after the target had been presented). When the cue remained onscreen for only 25ms, as with Jonides' original experiment, no congruency effects were observed. The authors proposed that the very short cue duration employed in the early study by Jonides may simply not have been long enough for participants to perceive the arrow cue fully. Indeed, when Gibson & Bryant, in a further experiment, forced participants to identify the cue as an arrow or as a bar (the arrow cue with the head removed) when presented for only 25ms, a congruency advantage did emerge. This latter finding suggests that in order to be automatically oriented by a cue's direction, its meaning must at least to some extent be interpreted. However, a recent study by Hermens, Sumner & Walker (2010) investigated the effect of masked arrow primes on saccadic reaction times and found that even very briefly presented arrows can influence saccadic responses. These authors presented arrow primes for 80ms followed by a mask, which was immediately followed by the presentation of the same arrow stimulus without the mask. The direction of this arrow target could be congruent or incongruent with the direction of the arrow prime. The task for the participants was to make a saccade towards a peripheral placeholder in the direction indicated by the arrow target. These authors found that even though the prime was visible for 80ms, participants were faster to make a correct saccade when the target and the prime were congruent than when they were incongruent. This finding further suggests that task irrelevant arrow cues are capable of influencing attentional orienting, even when they are barely detectable.

To summarise, evidence had emerged which contested the long standing view that symbolic cues like arrows, which were task-irrelevant, could cause a seemingly automatic

shift of attention in observers. Such studies cast doubt upon the claim that eye gaze cues held a “special” status as directional cues and prompted research aimed at directly comparing the effects of arrow and eye gaze cues on attention.

Ristic, Friesen and Kingstone (2002) compared the effects of nonpredictive eye gaze and arrow cues in adults and young children and found equivalent congruency advantages for both cue types over a range of SOAs. Quadflieg, Mason, and Macrae (2004) compared nonpredictive gaze and arrow cues and also found equivalent congruency advantages for the two cue types, although they did find that reaction times to gaze cues were faster overall than those made with arrow cues, even though the stimuli were well matched perceptually.

With equivalent effects for arrows and gaze cues being reported in the literature, adaptations on the standard spatial cueing paradigm were designed with the aim of shedding light on more subtle difference between the ways arrows and eyes were affecting attention. For example, Friesen, Ristic and Kingstone (2004) used schematic gaze cues which looked up, down, left and right and compared them to simple arrows. They altered the probabilities that the cues would point towards the correct location by designating one direction as being the likely target location on 75% of trials, whilst each of the other locations could be correct on 8% of trials (neutral trials where the face gazed straight ahead were also used). Therefore on any one trial, one location would be predicted, one location would be cued and the other two locations would be neither predicted nor cued. Together with a range of SOAs from 105ms nearly 2 seconds, it was hoped that the relative contributions of reflexive and volitional orienting could be determined by comparing reaction times to baseline trials (where targets were neither predicted nor cued) to the

reaction times on predicted and cued trials. For gaze cues their findings indicated that at the shortest SOA, participants experienced reflexive orienting of their attention towards the cued but most unlikely location. As the SOA increased to 600ms, participants showed equally fast reaction times to expected and cued locations, a finding which indicated that both reflexive and voluntary attention were co-occurring. However when participants were allowed at least 1200ms to respond, only the reaction times to predicted targets were quicker than the baseline, which reflected the sole involvement of voluntary mechanisms in shifting attention. In contrast to these findings, when the experiment was repeated with simple arrow cues, the cued location was never quicker than the baseline at any SOA. But as with the gaze cues, targets appearing at the most likely location produced the quickest responses at the longer SOAs. Friesen, Ristic and Kingstone proposed that their experiment had subjected both cue types to a more rigorous test of automaticity, which had demonstrated that gaze cues had a far greater and more reflexive effect on attention than arrow cues, the latter failing to show any reflexive orienting at short SOAs when cues were counter-predictive of target location. It also suggested that in response to eye gaze cues, attention could act both reflexively and voluntarily at the same time, reflecting competition between bottom-up and top-down control of attention. Recently however, a study by Tipples (2008) showed that counter-predictive arrow cues as well as gaze cues were able to cause an automatic shift in attention of observers

Directional cues other than arrows and eye gaze have received much less interest from researchers with very few studies having been reported in the literature. Although sparse, evidence does exist to show that the meaning of directional words can be automatically extracted and affect attention. As well as investigating the effects of non-

predictive arrow cues on attention as mentioned above, Hommel et al. (2001), in the same series of experiments, used the words LINKS, RECHTS, OBEN and UNTEN (German for LEFT, RIGHT, UP and DOWN) within a spatial cueing paradigm. They found that participants were quicker to correctly respond when the target location was congruent with the direction of the word. These results were further supported by a study by Ho & Spence (2006) who showed that the words LEFT and RIGHT presented at fixation caused participants to detect targets congruent with the word more quickly than when the cue and target were incongruent.

There is some recent evidence that other socially relevant cues as well as eye gaze may have automatic influence on covert attentional orienting. Finger pointing gestures have been shown to cause automatic orienting of attention in covert spatial cueing paradigms (Ariga & Watanabe, 2009; Sato, Kochiyama, Uono, & Yoshikawa, 2010; Tomonaga & Imura, 2009) and cause interference effects when presented simultaneously with spoken word and gaze cues (Langton & Bruce, 2000). Interestingly, one study (Ariga & Watanabe, 2009) showed that it was the index finger specifically which caused the maximal orienting effect. Although pointing cues other than index finger cues resulted in a congruency advantage for cued over uncued locations, even when little finger cues were digitally enhanced to extend the length of the finger to that of an index finger, the congruency effects were still greater for the genuine index finger cues than the enhanced little finger cues. This study suggests that the precise configuration of the pointing cue is of importance in eliciting cueing effects, but more generally that eye gaze may not be the only social/biological cue which can cause automatic orienting of attention.

In summary, work investigating the influence of eye gaze cues on covert spatial attention has provided a raft of evidence suggesting that such stimuli can cause orienting of attention which appears to be automatic in nature. Some researchers maintain that their work shows that arrows share these characteristics with eye gaze cues but others have suggested that gaze cues provide an example of a unique form of directional cue, based on anomalous effects seen only with this biologically and socially important method of indicating direction. However, recent work with other social cues indicates that it may be the category of cue, rather than eye gaze specifically, which causes automatic orienting of attention.

1.3.2 Overt orienting and symbolic cues

Consistent with the work on covert attention, other researchers have demonstrated direct effects of spatially non-predictive arrow and eye gaze cues on eye movements. In a so-called voluntary saccade task, participants are required to make an eye movement towards lateral targets flanking either side of a centrally presented cue. The correct direction for the saccade is stipulated usually by the colour change of a central fixation stimulus, where, for example green indicates that left is the correct target and red indicates that the right target is the correct one to saccade towards. Participants are instructed to make the saccade to the correct target as quickly and as accurately as possible whilst ignoring the centrally presented cue.

Using this paradigm, Ricciardelli, Bricolo, Aglioti and Chelazzi (2002) were the first group of researchers to investigate the effect of eye gaze and arrow cues on observers' oculomotor behaviour. These researchers found that in the presence of gaze cues, participants were quicker to make the correct saccade when the face gazed toward that

location than when it gazed at the other location or looked straight ahead. In addition, participants made more errors (where they looked towards the incorrect target) in the direction of the gaze than in the opposite direction. When Ricciardelli et al. completed the same experiment with arrow cues, they found that although participants were quicker to make a saccade on congruent trials than on incongruent and neutral trials, there was no difference in the number of errors produced in the three congruency conditions. The authors interpreted their results as suggestive of an inherent gaze-following tendency specific to this biologically relevant cue, a suggestion which has been referred to subsequently as the “gaze imitation hypothesis”. The authors suggested that observing the averted gaze of another person causes a corresponding oculomotor programme to be executed in the observer, resulting in an imitative saccade towards the gazed at location. Mirror neurons, found in monkey premotor and parietal cortex, fire when an action is performed but also when the monkey observes another performing the same action (Fogassi et al., 2005; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). As other forms of imitative behaviour had previously been reported as activating the mirror neuron system in humans (Heyes, 2001; Williams, Whiten, Suddendorf, & Perrett, 2001), Ricciardelli et al. suggested that the mirror neuron system could also be responsible for the oculomotor effects seen in response to their gaze cues. However these authors did not explore the possible mechanism underlying the congruency advantage for saccadic reaction times observed with arrow cues. It is possible that the stimuli used for the arrow cues may have lacked some features necessary to elicit saccades in the direction indicated by them. Nevertheless, the proposal of the gaze imitation hypothesis provoked further research into the effect of gaze cues on eye movements.

A study by Mansfield, Farroni, and Johnson (2003) showed that in a pro-saccade task, participants were 30ms quicker to saccade towards targets congruent with a centrally presented gazing face, than when the face gazed in the direction opposite the target. In addition, this study found that participants made small eye movements in the direction of the gaze cues on a small proportion of trials, before the target even appeared. Both findings added weight to the gaze imitation hypothesis proposed by Ricciardelli et al. (2002).

Friesen & Kingstone (2003) reasoned that if an imitative oculomotor response was initiated on seeing another's averted gaze, a saccadic congruency advantage ought to be augmented in comparison to that from an equivalent manual reaction time task, where participants maintain central fixation whilst withholding eye movements and make their response by pressing a key on a keyboard. On the contrary, Friesen and Kingstone found that the congruency advantage seen in their manual reaction time task was actually larger than that seen in the oculomotor version of the task. Furthermore, the congruency advantage in the covert task occurred under a wider range of conditions than that in the overt task. Friesen and Kingstone concluded from their findings that perceiving averted gaze did not trigger the generation of a saccade to the gazed at location and therefore did not support the gaze imitation hypothesis.

The most current work into the specific effects of perceiving gaze on eye movements in comparison to perceiving other symbolic cues has been conducted by Kuhn and colleagues (Kuhn & Benson, 2007; Kuhn & Kingstone, 2009; Kuhn et al., 2010). Kuhn & Benson (2007) investigated Ricciardelli et al.'s (2002) gaze imitation hypothesis by using a voluntary saccade task. These researchers wanted to establish if any differences existed between the effects of eye gaze and arrow cues on oculomotor behaviour. Further, Kuhn & Benson proposed that the reason Ricciardelli et al. did not find that participants

had a tendency to make saccades in the direction of their arrow cues as they did with their gaze cues was due to the stimuli's perceptual properties. Ricciardelli et al.'s gaze cues consisted of a photograph of a female face whereas the arrow cues were represented by "less than" (<<) or "greater than" (>>) signs and Kuhn and Benson suggested the latter cues were far from "real -world" unlike the gaze cues, and were therefore less likely to elicit responses from participants. Therefore, Kuhn and Benson used similarly constructed gaze and arrow cues, both consisting of simple shapes (circles and lines) in order to match the stimuli more effectively. Contrary to the gaze imitation hypothesis, Kuhn and Benson found that although participants were quicker to saccade to congruent targets than they were to neutral or incongruent targets with gaze cues, this was also true with the arrow cues. Further, participants made more erroneous saccades on incongruent trials (i.e. in the direction of the cues) but rather than this being specific to gaze cues, as found by Ricciardelli et al., it occurred also in the arrow condition. What they reported indicated that observing averted eye gaze or a pointing arrow had a direct effect on the oculomotor programming of the observer by interfering with the participant's own internal goal to make a saccade to the instructed location. One difference between the cue types was evident however and related to the latency of erroneous saccades made under the two conditions. The authors proposed that errors made on incongruent trials were evidence of a reflexive capture by the cue, made in the direction to which the cue pointed. This contrasted with correct saccades made on incongruent trials, which occurred by the participants' own volition. When they compared the latencies of correct and erroneous saccades on incongruent trials with the gaze cues, the error saccades were significantly quicker than the correct saccades, but this difference was not observed with the arrow cue. Kuhn and Benson argued that this difference between the two cue types reflected their respective

magnitudes of automaticity, with gaze cues having a more reflexive effect on saccade programming than arrow cues.

Having identified a possible difference in the mechanisms responsible for orienting to gaze and arrow cues, Kuhn (Kuhn & Kingstone, 2009) subjected these stimuli to a stronger test of their automaticity on eye movements. Friesen et al. (2004) and Driver et al. (1999) showed that in experiments testing the effects of gaze cues on covert attention, at short SOAs, attention was deployed to the cued location even when the cue predicted the wrong location for the target most of the time, so called “counter-predictive” cues. Kuhn and Kingstone adapted the voluntary saccade task to test whether this effect would be seen on oculomotor behaviour and whether similar or different effects would be seen with the arrow cues. The cues presented in their task therefore pointed towards the wrong target on the majority of trials, creating a conflict between the direction of voluntary orienting dictated by the central coloured fixation point, and the gazed at or pointed at location, which most of the time was incorrect. Kuhn and Kingstone predicted that if the cues had an obligatory and reflexive effect on eye movements, participants should be unable to suppress saccades to the location indicated by them at short SOAs, as they would not have enough time to inhibit the tendency in favour of directing their saccade to the more likely target. Their data supported this hypothesis. Participants were quicker to saccade towards targets which the eyes gazed at, even though the eyes usually gazed in the wrong location. Despite this, participants were unable to inhibit the orienting of their attention to the gazed at location. Moreover, more erroneous pro-saccades were made on incongruent trials, where the direction of the cue and the target direction were in conflict. The congruency advantage seen at the short SOA was an indication that the gaze cues were having a reflexive effect on the participants’ eye movements. As the SOA lengthened, Kuhn and Kingstone found that

the trend reversed, so that participants were quicker to saccade towards the most likely location, which was usually in the opposite direction to where the eyes were looking. This reversal effect was reflective of the participants' ability to use the advance knowledge within the increased time interval to direct their eye movements to the most likely location of the target. In order to establish whether this effect was unique to eye gaze cues, Kuhn and Kingstone compared them to arrow cues at the shortest SOA, where the maximal reaction time advantage for congruent trials had been observed with gaze cues. They discovered that the arrow cues caused an equivalent congruency advantage and pattern of erroneous pro-saccades to the gaze cues. For these reasons the authors concluded that automatic programming of saccades was not an exclusive property of biologically-relevant stimuli, thereby challenging the claims that eye gaze represents a unique form of directional cue.

Other oculomotor tasks have been used to attempt to demonstrate a special role for eye gaze cues on eye movements. Koval, Thomas, & Everling (2005) used an anti-saccade paradigm to investigate the effect of gaze cues on the production of voluntary saccades. Koval et al. reasoned that if viewing averted gaze causes a tendency to initiate a saccade to the gazed at location, participants should make most overt errors when the cue gazed towards the target, i.e. on congruent trials. Further, participants should be quicker to make correct anti-saccades on incongruent trials, as this would be the same location to which the cue was pointing and hence according to the gaze imitation hypothesis, the generation of a saccade to that location would already have been initiated by the cue. However, Koval et al. found quite the opposite. The quickest correct saccades were committed on congruent trials (where the face gazed at the target) i.e. in the opposite direction to the cue. Moreover, the

number of erroneous pro-saccades made incorrectly towards the target was greatest in the incongruent condition (where the gaze cue pointed away from the target, in the correct location for the anti-saccade) and therefore also in the opposite direction to the cue. For this reason, Koval et al.'s data did not support the gaze imitation hypothesis. Rather, participants seemed to be more likely to shift their attention away from the gazed at location. Koval et al. did not provide a thorough discussion of a likely mechanism for their results. However, a possible interpretation of their findings is that the detection of the target may have been facilitated by the gaze cues on congruent trials, thereby reducing the time necessary to make the anti-saccade and accounting for the reaction time advantage observed. Indeed, a study by Olk and Kingstone (2003) offered this interpretation to account for the relative increase in saccadic reaction times observed with anti-saccades relative to pro-saccades. These authors set out to investigate whether the reason that anti-saccades are slower than pro-saccades is due to the oculomotor inhibition required to inhibit the pre-potent pro-saccade or the need to generate a voluntary anti-saccade, or a combination of both. In two elegantly designed experiments, Olk and Kingstone demonstrated that even when the level of oculomotor inhibition and voluntary programming of saccades were equated for pro- and anti-saccade responses, anti-saccades were still more than 30ms slower than pro-saccades. These authors concluded that the reason for this discrepancy was because covert attention had to be shifted towards the target in order to ascertain whether a pro- or an anti-saccade was required and that such a shift was necessary before an eye movement could be programmed. On a pro-saccade trial, attention would have been covertly shifted to the correct location for the saccade. However, on an anti-saccade trial, covert attention would have been allocated to the wrong location for the correct saccade and so would need to be shifted to the opposite location, before a

saccade could then be executed to that location. The shifting of attention from one hemifield to the other is proposed to take time, thereby accounting for the increased latency of anti-saccades relative to pro-saccades. However, in terms of the Koval et al. (2005) study, it is difficult to see how this interpretation can account for the finding that participants, as well as being faster to saccade away from the gazed-at location, also made more overt errors in the opposite direction to the cues.

Regardless of the underlying mechanism at play, the data from the Koval et al. (2005) experiment did not support the idea that gaze cues act on observers by causing imitative eye movements in the same direction. In addition, the fact that this study did not look at other, non-social symbolic cues, leaves open the possibility that this same effect might occur with arrow cues, and may therefore be a common finding in an anti-saccade task rather than specific to gaze cues. Further use of this technique would be helpful in investigating whether gaze cues and non-social directional cues have different or similar effects on eye movement control, giving an indication of the degree of oculomotor activation occurring in response to these different stimuli.

Saccadic reaction time and error rates are not the only dependent measures to have been investigated in response to arrow and gaze cues. Nummenmaa and Hietanen (2006) used nonpredictive centrally presented gaze cues to determine whether an automatic activation of the oculomotor system would be evident in a change in the saccade curvature to targets. It is known that reflexive orienting to visual stimuli recruits the oculomotor system (Goldberg & Wurtz, 1972b) which can affect many facets of saccadic eye movements. One such feature is the trajectory of executed saccades which has been shown to be influenced by attention deployed to locations other than that of the saccade target. Saccades have been shown to deviate away from attended locations, when cued by

peripheral (exogenous) stimuli as well as when voluntarily directed to the location by centrally presented predictive cues (Doyle & Walker, 2001; McSorley, Haggard, & Walker, 2004).

In their task, Nummenmaa & Hietanen (2006) asked participants to make a saccade to a target located above or below a schematic gazing face which looked either left or right. It was anticipated that if the oculomotor system was affected by the task-irrelevant gaze distractor, evidence would be found in the trajectory of the saccade to the target. Indeed, this was what was observed. In comparison to a baseline condition, where the schematic face had no “pupils”, the vertical saccades curved away from the laterally gazed at location when the distractors were present. The authors therefore proposed that the oculomotor system is reflexively engaged by gaze cues. This finding appears to support the hypothesis that eye gaze has a privileged effect on the attentional system. However, a recent study by Hermens and Walker (2010) compared the effects of both gaze and arrows cues on saccade trajectories and found that both the social and non-social cues caused saccades to deviate away from the cued location at 300ms SOA. The influence of the arrow cues on trajectories was actually more robust than with gaze cues, occurring even at a very short SOA (10ms) where saccades deviated towards the location cued by arrows but not by gaze. This finding adds to the mounting body of evidence from oculomotor tasks which suggest that gaze cues are no more special in their influence on the saccadic system than arrow cues.

As discussed in an earlier section, when a fixation point is extinguished before the onset of the target, saccadic reaction times are characteristically reduced, caused by a reduction in activation of fixation neurons in the rostral pole of the SC which occurs at the same time as the inhibition of saccade-related cells decreases (Dorris & Munoz, 1995; Dorris et al., 1997). These processes act to disengage the oculomotor system from fixation

in preparation for a saccade. Furthermore, the offset of the fixation stimulus is also thought to act as a general warning signal, readying the oculomotor system for a saccade (e.g. Reuter-Lorenz et al., 1991). The resulting reduction in SRT and elevation in error rates associated with this manipulation is referred to as the gap effect. Friesen & Kingstone (2003) suggested that if observing averted eye gaze causes an automatic preparation to the gazed at location via activity in the SC, the gap effect ought not to occur with gaze cues which point left or right. They reasoned that if the cue's gaze was averted, the cue itself would have already pre-disengaged the saccadic system from fixation, and so introducing a temporal gap between fixation offset and target onset would not be able to cause further disengagement. The gap effect would occur however when the cue looked straight ahead, as no pre-disengagement of the oculomotor system would have occurred under these conditions. However, Friesen and Kingstone found equivalent gap effects for averted and straight gaze which led them to conclude that the oculomotor system was not involved in the orienting to eye gaze. Rather, these authors attributed the orienting effects to a novel cortical reflexive mechanism, mediated by the temporal and parietal cortices, specifically activated by gaze. Friesen and Kingstone did not compare gaze cues to any other cues in this study, and so the possibility exists that the effects they observed may be just as likely in response to other, non-social cues, such as arrows.

Oculomotor behaviour in response to directional cues other than arrows and eye gaze has received very little attention in the literature. However, as with studies of covert attention discussed in an earlier section, evidence has been provided for automatic effects of word cues on eye movements. Hodgson, Parris, Gregory, and Jarvis (2009) demonstrated that irrelevant directional words caused the programming and execution of saccades in the direction indicated by them in their oculomotor version of the classic Stroop task (Stroop,

1935). In Hodgson et al.'s task, participants were required to make a saccade to one of four coloured patches on a computer screen. The correct direction of the saccade was determined by the "ink" colour of a centrally presented colour or direction word, whilst the to be ignored identity of the word could be congruent or incongruent with the ink colour. These authors found that when the ink and identity of the word were incongruent, participants were slower to correctly initiate a saccade to the correct colour patch, but also that they made error saccades towards the patch indicated by the word identity. These findings suggest that the semantic meaning of words can be processed automatically, even when they are to be ignored, generating a corresponding oculomotor programme matching the meaning of the word. In Hodgson et al.'s study, it was necessary to attend to one aspect of the word cues, whilst ignoring their semantic meaning. Further work might investigate the influence of word cues on saccadic behaviour when they are entirely task irrelevant.

Unlike the literature on covert spatial attention, the effects of social cues other than eye gaze on oculomotor behaviour have received no interest. This is an obvious potential avenue for investigation. Evidence of automatic programming of saccades in response to social cues such as finger pointing would suggest that that assumptions made about the special nature of eye gaze as a directional cue may have been misguided.

In summary, to date there has been limited evidence from studies of oculomotor behaviour to suggest that eye gaze can qualify as a special directional stimulus. Similar results have been reported for arrow and gaze cues and no authors have managed to support Ricciardelli et al.'s (2002) gaze imitation hypothesis, which stipulated that saccade programming in the direction of gaze cues is specific to this biologically and socially relevant stimulus. Furthermore, there has been little consistency or concern about the use of

schematic versus real world cues. In addition, to date, very little research has been undertaken with other directional cues. It may be then, that eye gaze, although a powerful social cue, is no more effective at shifting attention than any other direction-implying stimuli.

1.4 The control of eye movements in relation to social and symbolic cues

1.4.1 Reflexive versus voluntary saccades

In section 1.2., attentional orienting was described as taking one of two forms: reflexive (alternatively referred to as exogenous, stimulus driven, visually guided or bottom-up) or voluntary (or endogenous, goal-directed, volitional, or top-down). The generation of saccades has been regarded to operate via these two mechanisms, and the two modes of orienting have been shown to be subserved by different neural networks to a degree (for reviews see Corbetta & Shulman, 2002; Johnston & Everling, 2008; McDowell, Dyckman, Austin, & Clementz, 2008). However, from the reported literature on symbolic cues and particularly eye gaze cues in the previous section, this dichotomy of attentional orienting seems to lack the ability to describe the findings from some oculomotor studies of both social and some non-social cues, which appear to operate via a mechanism which is neither truly reflexive nor endogenous. Current models of saccade generation generally continue to make the distinction between reflexive and voluntary saccades, however. The following section will briefly describe some of the models of saccade generation that have emerged in recent years and will discuss their ability to account for the kind of saccadic orienting observed with some symbolic cues.

1.4.2 Models of saccade generation

Two main themes emerge in the current models of saccade generation. The first represents exogenous and endogenously guided saccades as separate processes, with saccades evoked by each mechanism able to be processed in parallel with the program which runs to completion first, winning. The *independent horse-race model* holds this view (Godijn & Theeuwes, 2002; Theeuwes, Kramer, Hahn, Irwin, & Zelinsky, 1999). In this account, top-down saccade programming can be overcome entirely by the sudden onset of an exogenous cue if it occurs before the endogenous saccade can be initiated. The second theme in models of saccade generation is that of competition within the same system between endogenous and exogenous saccade targets. The *competitive integration model* first proposed by Godijn and Theeuwes (2002) and developed by Meeter, Van der Stigchel and Theeuwes (2010) (who also acknowledge an earlier model by Trappenberg, Dorris, Munoz and Klein (2001) is based on this idea, and holds that potential saccade targets compete within a topographically organised salience map (the SC being the proposed neurophysiological basis), with both stimulus-driven and goal-driven saccades competing within that map. A saccade is initiated when a location on the map reaches some threshold. Distant multiple saccade targets mutually inhibit one another, moving a potential saccade further from threshold, whilst proximate saccade target activity combines, resulting in one saccade target location which is closer to threshold than either of its individual components. Therefore, in this model, saccade location and latency are integrated.

Although a compelling account of saccade generation, which can account for several oculomotor phenomena with clear similarities to the neurophysiological accounts of saccade generation, it is not however obvious from this model how the social/biological and symbolic cues such as gaze cues may exert their effects on eye movements, apparently

being neither truly exogenous nor endogenous in their mode of action, according to the view of the literature presented thus far.

The competitive integration model has similarities with Findlay and Walker's (1999) model of saccade generation. Findlay and Walker's model also postulates that multiple saccade target locations compete via a salience map. However unlike the former model, in Findlay and Walker's model, the spatial and temporal parameters of the saccade are determined via two separate but parallel routes: The WHERE and the WHEN pathways. The WHERE pathway determines the spatial location of the saccade, and includes a *move centre* (the salience map) which is organised topographically. The point on the map with the greatest salience will be the location of the subsequent saccade. The WHEN pathway, which governs the latency of the saccade includes the *fixate centre*, the relative activity level of which determines the latency of the saccade. The competitive interaction between the fixate and move centres determines the overall metrics and timing of the saccade. As activity in one centre increases, there will be a decrease in activity in the other, and it is this competitive inhibition which determines to a large extent the SRT of the saccade (Findlay & Gilchrist, 2003). There is also competition within the salience map, if multiple saccade targets exist within the visual field. The model states that this competition within the move centre resolves via inhibitory connections, resulting in the point of greatest salience dictating the location for the subsequent saccade in a "winner takes all" manner (Findlay & Walker, 1999).

According to Findlay and Walker's model, the move and the fixate centres can be influenced by a range of factors occurring at hierarchically organised levels within the model. With Level 1 representing the motor response itself and Level 2 the decision as to where and when the saccade will be executed, Level 3 accounts for "hard-wired" and

“automatic” visual influences outside of cognitive control. Typical exogenous cues would be considered as acting at this level as are visual events at fixation. Levels 4 and 5 contain the cognitive influences on saccades, with Level 4, termed “automated” and Level 5 termed “voluntary”. The distinction is made between Level 4 processes which are generally outside of conscious awareness but may be based on learned responses, whereas Level 5 reflects more typically endogenous, goal-driven influences.

As already described, the traditional distinction between reflexive and voluntary orienting of eye movements does not appear to account for the obligatory effects observed in response to some task irrelevant spatial cues such as eye gaze. Although not explicitly discussing such cues, Findlay and Walker’s “automated” Level 4 processes may provide a framework within which the influence of task-irrelevant socio-biological and some symbolic cues can be interpreted. Operations at this level are described as being largely outside of conscious control and may be based on learned associations. Cues such as eye gaze and arrows, which have generally been referred to as endogenous cues, do however appear to exert apparently automatic effects on attention and eye movements. However although seemingly automatic, whether such effects should be termed “reflexive”, as many authors have done, is questionable. For example, it is unlikely that the saccadic system is predisposed to reflexively orient attention in the direction of arrows as it is to flashes of light. Therefore this form of orienting by some symbolic cues cannot be adequately situated at Level 3 of Findlay and Walker’s model and may therefore be more appropriately placed at Level 4.

The terms “automatic” and “reflexive” when used to describe covert and saccadic orienting are often used interchangeably and apparently indiscriminately in the wider literature. However, it seems more accurate, in light of the suggestions made above, to term

the orienting influence of to be ignored symbolic cues as *automatic* rather than reflexive, with endogenous, goal-directed orienting described as *voluntary*, with the term *reflexive* reserved for its original usage. This is the convention that will be adopted in the remaining chapters of this thesis.

1.5 Developmental issues

1.5.1 Development of gaze processing

Conflicting evidence has been provided in section 1.3 regarding the degree to which eye gaze can constitute a “special” example of directional stimulus. However, this intuitive idea is not simply based on anecdotal accounts. Rather, it is supported by decades of evidence from the developmental psychology literature where the importance of social cues and non-verbal communication has been acknowledged and extensively studied. The following section will present and evaluate evidence for the important role of social cues from the developmental perspective as well as from the area of autism research, where social difficulties are often accompanied by atypical responses to social cues.

Joint attention is a crucial component of healthy development, allowing infants to develop their understanding of the world, people and objects by sharing attention with others. It is a particularly important communicative device before the development of speech, as it enables the child to express its intentions and desires without the aid of language (Corkum & Moore, 1998). A behaviour which is critical to the development of joint attention is gaze following. It has been suggested that interpretation of eye gaze direction is an innate ability, mediated by the Eye Direction Detector module (Baron-Cohen, 1995). There is certainly evidence that newborns are able to perceive general face

related information such as attractiveness (Slater et al., 1998) and familiarity (Bushnell, 2001). Other work has shown that newborns spend more time looking at faces with eyes open than eyes closed, indicating a preference for observing the eyes of the face (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000). More specifically in support of the Eye Direction Detector, there is some evidence for gaze direction processing being present from birth (Farroni, Csibra, Simion, & Johnson, 2002; Farroni, Massaccesi, Pividori, & Johnson, 2004). Furthermore, in the laboratory, babies as young as 10 weeks old, have been shown to make saccades in the direction of gazing faces (Hood, Willen & Driver, 1998). However, in more natural settings, gaze following is observed for the first time between 6 and 12 months of age (Butterworth & Jarrett, 1991; Corkum & Moore, 1998; Morales, Mundy, & Rojas, 1998), although orienting to combined head and gaze cues has been reported by the age 4 months (Perra & Gattis, 2010). A study by Corkum and Moore (1998) investigated whether babies who were not already spontaneously gaze following, could be trained to do so over the course of an experimental session. They found that after a training period, where the experimenter's gaze turn (i.e. head and gaze) was paired with the activation of a toy at the gazed at location, most of the 10-11 month old children they tested continued to look at the gazed at location even when the toy was no longer activated in advance of the child's gaze shift, with 40% of 8-9 month olds able to develop gaze following over the training session. From these findings, the authors suggested that gaze following may be a learned ability acquired during the last few months of the first year of life, because children come to associate the cue of the gaze shift with interesting events at the gazed at location. In a second experiment by the same authors, the cues became counterpredictive in that they always looked in the wrong direction for the toy. They reasoned that if gaze following is simply a learned ability based on a stimulus-

response association, the babies should learn to look towards the direction opposite to where the gaze was directed as this was where the toy was being activated. However, contrary to this prediction, the babies still looked towards the direction to which the gaze was directed, even though this was not where the reinforcing stimulus (the toy) was located. This second experiment has correlates with the counterpredictive gaze cueing experiments conducted with adults (Driver et al., 1999; Friesen et al., 2004; Kuhn & Kingstone, 2009), where participants were still faster to respond in the direction of the cue, despite them predicting the wrong location for the target most of the time. However, the Corkum and Moore study investigated combined head and gaze cues, and it is therefore possible that the infants were responding to the head turn rather than the eye gaze itself. However, their findings are interesting as they may suggest that gaze following may not be simply a learned response which is acquired with repeated exposure. Rather, it suggests that there may be an innate tendency for infants to look towards where an adult is looking which may take precedence over any stimulus-response associations which might compete with it.

The reason that eye gaze processing is thought such a critical component of typical development is that it is considered to be one aspect of Theory of Mind (Baron-Cohen, 1995): The ability to attribute mental states to others and to understand that those mental states might be different from one's own. Evidence from neuroimaging tasks supports this, with common neural structures in frontal and temporal lobes being reported to be activated during Theory of Mind and gaze processing tasks (Calder et al., 2002; Williams, Waiter, Perra, Perrett, & Whiten, 2005). It has been proposed that Theory of Mind is achieved by imitating another's mental state and as such may be subserved by the brain's mirror neuron system (Gallese & Goldman, 1998; Schulte-Ruther, Markowitsch, Fink, & Piefke, 2007)

Recently, mirror neurons for eye gaze have been identified in macaques (Shepherd, Klein, Deaner, & Platt, 2009) further suggesting that the processes share a common neural basis. Additional evidence for the complex relationship between Theory of Mind, mirror neurons and gaze perception comes from the literature on Autistic Spectrum Disorders (ASD) and will be discussed in the following section.

1.5.2 Autistic Spectrum Disorders

The Autistic Spectrum Disorders (ASD) are a group of closely related neurodevelopmental disorders (generally referred to as just *autism*) which is characterised by amongst other things, abnormalities in Theory of Mind or “social intelligence” (Baron-Cohen et al., 2000). One of the first indications of autism is a reduced engagement in joint attention behaviours, one of which is gaze following (e.g. Baron-Cohen et al., 1996). There is limited evidence of gaze following behaviour in very young children with autism as it is a disorder which is rarely diagnosed before the age of two. However, retrospective analyses of home videos filmed at the first birthday parties of children who were later diagnosed with autism have revealed that these children respond less to social stimuli such as their name being called (Werner, Dawson, Osterling, & Dinno, 2000) and spend less time looking at the faces of others than typically developing children (Osterling, Dawson, & Munson, 2002). Deficits in spontaneous gaze following seem to be prevalent in young children with ASD. Whereas typically developing children will look towards where someone’s head and eyes are oriented by around 10 months of age (Corkum & Moore, 1998), children with autism fail to do so until much later, and even then only individuals with high mental ages seem able to acquire the ability and then only in a laboratory setting (Leekam, Hunnisett, & Moore, 1998). The problem lies not with perceptual abilities, as

children with autism are able to determine where someone is looking when asked (Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & Walker, 1995; Leekam, Baron-Cohen, Perrett, Milders, & Brown, 1997) but rather seems to lie with a lack of appreciation that eye gaze is an important stimuli to attend to. It has been proposed that in ASD, an inherent tendency to engage with faces and eyes, which is present in typically developing children, is absent or delayed.

Although gaze following seems to be diminished in natural settings in ASD, there is conflicting evidence from gaze cueing studies as to the presence of a deficit in the laboratory. Whilst some studies have shown that individuals with autism do not show automatic cueing effects to non-predictive gaze cues (Johnson et al., 2005; Ristic et al., 2005), others have demonstrated relatively normal cueing effects (Chawarska, Klin, & Volkmar, 2003; Kuhn et al., 2010; Kylliainen & Hietanen, 2004; Swettenham, Condie, Campbell, Milne, & Coleman, 2003)

So why are people with ASD uninterested in gaze, at least, in the real world? One possible answer lies with mirror neurons. As discussed in the previous section, imitative behaviour is thought to be mediated by mirror neurons. Imitation in young children is thought to aid learning (Tomasello, Savage-Rumbaugh, & Kruger, 1993) and is something which autistic children have characteristic impairments in (Williams et al., 2001). As gaze following is regarded as a form of imitation, with some evidence that eye gaze elicits its automatic effects on attention and eye movements via the mirror neuron system, it is possible that autistic children have a dysfunctional mirror neuron system, which would account for their deficits in gaze following and other forms of imitative behaviour (Frischen, Bayliss, & Tipper, 2007). Additional support for this has come from neurophysiological studies (Oberman et al., 2005). Furthermore, Theory of Mind is also

considered to be mediated by the mirror neuron system and Theory of Mind deficits are considered to be at the core of autism (Baron-Cohen, Leslie, & Frith, 1985), adding to the view that reduced influence of eye gaze cues in autism may be linked to a dysfunctional mirror neuron system.

An alternative explanation has been proposed for the lack of spontaneous gaze following in ASD. Social stimuli are thought to be inherently rewarding (Damasio, Tranel, & Damasio, 1990; Deaner, Khera, & Platt, 2005; Klein, Deaner, & Platt, 2008; Klein, Shepherd, & Platt, 2009; Rolls, 1999), so a reduction in the reward value of social interaction may account for the lack of learning of gaze following (Mundy & Sigman, 2006). Further support of this theory comes from evidence that amygdala function is impaired in autism (Baron-Cohen et al., 2000; Howard et al., 2000). This structure is involved in reward related behaviour (Cador, Robbins, & Everitt, 1989) and ablation of this area in primates has been demonstrated to significantly disrupt social behaviour (Aggleton & Passingham, 1981). In autistic individuals, a dysfunctional amygdala could result in social interaction being less rewarding and therefore less practiced, leading to reduced opportunities for learning about gaze following.

1.5.3 Gender differences in ASD and gaze following

The impairments in gaze processing in autism have been discussed but the relationship between gender, ASD and gaze following is worthy of further elaboration. The disorders are much more prevalent in males than in females, but even in typically developed adults there is a gender difference in autistic-like traits. The Extreme Male Brain Theory of autism (Baron-Cohen, 2002) proposes that ASD lies at the extremity of a continuum of a cognitive style which is typically male. The continuum ranges between two dimensions, empathising

and systemising. Empathising refers to the ability to identify and respond to other peoples' internal mental states, whilst systemising is the ability to understand the inner workings and rules governing the operation of systems. The former dimension is typically female and the latter, male (Baron-Cohen, 2002). For example, females talk more about emotions and feelings than men (Tannen, 2001), are found to score more highly on tests of Theory of Mind (Happé, 1995) make more eye contact (Lutchmaya, Baron-Cohen, & Raggatt, 2002; Swettenham et al., 1998) and score more highly on the Reading the Mind in the Eyes test, than men (Baron-Cohen, Jolliffe, Mortimore, & Robertson, 1997) whilst men show greater ability than women in tests of intuitive physics (Baron-Cohen, Wheelwright, Spong, Scahill, & Lawson, 2001) and more generally in academic disciplines of mathematics, physics and engineering, whilst professions which require a high level of systemising such as engineering and construction are dominated by men (Geary, 1998).

A covert spatial cueing study conducted by Bayliss, Pellegrino, & Tipper (2005) showed that men were less affected by gaze cues than women, and that higher scores on the Autism Spectrum Quotient (Baron-Cohen, S. Wheelwright, Skinner, Martin, & Clubley, 2001), a self-report questionnaire used for identifying autistic traits were associated with smaller cueing effects. In other words, for men and women, the greater the magnitude of cueing effect shown in the behavioural task, the lesser the severity of social and communication difficulties experienced in real-life. This finding may have implications for interpreting data from studies with variable ratios of males and females and also when considering single neuropsychological case studies.

1.6 Neural bases of processing of gaze and other symbolic cues

From the evidence presented so far, it is clear that gaze following is an important social behaviour with deficits related to severe impairments in development. However, behavioural studies of eye gaze cueing have failed to find many significant discrepancies between the effects of these cues and non-social cues such as arrows. The neural basis of gaze perception and gaze cueing has been the subject of intense research in an attempt to find evidence for the view that eye gaze really is a special directional stimulus, as the following section will present.

1.6.1 Neural substrates of gaze processing: An overview

Several structures including the amygdala, which is thought to be involved in the emotional response to eye gaze (Adams, Gordon, Baird, Ambady, & Kleck, 2003; Sato, Yoshikawa, Kochiyama, & Matsumura, 2004) and the fusiform gyrus, which is involved in face processing more generally, have been implicated in gaze processing (Calder et al., 2002; Pageler et al., 2003). One area which has been repeatedly linked to gaze perception is the superior temporal sulcus (STS). In fact, this area is not only sensitive to eye gaze stimuli, but has also been shown to be involved in processing biological motion in general (for a review see Allison, Puce, & McCarthy, 2000). Neurophysiological work on monkeys by Perrett and colleagues (Perrett & Emery, 1994; Perrett, Hietanen, Oram, & Benson, 1992; Perrett et al., 1985) showed that neurons in the STS were sensitive to the direction of gaze with some cells responding maximally to straight gaze and others to averted gaze. In humans, the region of the STS has also shown to be activated by meaningful gaze stimuli through neuroimaging studies of healthy participants (Hooker et al., 2003; Pelphrey, Viola, & McCarthy, 2004; Wicker, Michel, Henaff, & Decety, 1998). Further evidence for the role

of STS in gaze perception has been presented by Akiyama and colleagues (Akiyama, Kato, Muramatsu, & Kashima, 2008; Akiyama, Kato, Muramatsu, Saito, Nakachi, et al., 2006). Patient MJ had a circumscribed lesion confined to the right superior temporal gyrus (STG) which incorporated part of the STS. Although her intellectual, language and mnemonic skills were unaffected, MJ had difficulty determining the direction of gaze of the experimenter, was unable to maintain eye contact and did not orient to eye gaze cues in a spatial cueing paradigm, although she showed normal orienting to arrow cues. (Akiyama, Kato, Muramatsu, Saito, Umeda, et al., 2006). Further evidence of specific activation of STS by gaze but not arrows comes from an fMRI study by Kingstone, Tipper, Ristic, and Ngan (2004) (however see Tipper, Handy, Giesbrecht, & Kingstone, 2008).

Due to the inconclusive evidence from spatial cueing tasks regarding the special nature of gaze cues, several studies have attempted to identify brain regions involved in these type of tasks with arrow and gaze cues. One such study was conducted by Vuilleumier (2002), who performed gaze and arrow cueing tasks with patients with damage to the right parietal cortex. This author found that gaze cues but not arrows, caused automatic orienting of attention in these patients. As the parietal lobe is known to be involved in orienting of attention to symbolic cues (Corbetta & Shulman, 2002) this finding suggests that gaze cues may cause attentional orienting which is more reflexive than that caused by arrows, reliant upon a different neural network. However, a meta-analysis conducted by Grosbras et al. (2005) found evidence in support of a role for the intra-parietal sulcus (IPS) in the parietal lobe in gaze cueing. This area was found to be activated by gaze cues and also by visually guided attention. The authors suggested that gaze cueing appeared neuroanatomically, to have more in common with reflexive orienting

than voluntary orienting of eye movements and attention. Other work has further supported a role of the IPS in viewing averted eye gaze and has indicated that context of the gaze cues might be of importance in activating this region (Bristow, Rees, & Frith, 2007; Pelphrey, Singerman, Allison, & McCarthy, 2003).

A further study compared the activation of brain regions via fMRI, caused by gaze and arrow cues using a spatial cueing paradigm (Hietanen, Nummenmaa, Nyman, Parkkola and Hamalainen (2006). Although their behavioural data produced equivalent results for the schematic gaze and arrow cues (responses on congruent trials were quicker than incongruent), their imaging data identified differences between the two cue types. Arrow cues caused a generally more distributed pattern of activation including areas of the frontal cortices, including the FEF (thought to be particularly important for voluntary shifts of attention) whereas the gaze cues did not. Hietanen et al. proposed that the lack of frontal activity with gaze cues was attributable to the fact that eye gaze acts more reflexively on attention, without the need for frontal involvement, whereas arrow cues require interpretation and volition in order for them to shift attention. A recent fMRI study using more ecologically valid gaze cues reported reduced activity in the frontal-parietal attention network when orienting to gaze cues in comparison with arrows, further suggesting that gaze cues may be processed more automatically than other symbolic cues (Engell et al., 2010). Indeed, a study by Greene, Mooshagian, Kaplan, Zaidel and Iacoboni (2009) supported this hypothesis, by identifying similar areas of cortical activity for gaze cues as they did exogenous, peripheral cues. A study by Sato, Kochiyama, Uono and Yoshikawa (2009) has reported large areas of overlapping neural activation by photographic gaze and finger pointing cues and arrow cues, including areas of the parietal and frontal lobes. However they also reported greater cortical activation in parietal and temporal areas by

directional arrows than the socio-biological cues. This study may be harder to directly compare to those previously discussed as these authors were not investigating attentional orienting per se as participants passively viewed directional and non-directional versions of the stimuli, rather than performing a spatial cueing task. Nevertheless, it provides further suggestion that gaze cues may activate a less distributed cortical network than arrow cues, indicating that eye gaze may be processed more automatically by the brain.

Other areas of frontal cortex have been implicated in gaze processing in other studies. As noted in an earlier section, gaze perception and Theory of Mind have been linked not least by their common activation of areas of the medial frontal cortex (Calder et al., 2002; Williams et al., 2005). The orbitofrontal cortex (OFC) is included in this region and has been specifically implicated in gaze processing as well as in social behaviour, and will be discussed in the following section.

1.6.2 Orbitofrontal cortex, gaze processing and social behaviour

Evidence for the role of the OFC in gaze processing comes from a case in the literature who has been extensively studied with regards to his social behaviour. Patient EVR sustained a large bilateral orbitofrontal lesion after the removal of a meningioma. Although he experienced marked changes in his personality, resembling “acquired sociopathy”, his intelligence, memory, speech and face perception remained intact (Damasio et al., 1990). EVR performed as controls on a spatial cueing task involving peripheral cues, but in two studies using centrally presented gaze cues, Vecera and Rizzo showed that EVR did not shift his attention to the gazed at location when the cues were nonpredictive (Vecera & Rizzo, 2006) and could not even do so when the cues predicted

the correct target location most of the time (Vecera & Rizzo, 2004). The authors concluded that the processing of gaze stimuli and the subsequent shifting of attention to the gazed at location requires some degree of OFC involvement and was not solely reflexive in the sense that it relied mostly on subcortical mechanisms, as with exogenous orienting to peripheral cues. Vecera and Rizzo (2006) also demonstrated that EVR, unlike controls, could not orient towards the direction indicated by centrally presented, predictive word cues, such as LEFT and RIGHT. In this respect they proposed that gaze cues were no more special than words cues and suggested that the apparently reflexive effects observed in behavioural experiments may be due to gaze cues being an over-learned stimulus which has resulted in their ability to elicit aspects of automaticity on attention.

Although Vecera and Rizzo's conclusion did not attribute a specifically social role for the OFC in orienting to symbolic cues, there is a wealth of evidence that suggests that OFC does have a particular function in successful social behaviour, as studies of patients with lesions to this area have demonstrated. As already outlined, the Autistic Spectrum Disorders are associated with atypical social and emotional functioning, but patients with damage to the OFC show some of the same problems as those seen in ASD. Patient EVR, described above, and other OFC patients have been studied extensively and the core finding has been that patients with damage to this area of the frontal cortex display diminished emotional, behavioural and physiological responses to social stimuli in comparison to healthy controls and patients with lesions to other areas of the prefrontal cortex. Several tests of social perception and intelligence have been used with patients with OFC damage. For example, the Tests of Social Intelligence (O'Sullivan & Guildford, 1976) was used by Cicerone and Tanenbaum (1997) with patient SAL who had suffered traumatic brain injury to the OFC. In this test, the participant is required to interpret images depicting non-verbal

interactions and social exchanges between people in different contexts and to predict the most likely consequences of such exchanges. SAL was impaired in these tasks which relied on the interpretation of subtle behavioural nuances and associating emotional reactions to such cues. The authors noted that SAL's problems seemed to specifically relate to "... her failure to use all the relevant information available to her in a situation...[and she has] particular difficulty utilizing complex or subtle forms of information arising from social interactions" (Cicerone & Tanenbaum, 1997, p. 180). A similar task, but using video clips of real, unrehearsed social interaction, as opposed to clips using actors, is the Interpersonal Perception task (Archer et al. 1998). Participants are asked to explain the relationship between the people in the videos based on their non-verbal communication. Mah, Arnold, and Grafman (2004) used this task with OFC patients and showed that in comparison to neurologically healthy controls, this group were impaired in correctly judging the relationship between the people in the clips. The interpretation of such subtle exchanges would be problematic without an understanding of the emotions of the protagonists. Indeed, Hornak, Rolls and Wade (1996) showed that individuals with OFC lesions were impaired at decoding vocal and facial expressions and that the severity of this impairment correlated with the severity of their behavioural and emotional problems post-lesion.

A more cognitively complex test assesses participants' ability to detect whether a faux pas has been committed in a social interaction. A faux pas occurs when someone says something they shouldn't have said without realising that what they said maybe hurtful or insulting to another person who is present. In order to detect that a faux pas has occurred one must acknowledge that the person making the faux pas has a false belief (that what they are saying *is* appropriate in that circumstance) and that the other person would find what was said insulting or upsetting (Stone, Baron-Cohen, & Knight, 1998). Performance on this

test is poor in individuals with high functioning autism (Baron-Cohen, O'Riordan, Stone, Jones, & Plaisted, 1999) and was found to be equally poor in a group of OFC patients. However the same OFC patients were able to correctly perform a false belief task, with no affective component, which demonstrated that their deficit was not due to a general Theory of Mind impairment. Rather, it seemed that the attribution of emotional states to others' beliefs was affected in the OFC patients (Stone et al., 1998).

In addition to atypical behavioural responses, abnormal physiological responses to social stimuli have been observed in individuals with OFC lesions. For example, Damasio et al. (1990) showed that in response to social stimuli, a group of patients with OFC lesions exhibited reduced skin conductance responses (SCRs), a measure of autonomic arousal, in comparison to controls and patients with lesions outside the OFC. The OFC group showed normal SCRs to unconditioned stimuli such as a hand clap, indicating that it was not their autonomic arousal per se that was impaired, but rather that it was specifically their response to socially relevant stimuli that was atypical. Further evidence of abnormal autonomic responses in OFC patients has been presented by Bechara and colleagues (Bechara, Damasio, Damasio, & Anderson, 1994; Bechara, Damasio, Damasio, & Lee, 1999; Bechara, Tranel, & Damasio, 2000; Bechara, Tranel, Damasio, & Damasio, 1996). These authors assessed the behaviour of OFC patients in The Iowa Gambling Task and the SCRs produced during the test. They found that whilst healthy controls developed a preference for the low risk decks, OFC patients tended to persist with high risk decks which pay more in the short term but which have greater potential for large losses. In addition, whereas normal controls generate anticipatory SCRs prior to selecting high risk decks, OFC patients do not exhibit such autonomic arousal before making their choice. Evidence for a deficit in reward relating learning has also been shown in OFC patients, who were not able to update

their responses when reward contingencies changed, despite being able to verbalise the rules (Rolls, Hornak, Wade, & McGrath, 1994).

The fact that the OFC patients in Rolls et al.'s (1994) study often were able to verbalise that the rules of the game had changed but were nevertheless unable to modify their behaviour accordingly may be explained by the somatic marker hypothesis (Damasio et al., 1990). This hypothesis states that events become associated with physiological markers which can be positive or negative. The function of these markers is to associate an emotional valence to mental representations so that when a course of action is contemplated, an appropriate response can be selected on the basis of the somatic markers, without need for detailed analysis of all the possible responses and outcomes. A deficit in this short cutting mechanism could be responsible for the behaviour observed in the patients in the study by Rolls et al. and in those conducted by Bechara and colleagues in addition to the reduced SCRs found in OFC patients by Damasio et al (1990). Their impairments may be due to an inability to represent the emotional outcome of their choices because the somatic states associated with positive and negative outcomes are not activated appropriately. Rather, such patients appear to persist with behaviour which confers immediate rewards but results in long term negative consequences. The somatic marker hypothesis may also explain social perception deficits in OFC patients. For example, to acknowledge a faux pas may rely on the rapid identification of a somatic state associated with being embarrassed or offended.

In summary, there appears to be a clear role for the OFC in correctly associating stimuli with appropriate emotional and social valence, and damage to this part of the brain leads to inappropriate responses in these domains. In this respect there is a similarity with ASD, where social interaction appears to be unrewarding and the importance of social cues

are not acquired or appreciated. The case of patient EVR suggests that the eye gaze of another individual may not constitute a rewarding stimuli for OFC patients, as seems to be the case in autism. However, EVR's attentional orienting deficit may not be restricted to social cues, and being the only reported OFC patient with whom this paradigm has been carried out, future work with similar patients would aid in clarifying the role of OFC in attentional orienting to social and non-social cues.

1.7 Thesis overview

This chapter has presented and evaluated the literature which has sought to find evidence for a privileged role for eye gaze in orienting of attention and eye movements, in social interaction and the neural mechanisms which are responsible for its effects. Although there is strong evidence that eye gaze following is an important behaviour necessary for normal development and everyday social interaction, the behavioural literature on orienting to eye gaze presents few findings which support a special role for eye gaze over other non-social cues such as arrows. However, despite the intense interest in the subject of eye gaze, many avenues of research, which may shed light on the processes underlying orienting to gaze and other symbolic cues, remain unexplored and other issues which may have confounded previous research appear not to have been acknowledged. This thesis aims to address some of these unresolved and little considered issues.

To date, relatively few studies have explored eye movement responses to gaze and arrow cues. If gaze following is an imitative behaviour, as has been suggested by the gaze imitation hypothesis, then it would seem appropriate to study observers' overt behavioural responses to these cues, rather than measuring shifts of covert attention. In everyday life during social interaction, we use cues such as pointing with the finger as well as our eye

gaze, to refer to objects in order to share our attention of that object with others. The orienting responses of our social partner are almost always overt, that is they are made with their eyes, head and body. Furthermore, the use of oculomotor tasks allows for the extraction of a larger number of response parameters than covert attentional paradigms, which may uncover more subtle differences between the effects of different directional cues on eye movements. The pro- and anti-saccade tasks described earlier are suitable for adaptation to investigate the influence of directional cues on saccadic responses and both tasks have been used in this thesis. In addition, both have been modified to create *gap* versions to find evidence of automatic activation of the oculomotor system in response to gaze and arrow cues (Chapters 2 and 3). The use of the more cognitively demanding anti-saccade task as well as the pro-saccade task, will allow a comparison of the influence of the cues under high and low cognitive demands respectively.

There has been very little research addressing the effects of social biological and non-social symbolic cues other than gaze and arrows on eye movements. This research will address this issue by examining the effects of two further cues, finger pointing and directional words, on the saccadic system (Chapter 4).

The issue of ecological validity of the cues used in previous research has apparently been of little concern to researchers, with schematic gaze cues used in some studies and “real-world” gaze cues used in others, but with results often compared with little regard for this potentially confounding issue. Furthermore, no studies have attempted to increase ecological validity of arrow cues by using stimuli which convey a particular “real-world” meaning. This thesis will address this issue by using real-world, ecologically valid stimuli throughout, and then later comparing these results to those of schematic gaze and arrow cues (Chapter 5).

The relationship between autistic traits and the influence of eye gaze and arrow cues will be explored in young male controls (Chapter 6) and the relationship between damage to the frontal cortex, social behaviour and overt orienting to gaze and arrow cues will be explored with three neurological patients (Chapter 7), with the aim of finding evidence for a specific role of eye gaze cues in social interaction and the neural bases underpinning it. Finally, a model accounting for the influence of socio-biological and non-social cues on eye movements, by extending current theoretical accounts of attention and eye movement control, will be presented and the implications of a specific role of socially relevant cues in effective social functioning will be discussed. Finally, limitations and wider impact of the research will be discussed (Chapter 8).

Chapter 2: *The effect of real-world eye gaze and arrow cues on performance in pro- and anti-saccade tasks*

Experiment 1: Pro-saccades

2.1 Introduction

Previous studies of covert and overt orienting have demonstrated that uninformative, centrally presented eye gaze cues cause a facilitation of target detection (Driver et al., 1999; Friesen & Kingstone, 1998; Quadflieg, Mason, & Macrae, 2004; Sato, Kochiyama, Uono, & Yoshikawa, 2010; Tipples, 2005) or saccadic response time (Kuhn & Benson, 2007; Kuhn et al., 2010; Kuhn & Kingstone, 2009; Mansfield, Farroni, & Johnson, 2003; Ricciardelli, Bricolo, Aglioti, & Chelazzi, 2002) for targets presented in the direction of the cue, in comparison to targets in the uncued direction. This has even been found to occur when the cues are counter-predictive, in both covert (Friesen, Ristic, & Kingstone, 2004; Tipples, 2008) and overt (Kuhn & Kingstone, 2009) attentional orienting experiments. A further finding in many of these experiments has been that the cueing effects occur after only a very short presentation of the cue. This evidence has been used to assert that gaze cues act automatically or “reflexively” on visual attention mechanisms.

Although eye gaze has been regarded by some researchers to constitute a special example of a directional cue, a large and convincing body of recent evidence has also demonstrated that arrows, are also able to elicit apparently “reflexive” orienting in both covert (Gibson & Bryant, 2005; Hommel, Pratt, Colzato, & Godijn, 2001; Tipples, 2002)

and overt (Bonato, Priftis, Marenzi, & Zorzi, 2009; Kuhn & Benson, 2007; Kuhn & Kingstone, 2009) attention. A central aim of Experiment 1 was to test the suggestion that arrows are capable of producing automatic facilitation of saccadic responses in the direction of the cue in the same manner as gaze cues, by comparing gaze and arrows cues in a simple pro-saccade task. The cues were constructed to maximise their ecological validity. The gaze cues were comprised of colour photographs of a male pair of eyes, looking left or right, or with eyes closed, the latter representing the neutral condition. An image of closed eyes rather than eyes looking straight ahead was chosen as the latter has been shown to actively engage attention (Senju & Hasegawa, 2005) and would therefore prove unsuitable for a neutral condition. The eye region only, rather than whole face cues were used as previous work has suggested that facial properties such as emotion and attractiveness can interact with gaze direction to influence attention (e.g. Jones, DeBruine, Little, Conway, & Feinberg, 2006). As it was only directional effects which were under investigation, the images were cropped to include only the eye region. The arrow cues were represented by UK road signs for “keep left” and “keep right” with the neutral condition represented by the “mini-roundabout” sign. Previous similar studies have used a variety of stimuli to represent eye gaze and arrow cues, with some studies using photographs for the gaze cues but none using genuinely real-world arrows. This is important, as without such matching it is unclear what, precisely, previous studies were measuring. In this respect, Experiment 1 aimed to establish a baseline for future experiments with cues which were well matched in their ecological validity. However, although an attempt was made to match the stimuli in this respect (i.e. in their likeliness to everyday visual stimuli), it was impossible to match them in terms of their perceptual properties. However, rather than being a confounding issue, the stimuli’s dissimilarities in respect to their colour, shape and contrast merely reflected the

fact that such stimuli *are* inherently unlike and it was anticipated that the use of these more ecologically valid stimuli would uncover differences in eye movement responses to the cues which have been absent from studies using perceptually matched gaze and arrow stimuli.

In addition to the left and right versions of the cues, a neutral condition provided a baseline with which to calculate any reaction time costs or benefits for congruent and incongruent cue-target directions. A range of stimulus-response asynchronies (SOAs) were employed to investigate the temporal effects of the cues on saccades. If a reaction time advantage emerged for congruent cues at the shorter SOAs it could be argued that the cues are acting automatically on visual attention mechanisms, where as if a congruency advantage was evident at the later SOA it is possible that the participants may have been voluntarily shifting their attention in the cued direction, despite being told to ignore the cues.

2.2 Method

2.2.1 Design

This experiment had a 3 way, repeated measures design, with 2 levels on the factor cue type (arrow or eye gaze), 3 levels on the factor SOA (100, 300 or 800 ms) and 3 levels on the factor congruency (congruent, neutral, incongruent). The primary dependent measure was saccadic reaction time (SRT). Directional errors, where participants looked in the opposite direction to the target, were also measured.

2.2.2 Participants

Twenty healthy undergraduates from the School of Psychology, University of Exeter, (17 female) aged between 18 and 43 years ($M = 21.15$ years; $SD = 6.13$) took part in this experiment in exchange for course credit. All participants had either normal or correct to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

Apparatus and Materials

Stimuli were presented on a Dell Latitude D510 laptop computer with a 15" screen. Participants sat approximately 60 cm from the screen of the laptop. Eye movement recording was carried out by means of the head mounted EyeLink II system (SR Research, Canada) connected to a host computer with an Ethernet link connecting the host computer to the display laptop. Eye movements were recorded by a small camera mounted on the head band which sent the pupil position data to the host computer at a rate of 500 Hz. The position of the head was monitored by another camera mounted centrally on the headband which recorded illumination from four infra-red emitting LED markers mounted on the edges of the display computer's screen, which compensated for small head movements. The EyeLink II is accurate to less than 0.5° and is capable of detecting saccades as small as 0.05° . The system is very compatible with spectacles. Figure 2.1 shows a diagram of the EyeLink II eyetracker.

Images displayed were prepared using Corel Paint Shop Pro X image editing software.

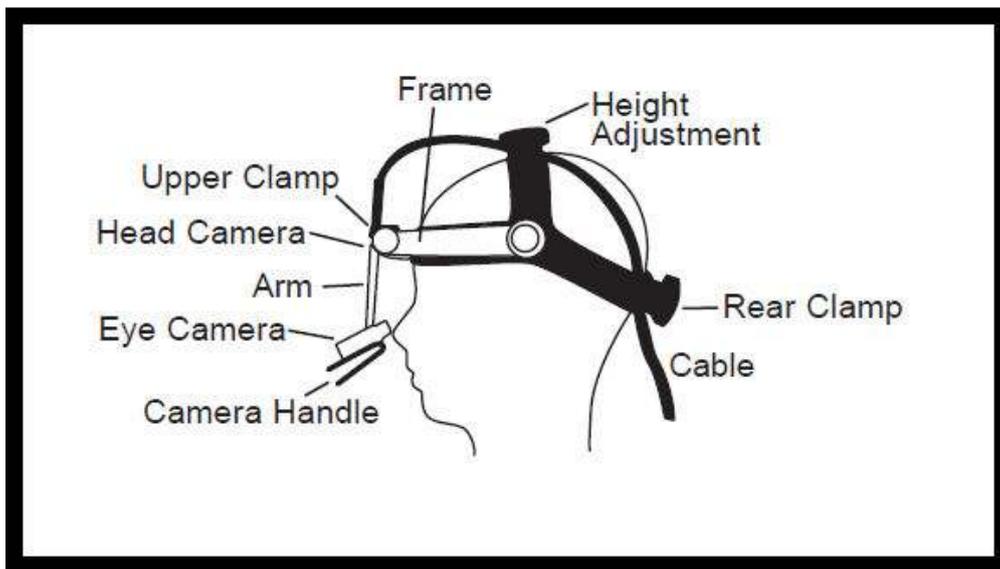


Figure 2.1: Eyelink II eye tracker. Adapted from SR Research Ltd. (2008).

Procedure

The experiment was blocked by the factor cue type (arrow or eye gaze). The order in which the cue types were presented was counterbalanced between subjects to prevent any order effects from emerging. Each cue type condition contained 180 trials, split into three blocks. This resulted in each participant completing 3 blocks of 60 trials with arrow cues and a further 3 blocks of 60 trials with gaze cues. At the beginning of each set of three blocks a calibration procedure was performed in order to map raw data into eye gaze position. The participant fixated a dot displayed on the display computer as it moved in steps around the periphery of the screen. In addition to this calibration, at the beginning of each block of 60 trials, a drift correct procedure was carried out in order to account for any headband slippage that may have occurred during the previous block. The participant

fixated a single central dot and the difference between that position and that expected from the calibration procedure was computed.

All trials were presented on a white background. Each trial began with the presentation of a black central fixation cross subtending 1° of visual angle, for the duration of 1000 ms. In the arrow blocks, a circular road sign, subtending 3.53° of visual angle, was presented behind the fixation cross. The road sign depicted a white arrow on a blue background pointing left or right, with the neutral condition represented by the UK road sign for “mini roundabout”, consisting of three small white arrows forming a circle, again on a blue background. The three road signs appeared with equal probability, each being presented 60 times over the course of the three blocks. The gaze cue condition comprised a rectangular photograph, subtending 4.38° of visual angle, showing a male pair of eyes. The eyes looked either left, right or they were closed (the neutral condition). Figure 2.2 shows the stimuli used in this experiment. Each condition occurred with equal probability and each was presented a total of 60 times over the course of the three blocks. After a period of 100, 300 or 800 ms, the target, a black dot with a diameter of $.76^\circ$ of visual angle, was presented. The dot could appear vertically centred at either the left or right of the screen at an eccentricity of 11.71° of visual angle, where it remained for 2000 ms. The target dot appeared on the left and right sides of the screen with equal probability and for a total of 90 left and 90 right presentations for each set of three blocks. The participants were instructed to maintain fixation on the central cross and ignore the road signs or eyes until the dot appeared, whereupon they were to make a saccade to the dot as quickly as possible. Participants were informed that the direction to which the arrows or eyes pointed in no way predicted the likely position of the target dot. An interval of 1000 ms separated each trial.

Figure 2.3 shows the sequence of events on a congruent gaze trial and an incongruent arrow trial.



Figure 2.2: Stimuli used for eye gaze and arrow cues. The neutral cues are presented in the third *column*.

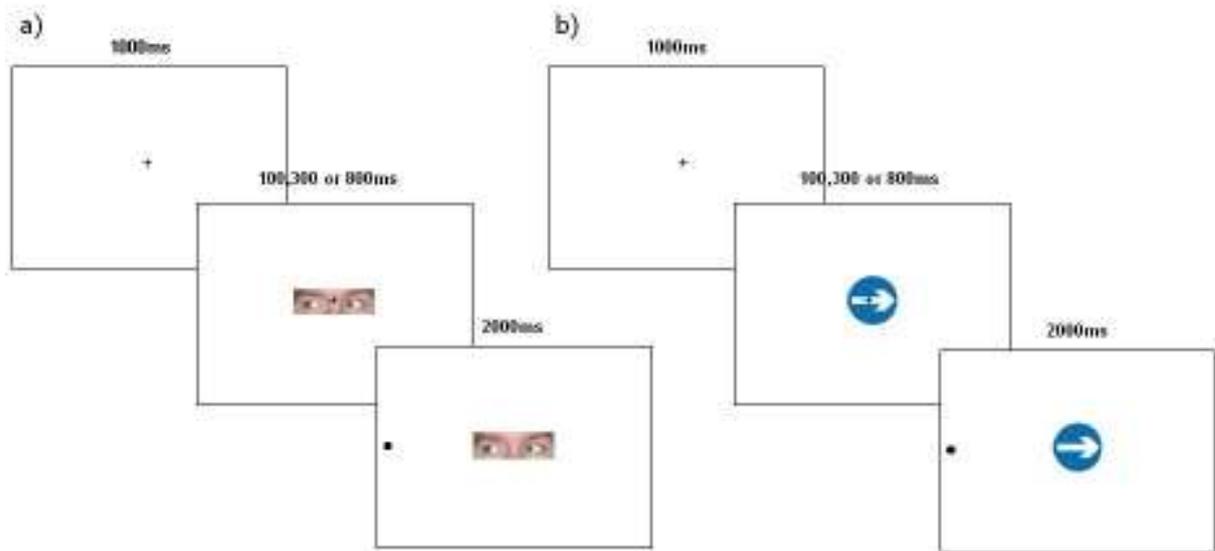


Figure 2.3: a) Procedure for a congruent trial with eye gaze cues. A fixation cross is displayed for 1000ms after which the cue is displayed. After an SOA of 100, 300 or 800ms the target is presented to the left or right of the cue, to which the participant saccades. The target remains on-screen for 2000ms. There is an inter-trial interval of 1000ms. b) Procedure for an incongruent trial with arrow cues. The figure is not drawn to scale.

Data preparation and analysis

The principle dependent measure of SRT was extracted offline using Eyelink Data Viewer, data analysis software produced by SR Research for use with the Eyelink II. The software presents a visual record of the trial, marking saccades, fixations, and samples as different coloured lines. In addition it is possible to “playback” the trial with the eye movements overlaid in real time. Figure 2.4 shows a screenshot of Dataviewer.

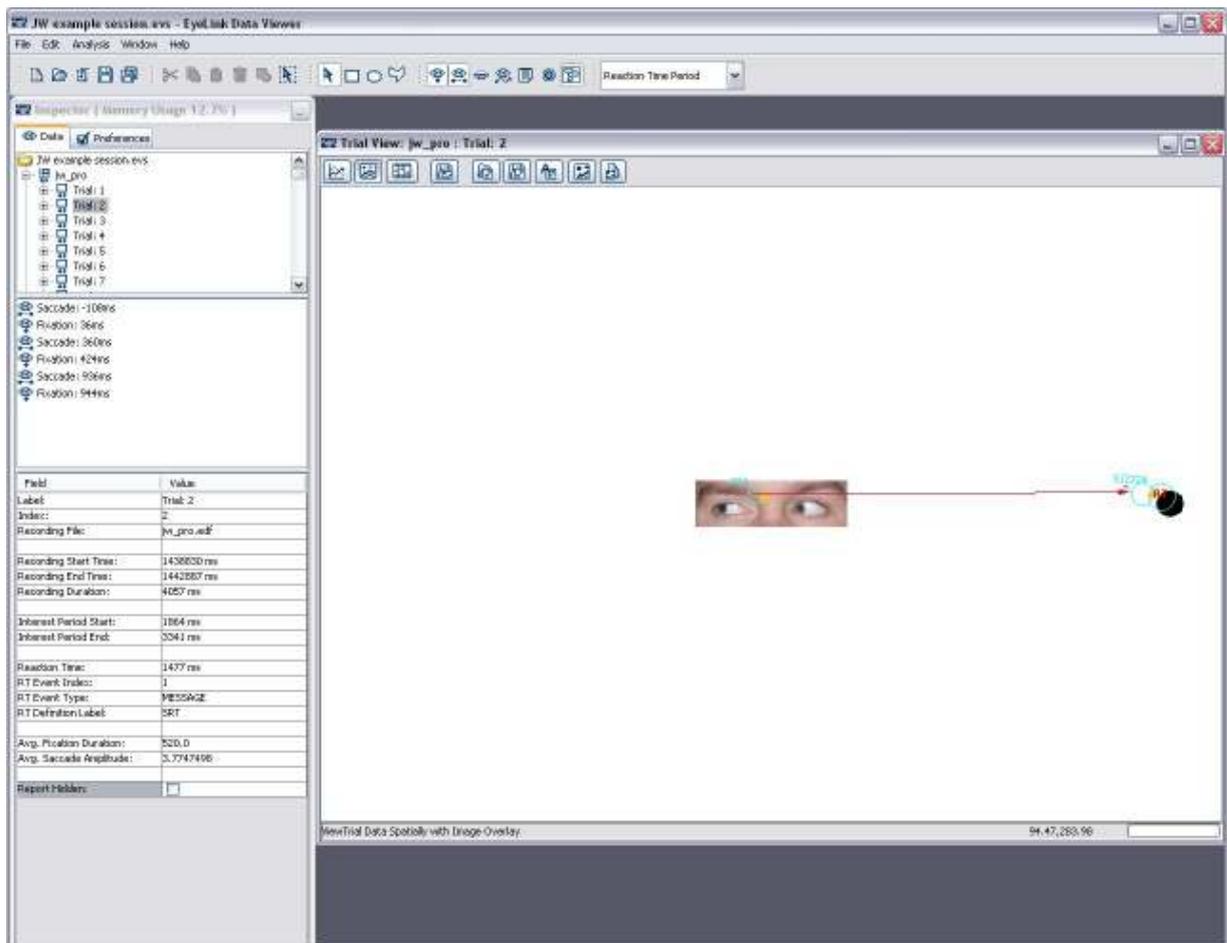


Figure 2.4: Screenshot of Dataviewer software. Screenshot shows visual display of a gaze trial during the reaction time period. The red line represents a saccade and the blue circles represent fixations. From top to bottom, the left hand panes show individual trials, the eye movement events for the current trial and the parameters of the currently selected trial.

SRT was defined as the time in *ms* of the first saccade initiated to the left or right. Of these saccades, only those with an amplitude of more than 2° and those which occurred between 80 and 699 ms after target onset were entered into the analyses, as saccades with latencies of less than 80 ms were considered to be anticipations whilst saccades with latencies of more than 699 ms were considered late responses, in accordance with the protocol presented in Fischer, Gezeck, & Hartnegg (1997). The latency and amplitude

criteria removed 178 trials which constituted 2.56% of total responses. Responses were considered to be correct if they met the above criteria and were initiated in the same direction as the target stimulus. Directional errors were also extracted offline with Dataviewer. Errors were defined as saccades meeting the above criteria initially made in the direction opposite to the target location.

2.3 Results

2.3.1 Saccadic reaction time

The mean correct SRT for each participant in each condition was calculated. SPSS version 15 was used to perform a 3 way repeated measures ANOVA on correct SRTs, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor SOA (100, 300, 800 ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent). There was a main effect of SOA, $F(2, 38) = 16.10, p < .001$ (H-F Criterion), with response times decreased at 800ms ($M = 187.97\text{ms}, SD = 3.83$) SOA relative to at 100ms ($M = 203.31\text{ms}, SD = 4.16$) and 300ms ($M = 203.49\text{ms}, SD = 5.07$) SOAs. There was a main effect of congruency, $F(2, 38) = 13.37, p < .001$. Planned comparisons showed that overall, responses on congruent trials were significantly quicker than on both neutral ($F(1, 19) = 34.79, p < .001$) and incongruent trials ($F(1, 19) = 8.53, p = .009$), but that there was no difference between neutral and incongruent SRTs ($F(1, 19) = 3.26, p = .087$). Table 2.1 below displays the mean SRT for congruent, neutral and incongruent trials, collapsed over SOA and Cue type. There was also a significant interaction between Congruency and SOA, $F(4, 76) = 2.65, p = .040$. From Figure 2.5 it is apparent that this interaction is the result of similar pattern of results SRTs at 100 and 300ms SOA (congruent quicker than neutral and incongruent) which is not present at 800ms SOA. The absence of a significant main effect of Cue type

in addition to this factor not interacting with SOA or Congruency strongly suggests that the gaze and arrow cues had an equivalent effect on correct responses in this experiment.

Figure 2.3 below shows the correct SRTs for gaze and arrow cues over the 3 SOAs.

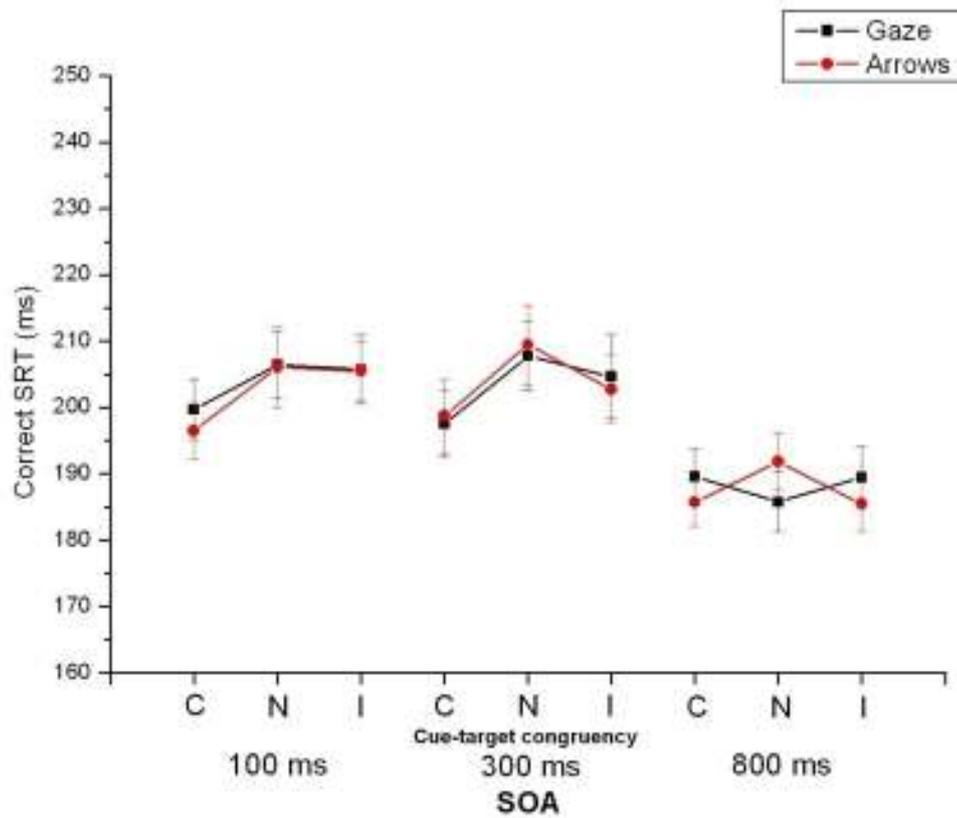


Figure 2.5: Mean correct SRTs in ms for congruent (C), neutral (N) and incongruent (I) gaze and arrow cues at the 3 SOAs. Error bars represent standard error of the mean.

Cue-target congruency	Mean SRT (ms)	Standard Error
Congruent	194.61	3.69
Neutral	201.23	4.24
Incongruent	198.93	4.23

Table 2.1: Mean SRTs and standard errors for correct saccades in the congruent, neutral and incongruent cue-target conditions, collapsed over SOA and Cue type in Experiment 1.

An unexpected result was that the responses on neutral trials were the slowest of the three congruencies. It is a possibility that the congruency effects observed were therefore the result of the neutral trials, which had been intended only as a baseline with which to compare responses on congruent and incongruent trials. Therefore a second, $2 \times 3 \times 2$ ANOVA, containing only data from congruent and incongruent conditions was conducted.

The removal of neutral trials made little difference to the results. The main effects of SOA was still significant, $F(2, 38) = 13.64, p < .001$ (H-F Criterion) as was the main effect of Congruency, $F(1, 19) = 8.53, p = .009$, indicating that there was a significant (albeit small – 4ms) difference between the SRTs of congruent and incongruent trials. The interaction between SOA and Congruency was no longer significant however, $F(2, 38) = 2.65, p = .083$ indicating that it was the difference in the effect of the neutral condition over the three SOAs which was responsible for the SOA by Congruency interaction observed in the first analysis.

2.3.2 Error rates

Participants made in total only two directional errors comprising 0.03% of trials and so these were not investigated further.

2.4 Discussion

The purpose of Experiment 1 was to investigate whether spatially uninformative real-world eye gaze and arrow cues were capable of producing a facilitation of saccades in the cued direction, in a simple pro-saccade task. The eye gaze and arrow cues could be congruent, incongruent or neutral in their agreement with the target location. It was hypothesised that if either of the cue types were able to automatically orient attention then trials where the cues were congruent with target location would produce shorter SRTs than incongruent trials and it was anticipated that incongruent trials would produce longer response times than neutral trials.

Trials where the cue and target location were congruent produced quicker SRTs than trials where the cue's direction was incongruent with target location or was neutral, for both the eye gaze and arrow cues. This finding adds weight to the ever increasing body of evidence showing that arrow cues are capable of producing comparable cueing effects to gaze cues, the latter having been regarded by some as "special" directional cues. In addition, it confirms that the stimuli used for the directional versions of these cues are effective in biasing visual attention in the cued direction to the same extent, both quantitatively and qualitatively. However, the congruency advantage observed in this experiment was only 4ms, a much smaller effect than has been observed in other overt orienting studies of this kind. For example, Kuhn & Benson (2007) reported a congruency advantage of 41ms in one voluntary saccade task. This difference in response time could be

attributed to the task itself. In the pro-saccade task, the participants must saccade to a sudden-onset stimulus, whereas in the voluntary saccade task, there is no such stimulus to cause a rapid capture of the oculomotor system. It may be that there is a greater influence of the cues when a voluntary saccade is required than when a more reflexive saccade is generated, the reflexive response to some extent over-riding the effects of the cue in the pro-saccade task.

An unexpected result was that the neutral trials did not produce shorter SRTs than the incongruent trials: It had been anticipated that incongruent cues would cause a SRT cost relative to neutral. Removing the neutral trials did not dramatically influence the results, but did serve to eliminate the interaction between Congruency and SOA, indicating that the advantage of congruent cues over incongruent cues was stable over the time course of the 3 SOAs but that the effect of the neutral cues varied. Neutral cues had been used to provide a baseline with which to compare the directional effects of the congruent and incongruent cues. However, the neutral cues for each cue type appeared to have a more inhibitory effect on responses than the incongruent cues. Moreover, at the longest SOA, the neutral gaze and arrow cues caused differential effects on responses, causing the observed SOA by Congruency interaction, indicating that they were not similarly acting on visual attention mechanisms, as had been their purpose. For these reasons, the usefulness of these particular neutral cues as a baseline is questionable.

Despite the fact that the removal of the neutral cues from the analysis resulted in the SOA by Congruency interaction becoming non-significant, there is a suggestion from Figure 2.5, of an early facilitation of responses to the cued location over the uncued location at the shorter SOAs, which seems to dissipate by the longest SOA. If so, this would be consistent with the cues acting automatically on attention. Further work may

provide more statistically robust evidence for this suggestion. The finding that overall saccadic response times were shorter at 800 ms SOA than at the shorter SOAs is a frequent finding when SOAs are increased. This is thought to occur because the increased period of preparation time acts as a warning signal and allows for non-directional preparation of an eye movement (an increase in oculomotor readiness) before the target appears (Posner, 1978; Spence & Driver, 1997).

Experiment 2: Anti-saccades

2.5 Introduction

The gaze imitation hypothesis, introduced in Chapter 1, refers to the idea that people tend to make involuntary, imitative eye movements in the direction of observed averted gaze and that such responses are absent when confronted with other directional symbols such as arrows. Although there is significant real-world, observational research supporting the idea that people look where others are looking, particularly in the developmental literature (e.g. Baron-Cohen, 1995; Corkum & Moore, 1998; Farroni, Massaccesi, Pividori, & Johnson, 2004; see also Kuhn, Tatler, & Cole, 2009) the findings of only one experimental oculomotor study specifically supports this hypothesis (Ricciardelli et al., 2002). Other researchers who have attempted to investigate this assertion have found that arrow cues are just as capable of eliciting involuntary eye movements in the direction of the cue as are gaze cues. In addition, the only study to utilise the anti-saccade paradigm with gaze cues (Koval, Thomas, & Everling, 2005) found that participants made more erroneous pro-saccades towards the target when the cue pointed *away* from it, i.e. on incongruent trials, than on congruent trials, a finding which is contrary to the predictions of the gaze imitation

hypothesis. Furthermore, Koval et al. found that participants were faster to make a correct anti-saccade in the direction *opposite* to where the cue was directed, which again is entirely contrary to predictions of the gaze imitation hypothesis. The latter study investigated only gaze cues and therefore it is impossible to know what affect arrows might have had within this task, as no other studies to date have investigated the effects of centrally presented, non-predictive cues in the anti-saccade task. Two questions are therefore raised by the Koval et al. study: How can the facilitation of overt orienting and response time in the opposite direction to the gaze cues be explained? What influence, if any, would other types of cue, such as arrows have on performance in an anti-saccade task?

The anti-saccade task has advantages over the voluntary saccade task used by Ricciardelli et al. (2002) and Kuhn et al. (Kuhn & Benson, 2007; Kuhn et al., 2010; Kuhn & Kingstone, 2009) when studying the effects of cues on oculomotor behaviour, as it is a more cognitively complex task, requiring several extra processes not involved in the voluntary saccade task. The predominant account of the mechanism underlying the successful completion of the anti-saccade task involves the inhibition of a reflexive saccade towards the sudden onset stimulus and the generation of a voluntary anti-saccade to the mirror opposite location to the target (Everling & Fischer, 1998; Guitton, Buchtel, & Douglas, 1985; Munoz & Everling, 2004). However, it could be considered that these are not the only subcomponents required to successfully complete the anti-saccade task. Firstly, in the anti-saccade task, before a response can be programmed, the location of the peripheral stimulus must be determined whilst maintaining fixation in the centre of the screen. There is no such stimulus detection process in the voluntary saccade task, as the imperative stimulus, the fixation point which changes colour to indicate the instruction for the saccade, is under foveation at the time of instruction. As mentioned above, the

prepotent reflexive saccade, the “visual grasp reflex” (Hess et al., 1946; Machado & Rafal, 2000a, 2000b, 2004), must be inhibited, a process which again has no counterpart in the voluntary saccade task. Further, the knowledge of the location of the peripheral stimulus must be used to programme a saccade to the mirror opposite location, often referred to as a vector inversion process (Munoz & Everling, 2004), which also does not occur in the voluntary saccade task. Finally, the anti-saccade is generated to the computed location, a process which *is* analogous to the generation of a voluntary saccade, based on a coloured fixation cross, required in Ricciardelli et al. (2002) and Kuhn et al.’s (Kuhn & Benson, 2007; Kuhn et al., 2010; Kuhn & Kingstone, 2009) tasks. Presenting a non-predictive directional cue centrally within this paradigm may affect one or several of these processes: The detection of a target, the inhibition of a reflexive saccade, a vector inversion and the voluntary execution of a saccade.

It is clear from this description of the components involved in the anti-saccade task, that it encompasses processes that are not involved in the pro-saccade task, used in Experiment 1. In the pro-saccade task it should be apparent that there exists the same initial stimulus detection process. However, the reflexive saccade to the stimulus does not need to be inhibited, as the stimulus is in this case, the target. There is clearly no vector inversion involved, and the extent to which the response saccade is voluntary in nature is difficult to ascertain, being as it is, directed towards a sudden onset stimulus. Correct saccades are likely therefore, to be a combination of reflexive and voluntary responses, unlike in the anti-saccade task, where voluntary saccades (correct responses) and reflexive saccades (erroneous pro-saccades) are dissociable.

The purpose of Experiment 2 was to investigate whether participants make imitative eye movements in the direction of gaze cues and also arrow cues, in the anti-saccade task.

The gaze imitation hypothesis suggests that this should happen only for gaze cues. However, the study by Koval et al. (2005), which investigated the effects of gaze cues only in the anti-saccade task, produced results which were contrary to those predicted by the gaze imitation hypothesis, as people were faster to respond in the opposite direction to the cues. Experiment 2 therefore compared the effects of the real-world arrow cues used in Experiment 1, with the gaze cues used in the same experiment, to ascertain whether the counter-intuitive results obtained by Koval et al. are unique to gaze cues or whether they are common when other directional cues are used in an anti-saccade task. If similar results are obtained for arrow and gaze cues which concur with the general finding of Koval et al., then a possible mechanism underpinning the apparent facilitation of responses in the opposite direction to the cue, will require exploration. If anti-saccade performance is influenced differentially by gaze and arrow cues, this may indicate that the two cues are being processed differently. As Experiment 1 showed equivalent effects of the two types of cue in the pro-saccade task, any dissociation between the effects of the cues in this task may be due to their influence on “voluntary” oculomotor programming.

2.6 Method

2.6.1 Design

This experiment had the same, 3 way, repeated measures design as Experiment 1, with 2 levels on the factor cue type (arrow or eye gaze), 3 levels on the factor SOA (100, 300 or 800 ms) and 3 levels on the factor congruency (congruent, neutral, incongruent). There were 2 dependent measures: anti-saccade reaction time and the number of erroneous pro-saccades. In this task, as in Experiment 1, “congruent” and “incongruent” refers to the cue-target congruency. Figure 2.4 illustrates a congruent and an incongruent trial and the

position of the correct anti-saccade end point. As in Experiment 1, only correct anti-saccades between 80 and 699 ms in latency were entered into the analysis. (Fischer et al., 1997).

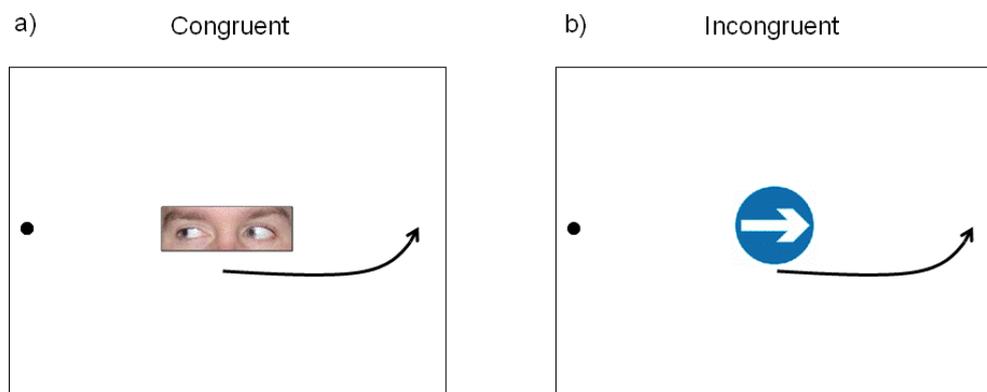


Figure 2.6: a) A congruent trial with gaze cues and b) an incongruent trial with arrow cues. The black arrow denotes the correct saccade direction. Congruency relates to cue-target congruency. Images are not to scale.

2.6.2 Participants

Fourteen Psychology undergraduates (13 female) aged between 18 and 43 years ($M = 23.00$ years ; $SD = 7.93$) took part in this experiment in exchange for course credit. All participants had either normal or correct to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

2.6.3 Apparatus and Materials

The apparatus and materials were identical to those of Experiment 1, but with the following exception. Stimuli were presented on a 19" Iiyama MA901U Vision Master Pro 452 CRT monitor connected to a Dell Optiplex GX260 desktop computer. Participants sat approximately 60 cm from the monitor. Eye movement recording was carried out by means of the head mounted EyeLink II system (SR Research, Canada) connected to a second Dell Optiplex GX260 desktop computer with an Ethernet link connecting the host computer to the display computer.

2.6.4 Procedure

The procedure was identical to that of Experiment 1, except that participants were this time instructed to look in the opposite direction to the "target" as quickly as possible. The fact that the experiment was presented on a larger monitor than in Experiment 1, meant that on-screen dimensions of the stimuli and their location on screen were not the same in Experiment 2. The gaze cues measured 5.52° , the arrow cues 4.45° and the target eccentricity was 14.75° of visual angle. The target and fixation stimuli measured $.95^\circ$ and 1.26° of visual angle respectively.

2.6.5 Data preparation and analysis

As in Experiment 1, eye movement data were extracted offline using Dataviewer (SR Research, Canada). Dataviewer indexes saccades according to their position in the trial using very broad inclusion criteria. The saccade given an index of 1 by Dataviewer was taken as the response for each trial for each participant. Of these saccades, only those which were executed towards the left or the right were retained for further analysis. Of these left and right responses, those with latencies between 80 – 699 ms, an amplitude of more than

2.0°, and which began in the central region of the screen were retained and the remainder of the trials were removed. This data preparation procedure (removal of trials based on the directional, latency, amplitude and start position criteria) removed 1.53% of the data. Of these remaining saccades, those which were initiated in the direction opposite to the peripheral stimulus were considered as correct responses, whilst those made in the same direction of the peripheral stimulus were classed as errors.

2.7 Results

2.7.1 Saccadic reaction time

The mean correct SRT for each participant in each condition was calculated. As with Experiment 1, SPSS version 15 was used to perform a 3 way repeated measures ANOVA on these data, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor SOA (100, 300, 800 ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent). There was a main effect of SOA, $F(2, 26) = 34.85, p < .001$ (sphericity assumed), with response times again decreased at 800ms ($M = 245.64, SD = 8.00$) SOA relative to at 100ms ($M = 282.64$ ms, $SD = 7.34$) and 300ms ($M = 264.89, SD = 6.81$) SOAs. There was also a main effect of Congruency, $F(1, 13) = 9.47, p < .001$, with congruent trials producing the fastest responses ($M = 258.96$ ms, $SD = 7.00$), followed by incongruent trials ($M = 264.30$ ms, $SD = 7.31$), with the slowest responses on neutral trials ($M = 269.91$ ms, $SD = 6.98$). Planned comparisons showed that congruent trials were quicker than neutral, $F(1, 13) = 20.24, p = .001$ and that incongruent trials were also quicker than neutral $F(1, 13) = 5.60, p = .034$, but the difference between congruent and incongruent did not quite reach significance, $F(1, 13) = 3.85, p = .072$. There was no main effect of Cue type, but this factor did interact with SOA, $F(2, 26) = 4.81, p = .017$,

indicating that the effects of the cues on reaction time changed over time. In addition there was an SOA by Congruency interaction, $F(4, 52) = 2.59, p = .049$, indicating that there was some change in the congruency effects over the 3 SOAs.

Figure 2.7 shows the correct SRTs for congruent, neutral and incongruent gaze and arrow cues over the 3 SOAs..

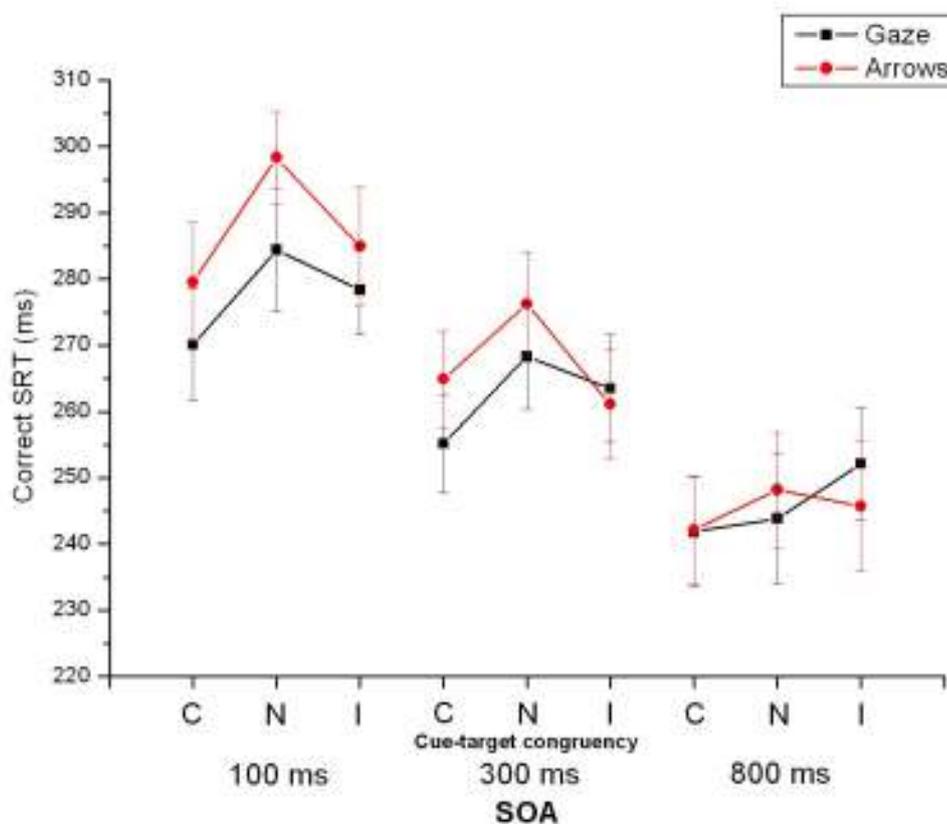


Figure 2.7: Mean correct SRTs in ms for congruent (C), neutral (N) and incongruent (I) gaze and arrow cues at the 3 SOAs. Error bars represent standard error of the mean.

As in Experiment 1, a second ANOVA was conducted which excluded the data from neutral trials. The neutral trials in Experiment 1 appeared to be responsible for some of the congruency effects, as their removal from the analysis eradicated a SOA by Congruency interaction. Having been intended as a baseline with which to compare the

relative costs and benefits associated with incongruent and congruent cues, the finding that these trials produced the longest SRTs was unexpected and may have masked the more interesting differences between the effects of congruent and incongruent cues on SRTs. It was for these reasons that a second, $2 \times 3 \times 2$ ANOVA was conducted here.

The removal of the neutral trials has a marked effect on the results. The main effect of SOA remained, $F(2, 26) = 27.75, p < .001$ (H-F Criterion). However the main effect of Congruency did not reach significance, $F(1, 13) = 3.85, p = .072$, indicating that the neutral trials were largely responsible for the main effect of Congruency in the first analysis. The Cue by SOA interaction was still significant, $F(1, 13) = 3.58, p = .042$. However, a new interaction emerged between Cue and Congruency, $F(1, 13) = 8.16, p = .014$, indicating that there was a difference between the effects of the congruent and incongruent arrow and gaze cues on reaction times.

In order to investigate the nature of the Cue by Congruency interaction, t tests were conducted on gaze and arrow congruent/incongruent pairs, collapsed over SOA. It was found that for gaze cues, SRTs on congruent trials were significantly quicker than on incongruent trials, $t(13) = 2.92, p = .012$, but that for arrows cues there was no difference between congruent and incongruent trials, $t(13) = .59, p = .568$. Figure 2.8 shows the SRTs of congruent and incongruent gaze and arrow cues collapsed over SOA.

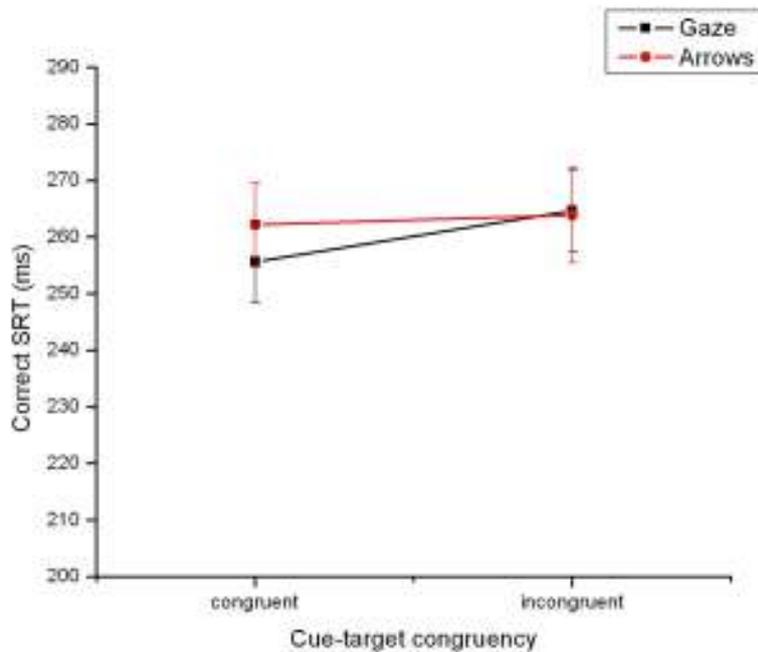


Figure 2.8: Mean correct SRT for congruent and incongruent arrow and gaze cues, collapsed over SOA. Error bars represent standard error of the mean.

2.7.2 Error rates

In 455 trials (10.68% of the total completed trials), the first response was an error: a saccade incorrectly initiated towards the peripheral target.

The percentage of errors committed in each condition was calculated for each participant by dividing the number of errors committed by the total number of trials for each condition, converted to a percentage.

An initial 3 way repeated measures ANOVA was conducted on these data with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor SOA (100, 300, 800 ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent). The main effect of SOA was significant, $F(2, 26) = 15.53, p < .001$ (H-F Criterion), with most errors

executed at the 100ms SOA and the least at 800ms SOA. There was an interaction between Cue and Congruency, $F(2, 26) = 4.91, p = .016$. However, when a second ANOVA was conducted without the neutral trial data, this interaction became non-significant, $F < 1.0, p = .747$, indicating that it was the difference in the effects of the neutral gaze and arrow cues, rather than the difference between congruent and incongruent cues, which was responsible for the interaction between Cue and Congruency in the initial analysis. No other main effects or interactions reached significance, in either the analysis with or without neutral trials. Figure 2.9 shows the error rates for congruent, neutral and incongruent gaze and arrow cues over the 3 SOAs.

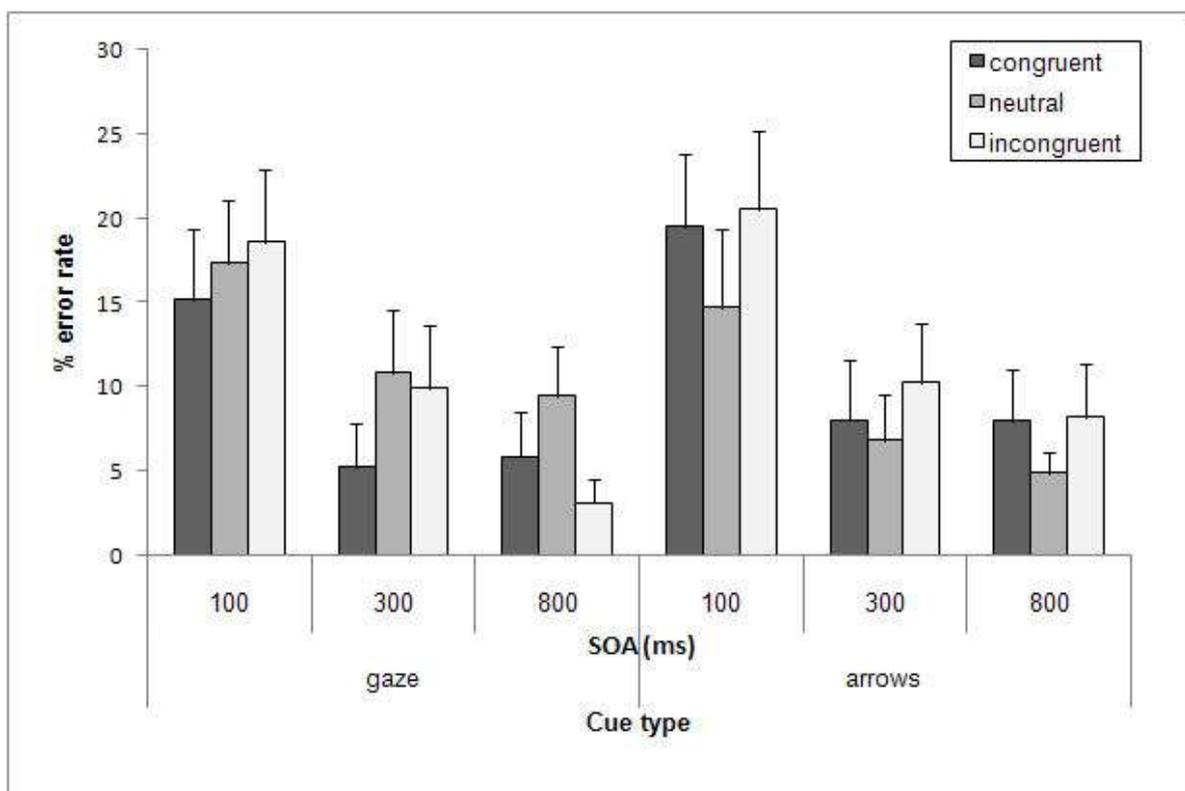


Figure 2.9: Mean percentage error rates per participant for congruent, neutral and incongruent arrow and gaze cues over the 3 SOAs. Error bars represent standard error of the mean.

Despite the lack of a significant Cue by Congruency interaction in the analysis excluding the data from neutral trials, by looking at Figure 2.7, a suggestion of a trend for more errors on incongruent trials in general, and specifically for gaze cues at short SOAs, is apparent. The relatively small number of errors produced in Experiment 2 may mean the study lacked statistical power to detect differences in error rates. A paradigm capable of eliciting a greater number of errors might overcome this and reveal statistically significant effects of Cue type and Congruency on error rates. One of the aims of Chapter 3, which investigates the gap effect and its interaction with gaze and arrow cues, is to address this issue.

2.8 General Discussion

Experiment 2 investigated whether participants make imitative eye movements in the direction of gaze but also arrow cues, in the anti-saccade task. The gaze imitation hypothesis predicts that this should occur for gaze cues only. However, it was possible that participants may be faster to respond in the opposite direction to the gaze cues, as was demonstrated by Koval et al. (2005). If so, it was also of interest whether the direction and magnitude of facilitation of responses was the same for arrow cues as for gaze cues or whether they were specific to gaze cues and are therefore in some way a consequence of their unique effect on the attentional system.

In respect to SRT, the results of Experiment 2 replicate those of Koval et al. (2005). In the present experiment, participants were quickest to make correct anti-saccades in the opposite direction to the gaze cues (on congruent trials - when the gaze cues pointed towards the peripheral stimulus and therefore in wrong direction for the correct response). Although analyses of error rates did not yield any statistically significant differences

between congruent and incongruent trials, there was a suggestion of a trend for more errors in the opposite direction for gaze cues, as found in the Koval et al. study.

The second notable finding of Experiment 2 was that the SRT congruency advantage seen with gaze cues was not present with arrow cues. The initial analysis which included neutral trials, masked this effect but the analysis including only congruent and incongruent trial data showed clearly that it was only the gaze, but not arrow cues which affected response times. This finding adds weight to the idea that gaze cues are processed more automatically than non-social directional cues. It does not however, provide evidence for the gaze imitation hypothesis specifically, as the response advantage was restricted only to facilitation of SRT, not overt responses (i.e. errors) and in any case, was in the opposite direction to the cues.

The role of the neutral trials in this experiment has already been touched upon but is worthy of further discussion. The initial analysis of SRT included neutral trials and yielded a significant main effect of Congruency, whilst in the second analysis without neutrals, this effect was absent. It is therefore clear that the neutral trials were responsible for the main effect of Congruency in the initial analysis and planned comparisons showed that neutral trials were slower than congruent and incongruent trials. Turning to error rates, the analysis including neutrals yielded effects of Congruency, this time by way of an interaction with Cue type, which again was not present when they were excluded in a second analysis. This particular interaction further supported the idea posed earlier in the discussion of Experiment 1, that the stimuli chosen for neutral cues might not constitute the reliable baselines they had been intended to be, as the neutral gaze and arrow cues seemed to have different effects on error rates as can be seen from Figure 2.9. Indeed, the issue of neutral cues in general in cost-benefit analyses has been raised and discussed in detail in an article

by Jonides and Mack (1984). These authors suggest that the inherent problem with using neutral cues is that many choices of stimuli will be made on subjective judgments of neutrality which are effectively arbitrary choices. It is generally assumed that aside from being devoid of directional meaning, a neutral cue will otherwise be comparable to congruent and incongruent cues. However, this assumption is not warranted according to Jonides and Mack who argue that there may be fundamental differences in the way that a neutral cue is processed in comparison to directional cues. The primary concern put forward is that participants may be less attentive towards neutral cues than directional cues. Directional cues, it is argued, may confer general, non-directional preparatory effects on the attention system, whereas neutral cues may not. Also, they may be more easily ignored. Furthermore, their visual dissimilarities to the directional versions may also affect their processing. In all, Jonides and Mack do not advise the use of neutral cues in experiments where differences between congruent and incongruent conditions are to be investigated. Despite this, neutral cues have been used extensively in studies of covert and overt attentional orienting, although their interpretation is often treated with caution. In addition, to circumvent the problems which may arise from one badly chosen neutral cue, some authors have chosen to use two or more neutral conditions, whilst remaining tentative in their interpretation of responses to such cues, whilst concentrating on differences between congruent and incongruent conditions (e.g. Langdon & Smith, 2005).

Four further results which relate to the time course of cue-response interactions require discussion. Firstly, in analyses of SRT, both with and without neutral trials, a Cue by SOA interaction emerged, indicating that the two cue types had different (non-directional) effects on SRT at different SOAs. This appears to be related to the fact that SRTs at the shortest SOA, 100ms, were quicker for gaze cues than arrow cues, whereas at

the other SOAs mean SRTs for gaze and arrow cues were of a similar magnitude. One interpretation of this finding is that the gaze cues caused greater disengagement of the saccadic system relative to arrow cues at short SOAs. Averted gaze cues have been shown to cause a disengagement of attention relative to neutral cues (Senju & Hasegawa, 2005) and due to their proposed “reflexive” influence on attention and saccadic systems, it is possible that this effect is unique to gaze cues. The influence of gaze and arrow cues on disengagement of the oculomotor system will be addressed in Chapter 3.

A further result worthy of mention is that a marginally significant interaction between SOA and Congruency was apparent when neutrals were included but disappeared when they were removed and the analysis rerun, indicating that SRTs on neutral trials varied over the three SOAs. Thirdly, overall, significantly more errors were produced at the 100ms SOA, than at the longer SOAs. This has been observed elsewhere (Weber et al., 1998) and may be a result of inadequate inhibition of the prepotent response (the visual grasp reflex) given such a short response preparation period at very short SOAs. With an extended SOA, participants may be more able to successfully suppress the reflexive saccade towards the sudden onset of the peripheral stimulus reflected in lower error rates at longer SOAs. Finally and perhaps most notably, the fact that the three way interaction between Cue type, Congruency and SOA was not significant, either with or without neutral trials, shows that the congruency effect of gaze cues on SRT was stable over time and therefore that it emerged rapidly by 100ms and was sustained up to 800ms after the cues were presented. The early effects suggest that the cues were acting automatically, as 100ms would not be long enough for the cues to be processed and acted upon voluntarily. However, at 800ms the cues would have received a degree of conscious interpretation and

so it is likely they were influencing voluntary processes, despite the explicit instruction for the participants to ignore them.

The results from Experiment 2, presented here, support a general hypothesis within the literature that gaze cues have a privileged status within the brain's attentional systems. However, the mechanism via which these cues act is not clear, with results from this experiment supporting those from Koval et al. (2005) that gaze cues in an anti-saccade task, far from facilitating responses in the gazed at direction, appear to facilitate response times and perhaps even the production of involuntary saccades, *in the opposite direction* to the cue. This finding requires some explanation.

In the introduction of Experiment 2, the possible stages of successful performance of the anti-saccade task were presented. To summarise, they include detection of the peripheral stimulus ("target"), inhibition of a reflexive saccade to that stimulus, vector inversion of stimulus location onto correct anti-saccade location, and finally generation of an anti-saccade to that location. In order to explain the finding that responses are facilitated in the opposite direction to the cue it is useful to consider at which of the stages above, the cues might be exerting their influence. It seems unlikely that the cues were influencing the inhibition of the prepotent saccade to the stimulus, as an elevated error rate on congruent trials (where cue points to stimulus) was not observed. On the contrary, there was a suggestion of a higher rate of errors on incongruent trials. It is difficult to ascertain whether the vector inversion process was influenced by the cues. There is some evidence however that the production of "voluntary" saccades, in this case, correct anti-saccades, was affected by the cues as any effect of congruency on error rates would indicate such influence. Indeed, a trend for more errors on incongruent trials was suggested. It is of interest to note

however that if the production of correct anti-saccades was influenced by nonpredictive cues, the degree to which such saccades should be considered “voluntary” might be questionable. A further process that may have been subject to the influence of the cues is that of target detection. If the gaze cues facilitated this process, so that targets presented in the cued direction were detected faster than those in the opposite direction, an explanation for the observed effects might have been found. Suppose that a leftward pointing cue enhanced the speed of detection of a left positioned stimulus (cue and target are congruent); the subsequent processes might also be speeded, ultimately resulting in a reduction of the correct anti-saccade latency, which would be in the direction opposite the cue. This would explain the finding from this experiment and that of Koval et al. (2005), that SRTs of correct anti-saccades are faster when made to the side opposite that indicated by the cue. It may also go some way to explaining the effect of increased error rates when cue and target are incongruent. If a attentional shift occurs in the direction of the cue, stimuli appearing at the non-attended location may have a more pronounced sudden-onset or “capturing” effect, resulting in more reflexive saccades towards the stimuli appearing at that location (Machado & Rafal, 2000a; Theeuwes et al., 1999).

The process by which this enhancement of detection is likely to be due is by allocation of covert visual attention to the cued location. The underlying mechanisms for the shift of visual spatial attention are of debate, with some authors suggesting that covert attention is separable from the oculomotor generation processes (e.g. Klein, 1980) whilst others have provided evidence in favour of the hypothesis that shifting covert attention is actually the same process as preparing an eye movement to a location, except with the ultimate motor response withheld, known as the premotor theory of attention (Rizzolatti et al., 1994, 1987; Sheliga et al., 1997). Whatever the underlying mechanism for the

facilitation of responses in the opposite direction to the gaze cues observed here, Experiment 2 has provided further evidence for the hypothesis that eye gaze may be an exceptional form of directional cue. It has not however, provided support for the gaze imitation hypothesis.

Although the pro-saccade task of Experiment 1 demonstrated very similar effects of the cues, albeit without clear statistical support for the idea that the cues were acting automatically (which would be observable as congruency effects only at short SOAs), Experiment 2's anti-saccade task provided evidence that eye gaze may indeed be processed differentially by the brain. Furthermore, the gaze cues acted equivalently on SRTs at all 3 SOAs, demonstrating rapidly emerging automatic effects followed by a more sustained and presumably more voluntary component. This goes to highlight the sensitivity of the anti-saccade task relative to the pro-saccade task, and the former's utility in studying the effect of directional cues on eye movements over other tasks commonly used in the literature.

Experiments 1 and 2 together also call into question the validity of using the particular neutral stimuli chosen as baselines with which to explore the relative costs and benefits of incongruent and congruent trials on SRT and error rates. However, the overarching finding in both experiments, that the neutral trials appeared to have an inhibitory effect on SRTs, is worthy of discussion. A possible reason for this may be that neutral cues have a more engaging effect on attention and/or oculomotor systems than their directional counterparts. It has been postulated by both attention (Posner, Walker, Friedrich, & Rafal, 1984) and oculomotor (Findlay & Walker, 1999) researchers that in order for a shift of attention or a saccade to be initiated, some process of disengagement from the currently fixated/attended position must be achieved and that this disengagement

process is time consuming. The directional versions of the cues in these experiments may not only cue a particular direction but may also act to generally disengage the oculomotor system in readiness for some form of action. The neutral cues may therefore not only lack direction, but may also lack this disengaging property, thereby slowing SRTs via both mechanisms, resulting in the longer SRTs in the present studies.

Experiment 1 showed that in a pro-saccade task, under conditions where gaze and arrow cues were carefully selected for their ecological validity, they had very similar effects on eye movements. However, matching of the cues in this respect was not sufficient to produce similar effects in the anti-saccade task in Experiment 2. The reason that some studies of attention have found that arrows have less pronounced effects on attention than gaze is therefore not likely to be solely because they did not use arrow stimuli which were ecologically valid as originally suggested. However, without the consideration of this issue in the present experiments, this would have remained an unchallenged possibility.

2.9 Conclusions

Whilst Experiment 1 demonstrated equivalent effects for real-world gaze and arrow cues in a pro-saccade task, Experiment 2 showed that gaze cues, but not arrow cues, influenced oculomotor responses in an anti-saccade task. These findings demonstrate that given a sufficiently complex task, differences between the oculomotor responses produced in the presence of gaze and arrow cues do emerge. The direction of the facilitation by gaze cues was actually opposite to that predicted by the gaze imitation hypothesis: correct SRTs were quicker when they were made away from the cued location. This was perhaps due to enhanced target detection, and therefore response generation, when the target was congruent with the cue. However, there were no statistically significant effects of error rate,

although there was a suggestion of more errors on incongruent trials with gaze cues. The neutral cues employed in these experiments did not provide the baseline for congruent and incongruent comparisons as had been intended and it was suggested that this was because they were actively engaging attention in comparison to the directional versions of the cues. In the following chapter, these issues will be addressed by the use of a variable fixation offset, which is likely to modulate error rate as well as attentional or oculomotor disengagement.

Chapter 3: *An investigation into the gap effect in pro-and anti-saccade tasks with gaze and arrow cues*

Experiment 3: Pro-saccades

3.1 Introduction

Chapter 2 demonstrated that in a pro-saccade task, both eye gaze and arrow cues enhance response times to targets located at the cued (congruent) location, relative to the uncued (incongruent) location. However, the neutral trials unexpectedly resulted in SRTs which were no faster than incongruent trials: the anticipated cost of incongruent trials, relative to neutrals did not emerge. An explanation for this finding is that the left/right versions of the cues, as well as imposing spatially specific effects may also act to prepare the oculomotor system more generally for a saccade, a process of disengagement from fixation like that thought to be involved in the gap effect (similar suggestions have been made elsewhere: see Friesen & Kingstone, 2003; Senju & Hasegawa, 2005). In contrast, the neutral cues may have lacked not only the spatial cueing property of the directional versions, but also the ability to disengage the saccadic system from fixation (i.e. enhancing fixate and engage mechanisms). A manipulation thought to act to disengage the saccadic system in readiness for a saccade is to introduce a temporal gap between fixation offset and target onset. The resultant characteristic reduction in saccadic latency and increase in error rates is known as the gap effect. The gap effect is caused by a reduction in activation of fixation neurons in the rostral pole of the SC which occurs at the same time as the inhibition of saccade-related cells decreases (Dorris & Munoz, 1995; Dorris et al., 1997). These processes act to

disengage the oculomotor system from fixation in preparation for a saccade. Furthermore, the offset of the fixation stimulus is also thought to act as a general warning signal, readying the oculomotor system for a saccade (Reuter-Lorenz et al., 1991; Reuter-Lorenz, Oonk, Barnes, & Hughes, 1995; Ross & Ross, 1980, 1981). In the current work, the introduction of such a temporal gap between fixation offset and target onset should disengage the saccadic system regardless of the directionality of the cue (i.e. to an equal extent for congruent, incongruent and neutral cues), so it might be anticipated that just the directional effects of the cues would be reflected in SRTs. Under such circumstances, it would be expected that neutral cues may exert the effects on response latencies which were expected in the first two experiments: Specifically, slower than congruent, but faster than incongruent (a benefit and a cost). Therefore, Experiment 3 modified the pro-saccade task of Experiment 1 to include three fixation offset conditions to examine the role of a variable temporal gap between fixation offset and target onset. If directional versions of gaze and arrow cues influence fixation mechanisms more than the neutral cues, an interaction between congruency and fixation conditions should emerge.

In Experiments 1 and 2, a small number of anticipatory saccades were observed in the presence of the cues, but before the onset of the target. If a temporal gap between fixation offset and target onset disengages the oculomotor system, then a higher rate on anticipatory saccades should be observed in this condition, relative to conditions where there is no gap. Furthermore, if the rate of these anticipations is greater in the direction of the cues than in the opposite direction, then the evidence would strongly suggest that the cues were directly causing automatic programming of motor responses. Experiment 3, as well as examining these visible (and therefore relatively large amplitude) overt anticipatory saccades, also investigated the rate of small amplitude anticipatory responses. *Micro-*

saccades, although smaller than the “small saccades” which will be examined here and detected by algorithms which consider additional factors such as velocity and binocularity, may be an indication of the shifts of covert attention, some work has suggested (Engbert & Kliegl, 2003). As such, the influence of the cues on the generation of small saccades (< 2.00°) might reflect the involvement of additional attentional processes, perhaps caused by low level stimulus properties, which may be separate from those underlying the production of larger amplitude saccades. However, the functional role of microsaccades remains a contentious issue, and it may be that rather than a greater frequency of small saccades during the gap period, there may be fewer small saccades produced. It has been shown that one role of microsaccades is to stabilise the image on the retina by counteracting oculomotor drift and preventing visual fading. Microsaccades are suggested to occur only in the presence of a fixation stimulus, which is thought to occur via activity in fixation cells of the SC (Hafed, Goffart, & Krauzlis, 2009; Martinez-Conde, Macknik, & Hubel, 2004). Therefore, removing the fixation cross may actually reduce the frequency of small saccades in comparison to when the cross remains visible. However, as the current experiment will not be specifically identifying microsaccades per se, this may not be the case.

In relation to the above discussion of microsaccades/small saccades, there is a possibility that the geometric asymmetry of the cues could be causing participants to fixate towards the left or right of the fixation cross prior to the onset of the target, albeit still in the central portion of the screen. The “spatial correspondence” or “spatial compatibility” account of symbolic cueing has developed from covert spatial cueing paradigms and suggests that the asymmetry of cues results in facilitation of attentional processing on the side of the cue with greatest perceptual information (Downing, Dodds, & Bray, 2004; Lambert & Duddy, 2002; Lambert, Roser, Wells, & Heffer, 2006; Muller & Rabbitt, 1989).

A previously discussed eye movement study by Mansfield et al. (2003) demonstrated that participants do make small eye movements around fixation in the direction of gaze cues, although fixation position prior to target onset was not measured. A fixation bias in the direction of the cues could account for the congruency advantage in Experiment 1, as the fovea would be closer to the target on congruent trials, making it easier to detect. For this reason, the position of the fixation before the saccadic response was also examined in Experiment 3.

Therefore, to investigate these possibilities, Experiment 3 used a pro-saccade task, with the same arrow and gaze cues used in Experiments 1 and 2, with a fixed SOA of 300ms, but with a variable temporal gap between the removal of the fixation cross and the appearance of the target. This was achieved by using three conditions: a gap of 200ms between the two events; simultaneous removal of the fixation cross and appearance of the target stimulus; a temporal overlap of 200ms of the fixation cross with target stimulus.

There were several predictions of Experiment 3. One was that the robust gap effect on SRT would be observed: That is that SRTs would be shortest in the gap condition and longest in the overlap condition. Further, an interaction between the fixation and congruency conditions might emerge if only neutral cues do not disengage the saccadic system. In addition, it was anticipated that more errors (where participants initiate a saccade in the wrong direction for the target) would be committed in the gap condition than in the other conditions and in Experiment 1, due to the disengagement of the saccadic system from fixation, and that the direction of these errors might be influenced by the direction of the cues. Further, it was predicted that participants might make large and perhaps also small amplitude anticipatory saccades in the direction of the cues before the onset of the target

which again were likely to be more prevalent in the gap condition. A fixation bias in the cued direction might also become apparent.

3.2 Method

3.2.1 Design

This experiment had a 3 way, repeated measures design, with 2 levels on the factor Cue type (arrow or eye gaze), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 3 levels on the factor Congruency (congruent, neutral, incongruent). The primary dependent measure was saccadic reaction time (SRT). Directional errors were also measured.

Frequency of anticipatory saccades and pre-saccadic fixation position (i.e. fixation position at target onset) were further measures.

3.2.2 Participants

Fourteen healthy undergraduates and postgraduates from the School of Psychology, University of Exeter, (9 female) aged between 19 and 43 years ($M = 22.21$ years; $SD = 6.55$) took part in this experiment in exchange for course credit or £5. All participants had either normal or correct to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

3.2.3 Apparatus and Materials

Apparatus and materials were identical to those of Experiment 2 (Chapter 2).

3.2.4 Procedure

As with Experiments 1 and 2, Experiment 3 was blocked by the factor Cue type (arrow or eye gaze). The order in which the cue types were presented was counterbalanced between subjects to prevent any order effects from emerging. Each cue type contained 180 trials, split into three blocks. Again, as in the previous experiments, this resulted in each participant completing 3 blocks of 60 trials with arrow cues and a further 3 blocks of 60 trials with eye cues. At the beginning of each set of three blocks a calibration procedure was performed, as in Experiments 1 and 2. In addition to this calibration, at the beginning of each block of 60 trials and every 10 trials thereafter, a drift correct procedure was carried out in order to account for any headband slippage (which can result in reduction of gaze position accuracy) that may have occurred during the previous trials.

The stimuli were the same as those used in the previous experiments and were presented on the same monitor as used in Experiment 2. Therefore cue size and position, as well as possible target locations, were the same as in Experiment 2. The procedure was similar to that of Experiment 1, except that fixation offset duration (“Fixation”) was manipulated rather than SOA. The duration of the presentation of the fixation cross was manipulated to produce the three Fixation conditions. In the gap condition, the cross was extinguished 100ms after the cue appeared and 200ms before the target appeared, resulting in a “gap” of 200ms, which has been proposed as the optimum duration for reducing SRT whilst increasing error rates (Fischer & Weber, 1997). In the simultaneous condition, the cross was extinguished at the same time as the target. Finally in the overlap condition, the fixation cross was extinguished 200ms after the target appeared. In all conditions, 300ms after the cue onset, the target stimulus was presented, vertically centred at either the left or

right of the screen, with the same measurements and at the same eccentricity as in Experiment 2. Figure 3.1 shows the procedure for the three gap conditions.

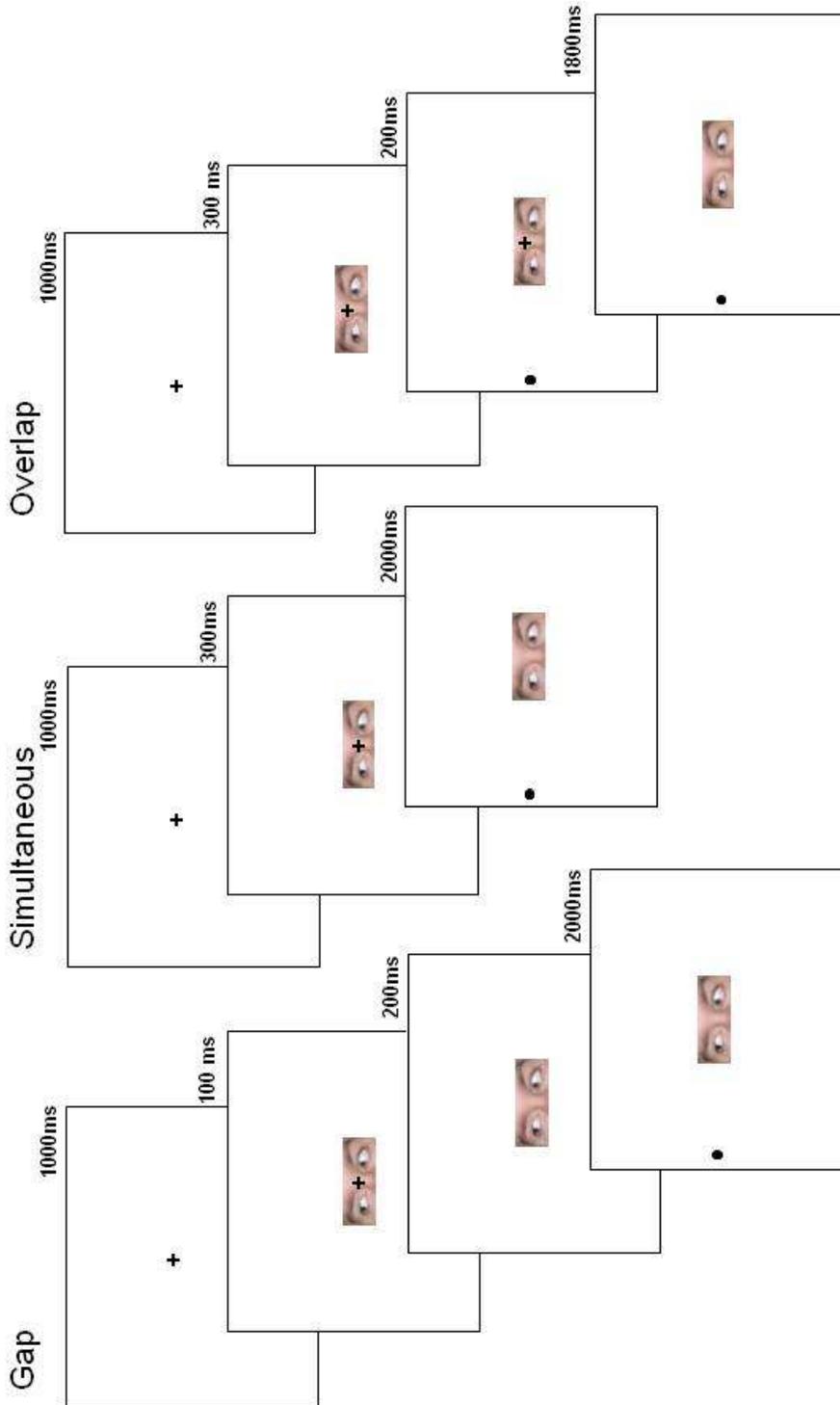


Figure 3.1: Procedures for gap, simultaneous and overlap Fixation conditions with gaze cues. Figure is not drawn to scale.

3.2.5 Data preparation and analysis

Completed trials were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in Experiments 1 and 2. This procedure removed 741 trials representing 15.02% of trials.

3.3 Results

3.3.1 Saccadic reaction time

The mean correct SRT for each participant in each condition was calculated. A 3 way repeated measures ANOVA was performed on correct SRTs, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 3 levels on the factor Congruency (congruent, neutral, incongruent). There was a main effect of Fixation, $F(1.33, 17.31) = 32.75, p < .001$ (H-F criterion), with shortest SRTs in the gap condition ($M = 152.12$ ms, $SD = 5.23$), followed by the simultaneous condition ($M = 173.09$ ms, $SD = 6.76$), with the longest in the overlap condition ($M = 185.88$ ms, $SD = 9.27$). There was also a main effect of Congruency, $F(2, 26) = 14.40, p < .001$. Planned comparisons showed that congruent trials were quicker than both incongruent, $F(1, 13) = 22.24, p < .001$, and neutral trials, $F(1, 13) = 16.67, p = .001$, but there was no difference between neutral and incongruent, $F(1, 13) = 1.23, p = .287$. There was no effect of Cue type. The Fixation by Congruency interaction did not reach significance, $F(4, 52) = 1.96, p = .115$ and neither did the other interactions, $F_s < 1.60, p_s > .200$. Figure 3.2 displays the mean SRTs for congruent, neutral and incongruent gaze and arrow cues over the three gap conditions.

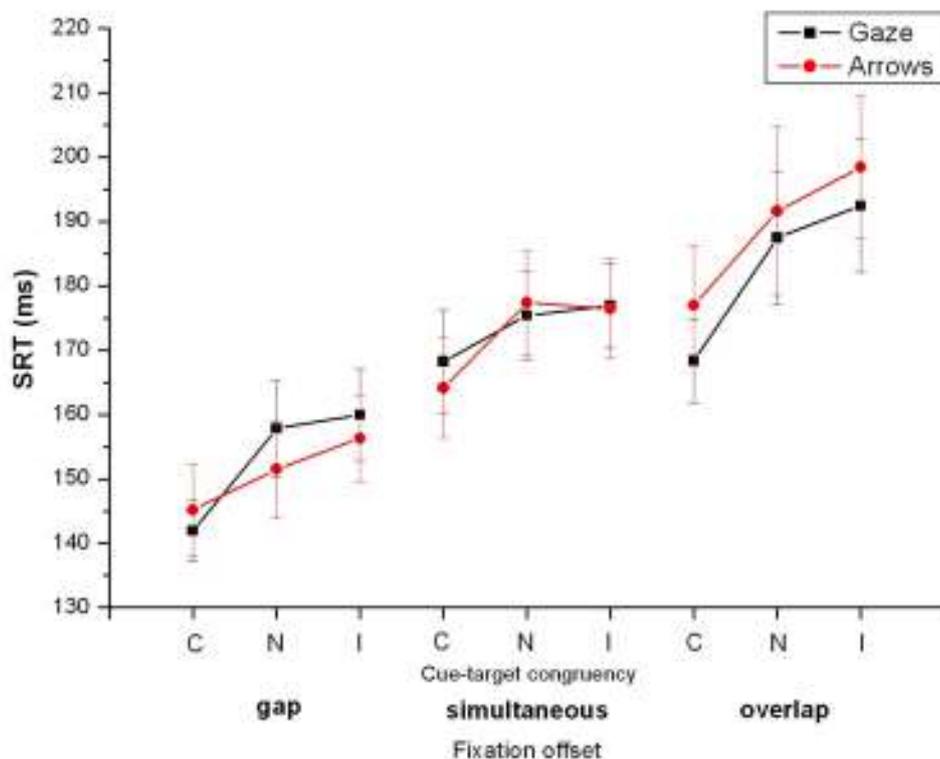


Figure 3.2: Mean SRTs for congruent (C), neutral (N) and incongruent (I) gaze and arrow cues over the three Fixation conditions. Error bars represent standard error of the mean.

As in Experiments 1 and 2, the neutral trials in Experiment 3 did not produce SRTs which were shorter than incongruent but longer than congruent. Therefore the neutral cues did not appear to provide the baseline with which to compare the other congruency conditions, as had been originally anticipated. The neutral trials were therefore excluded from a further 3 way ANOVA which was conducted on congruent and incongruent SRTs only.

With neutrals excluded, main effects of both Fixation, $F(1.35, 17.61) = 38.65, p < .001$ (H-F criterion), and Congruency, $F(2, 26) = 22.34, p < .001$, remained. There was

now an additional significant result, an interaction between Fixation and Congruency, $F(2, 26) = 4.70$, $p = .018$. Table 3.1 displays the means, standard errors and p and t values for t tests conducted on congruent/incongruent pairs at each of the gap conditions, collapsed over cue type. Although congruent trials are quicker than incongruent at all three gap conditions, it is apparent that the difference is greatest in the overlap condition and smallest in the simultaneous condition.

Fixation condition	Mean Congruency advantage (ms)	Standard Error	t	Significance (2 tailed)
Gap	14.58	3.80	3.84	.002
Simultaneous	10.54	3.48	3.03	.010
Overlap	22.77	4.94	4.61	<.001

Table 3.1: Mean congruency advantage, t values and significance values in gap, simultaneous and overlap conditions, collapsed over Cue type.

3.3.2 Error rates

Participants made in total only 15 directional errors comprising 0.37% of trials. 11 of these saccades were initiated in the gap condition, with 2 in the simultaneous condition and 2 in the overlap condition. Overall, 11 errors were made on incongruent trials (that is, in the direction of the cue) and only 4 on congruent trials (in the direction opposite the cue). This does suggest that participants tended to make spontaneous saccades in the direction of the cues. However, due to the small numbers, error rates were not investigated further.

3.3.3 Anticipations

Frequency of anticipatory left and right saccades made during the period after the cue had been presented and 80ms after the target's appearance was calculated (as saccades occurring up to 80ms after the target's onset would not be considered to be target elicited, as the time period is too short (Findlay & Walker, 1999). This was achieved by calculating a new interest period in Dataviewer which corresponded to this period, and resulted in data entirely orthogonal to that included in the SRT analyses. Saccades were then classified as being executed in either the same or the opposite direction to the cue (data from neutral trials were excluded from this analysis). The resulting anticipatory saccades were further classified as either large (greater than 2.00° amplitude) or small (1.99° amplitude or less). The presence of large anticipatory saccades might indicate that the cues were causing the preparation of an automatic or even "imitative" eye movement in the cued direction. Small anticipatory saccades may occur without conscious awareness and may act to bring the fovea closer to the target on congruent trials. In total, anticipations were made on 10.60% of trials.

Large anticipatory saccades

353 large anticipatory saccades were executed, representing 7.00% of trials.

A 3 way repeated measures ANOVA was conducted on the frequency of large anticipations, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the new factor, Direction (same, opposite).

There was a significant main effect of Fixation, $F(1.16, 15.08) = 29.93, p < .001$ (H-F Criterion), with most large anticipatory saccades occurring in the gap condition (gap: $M = 3.66, SE = .62$; simultaneous: $M = .95, SE = .20$; overlap: $M = .86, SE = .27$). There was also a significant main effect of Direction, $F(1, 13) = 22.76, p < .001$, with most large anticipatory saccades occurring in the same direction as the cue (same: $M = 3.27, SE = .62$; opposite: $M = .37, SE = .07$). In addition, there was an interaction between Fixation and Direction $F(2, 26) = 19.50, p < .001$, which appeared to be due to a greater difference between the number of large anticipatory saccades in the same and opposite direction to the cue, in the gap condition than in the other conditions. The other interactions did not reach significance however, $F_s < 1.60, p_s > .200$. Figure 3.3 shows the difference between the rates of large anticipations in the same and opposite direction to the cues in the three Fixation conditions.

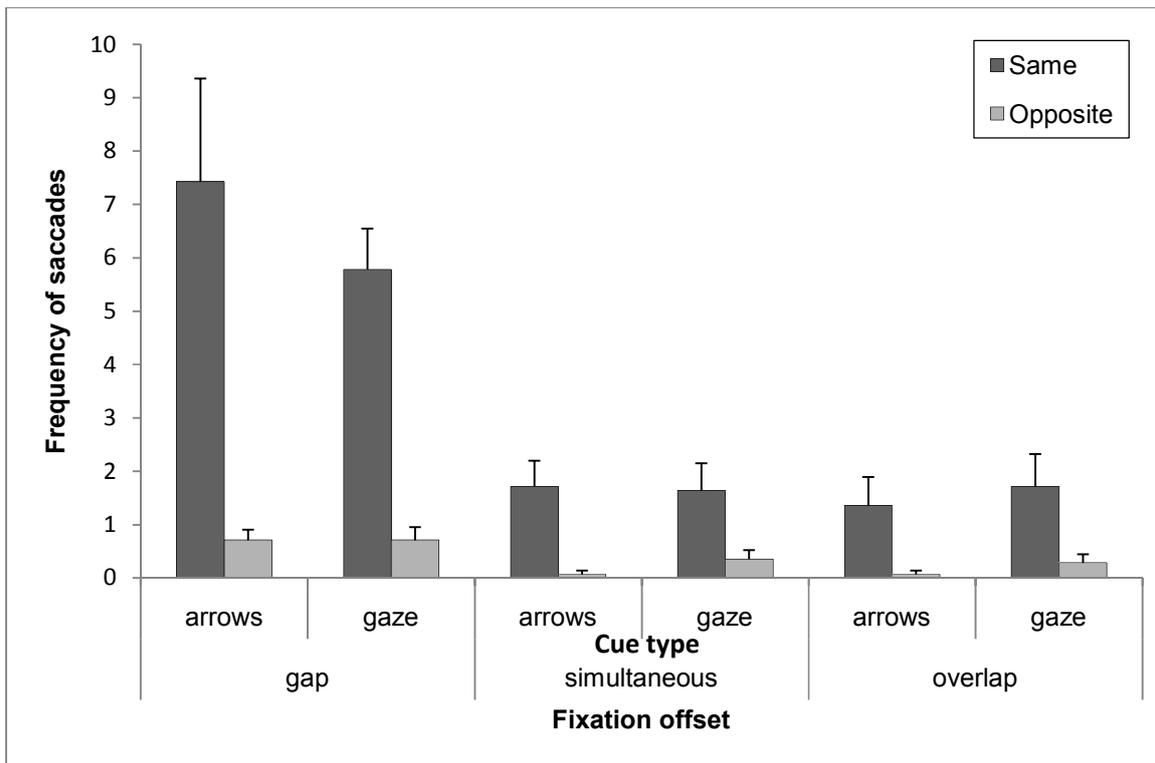


Figure 3.3: Mean frequencies of large anticipatory saccades, made per participant, in the same and opposite directions to the arrow and gaze cues, over the three fixation conditions. Error bars represent standard error of the mean.

Small anticipatory saccades

181 small anticipatory saccades were made, representing 3.60% of trials.

As with the large anticipatory saccades, a 3 way repeated measures ANOVA was conducted on the frequency data, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the new factor, Direction (same, opposite). There was a significant main effect of Cue type, $F(1, 13) = 9.19, p = .010$ with more anticipations with gaze cues than arrow cues (gaze: $M = 1.63, SE = .42$; arrows: $M = .49, SE = .14$). There was also a main effect of Direction, $F(1, 13) = 16.00, p = .002$, with more anticipations in the same direction as the cue than in the

opposite (same: $M = 1.70$, $SE = .41$; opposite: $M = .42$, $SE = .12$). In addition, there was a significant interaction between Cue type and Direction, $F(1, 13) = 7.32$, $p = .018$, with the biggest difference between the frequency of small anticipatory saccades occurring in the same and the opposite direction to the cue occurring for gaze cues. Figure 3.4 displays this interaction.

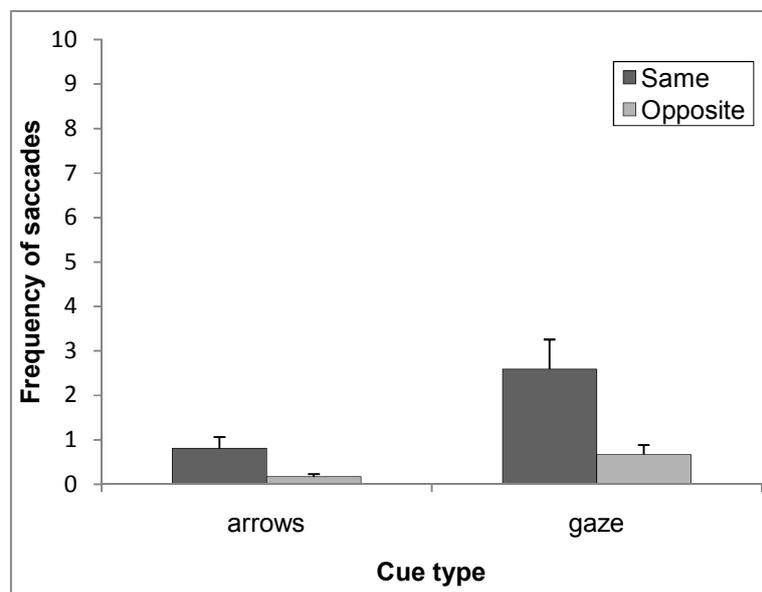


Figure 3.4: Frequency of small anticipatory saccades per participant in the same and opposite direction as gaze and arrow cues. Error bars represent standard error of the mean.

3.3.4 Pre-saccadic fixation position

It is possible that the congruency advantages observed so far may be due to a fixation bias in the cued direction, albeit still within the central region of the screen, bringing the fovea closer to the target on congruent trials. It has been suggested that when an asymmetric stimuli is perceived, In order to investigate this possibility, the mean fixation position prior to the saccade entered into the SRT analysis (i.e. the saccade start position), measured by its co-ordinate in pixels on the x axis, was calculated (possible fixation bias in response to the

cues was only anticipated on the x axis) (referred to below as “*SRT data*”). The centre of the screen was 510 pixels on the x axis.

In addition, a further dependent measure was calculated, encompassing the mean pre-saccadic fixation position of all trials (referred to below as “*all data*”), including those excluded from the main analyses. This analysis therefore included trials where participants were not fixating the central region when the target was presented. The rationale for investigating this variable was to uncover any general fixation bias in the cued direction, regardless of subsequent response.

SRT data

A 3 way, repeated measures ANOVA was conducted on the data, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Cue direction (left, right). Although there was a main effect on Cue type on fixation position, $F(1, 13) = 5.94, p = .030$, with participants fixating slightly towards the right with gaze cues (arrows: $M = 509$ pixels; gaze: $M = 513$ pixels), there were no effects of Fixation or Cue direction, showing that participants did not tend to fixate in the direction of the cue before they made their responses.

All data

A 3 way, repeated measures ANOVA was conducted on the data, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Cue direction (left, right). There were no significant main effects or interactions, demonstrating that participants did not tend to fixate an area of the screen congruent with the cued direction, prior to making a response.

In summary, correct responses on congruent trials were quicker than those on incongruent and neutral trials. There was no difference between neutral and incongruent, however. Responses were quickest when there was a temporal gap between fixation offset and target onset. The congruency advantage was greatest when there was an overlap between the presentation of the fixation cross and the cue's presentation. Participants made very few errors, but those that were executed were mainly in the cued direction. Further, participants appeared to make anticipatory saccades in the direction of the cues which were both large and small in amplitude, primarily in the gap condition. There were more small anticipatory saccades with gaze cues. However, there appeared to be no overall fixation bias in the direction of the cue, before the target appeared.

3.4 Discussion

Experiment 3 employed a pro-saccade task, with a variable gap between removal of the fixation cross and the appearance of the target, with a fixed SOA of 300ms, using the same gaze and arrow cues from Experiments 1 and 2. There were three aims of Experiment 3. The first was to uncover any masked differences between SRTs to congruent and incongruent cues in general, and perhaps more specifically for gaze cues, caused by the simultaneous fixation offset/target onset procedure used in Experiment 1. The second related to the neutral cues in the previous experiments, which did not result in reaction times which were greater than congruent but less than incongruent, as had been expected. One explanation was that the choice of stimuli had been inappropriate, as the assessment of their neutrality may have been misguided (Jonides & Mack, 1984). An alternative explanation for the unexpected effects of the neutral cues was that they were actively engaging the saccadic system relative to their directional counterparts. To investigate

whether a more typical pattern of SRT benefit and cost for congruent and incongruent trials relative to neutrals might emerge given the known disengaging properties of the gap condition on the oculomotor system, a variable fixation offset procedure was used. Thirdly, it was predicted that participants might make involuntary, anticipatory saccades in the gap condition, the direction of which might be modulated by the cue direction. More generally, the variable fixation offset procedure was anticipated to produce a gap effect on SRTs and also error rates.

The overall gap effect on SRT was seen in Experiment 3. Participants were quicker to correctly respond in the gap condition than the simultaneous condition, and were slowest in the overlap condition, in analyses both with and without neutral trials. However the effect on error rates was not investigated as participants made too few errors to enable an analysis, although those that were committed were largely in the cued direction. The general congruency effect on SRT, observed in Experiment 1, was replicated here, but to a greater magnitude. Responses on trials where the cue and target were congruent were significantly quicker than when cue and target were incongruent and when the cues were neutral. That the congruency effect did not vary across the two cue types suggests that both gaze and arrow cues are able to cause a facilitation of saccadic responses to the cued location. The fact that this facilitation occurred at a short SOA suggests that this effect may have been occurring automatically. As with Experiment 1, there was still no overall difference between the SRTs on neutral and incongruent trials. It was suggested that the reason neutral cues had not produced SRTs longer than congruent cues but shorter than incongruent cues, was that the neutral cues caused a prolonged engagement of the oculomotor system at fixation, relative to the left and right versions of the cues. It was argued that introducing a temporal gap between fixation offset and target onset, should

disengage the participant's oculomotor system equally from all three cue congruencies, allowing only the directional effects of the cues to influence SRTs. Therefore, it was anticipated that in the gap condition, there may be a more usual benefit and cost of congruent and incongruent cues relative to the neutrals, due to this general disengagement, resulting in an interaction between Fixation and Congruency. However, this interaction did not reach significance (despite graphically there appearing to be a more usual cost and benefit relative to neutrals pattern in gap and overlap conditions, as predicted) indicating that the gap effect occurred equally for the three cue congruencies. This finding does not support the proposal that neutral cues cause prolonged engagement relative to directional cues. A study by Friesen & Kingstone (2003) used a pro-saccade task with gaze directional and neutral gaze cues, and found similar results to those presented here. Friesen and Kingstone argued that if averted gaze causes a disengagement of overt attention and that neutral gaze cues do not, incorporating a gap between fixation offset and target onset should disproportionately affect neutral cues. They reasoned that in a gap condition, averted gaze cues would already have disengaged the saccadic system, which could not be further disengaged by the removal of the fixation stimulus. However, they found that the gap condition affected both directional and neutral cues to a similar extent, and argued that this was evidence that averted gaze cues do not cause a disengagement of the saccadic system relative to neutral cues. Another study investigating the covert attentional engaging properties of direct and averted gaze, as well as eyes closed cues and found comparable gap effects of eyes closed and averted gaze cues (Senju & Hasegawa, 2005), further suggesting that neutral gaze cues may not be more engaging than directional gaze cues. There is another factor however which needs to be considered when interpreting the results of Experiment 3. As previously discussed, the gap effect is not only thought to occur because

of attentional disengagement. The offset of stimuli at fixation is also thought to act as a warning signal that a target will appear imminently (Reuter-Lorenz et al., 1991, 1995; Ross & Ross, 1980, 1981). However, warning effects need not relate specifically to visual offsets at fixation. Acoustic warning signals presented in fixation gap and overlap conditions have been shown to reduce the size of gap effect (i.e. the difference in reaction time between gap and overlap conditions) (Reuter-Lorenz et al., 1995) and visual onsets or changes of stimuli at fixation have also been shown to cause gap-like effects on saccadic reaction times (Ross & Ross, 1980). In the current experiment, although the fixation point offset was manipulated, so that on a third of the trials a temporal delay existed between the offset of the fixation cross and the onset of the target, the cue remained visible throughout. It might be argued that under such conditions, the offset of the cross acted as a warning signal that the target was about to be presented, rather than it acting to disengage the oculomotor system from fixation, as the cue stimulus remained on the screen at fixation. If the offset of the cross was not sufficient to disengage the saccadic system, this may account for why the gap manipulation affected all three cue congruencies (congruent, incongruent and neutral) to the same degree. Based on the lack of a Fixation by Congruency interaction in the current experiment, the proposal that the neutral cues caused prolonged engagement relative to the directional cues was earlier dismissed. However, it is possible that the gap manipulation did not cause the predicted disengagement to occur at all, and rather acted only as a warning effect that a response would be imminently required. However, one further observation may indicate that the oculomotor system was disengaged during the fixation offset. Although participants tended to make anticipatory saccades in the direction of the cues in all Fixation conditions, the rates were particularly pronounced in the gap condition (as reflected by the Fixation by Direction interaction). This suggests that saccades

were being automatically programmed during the gap with their direction influenced by the direction of the cues. It is difficult to understand how saccades can be programmed and executed whilst the saccadic system is still engaged at fixation and therefore it seems unlikely that a warning effect account can completely explain the results presented here.

The use of the gap procedure did not provide any further explanation of the effect that the particular neutral cues had in the preceding experiments. The repeatedly inconclusive findings suggest that the removal of neutral cues from following experiments might aid clarity in the interpretation of the results with greater import: the difference between response times with congruent and incongruent cues.

A further analysis of SRT without neutrals yielded an effect of the gap conditions on the congruency advantage. The largest congruency advantage occurred in the overlap condition and the smallest in the simultaneous condition. This goes some way to explaining why the congruency advantage in Experiment 1, which used a simultaneous fixation offset target onset, was smaller than anticipated: It was the least effective condition for producing an SRT congruency advantage in the current study. It is clear from Figure 3.2 that the larger congruency advantage in the overlap condition is a result of a increased cost on incongruent trials, with congruent trials approximately the same latency as in the simultaneous condition. This effect may be explained in terms of Findlay and Walker's model of saccade generation. In this model the WHEN and WHERE pathways proceed in parallel and competitive inhibition between the two determines the time and location of the saccade. The WHERE pathway contains a salience map with peaks corresponding to locations of activation caused by visual stimuli. The location of the saccade is determined by the highest peak on the map. Although not specifically mentioning symbolic cues, it is possible that the location indicated by the cues can also activate a peak on the salience map in this model, as

would the target and the fixation cross. In the overlap condition, a permanent activation occurs at fixation. Whilst on congruent trials, the same location on the map is activated by the cue and the target, on incongruent trials the cue and target may activate two separate locations, in addition to the fixation location increasing the competition within the map, thereby increasing reaction times, particularly in this condition. Figure 3.5 demonstrates the peaks on the salience map which might arise on congruent and incongruent trials.

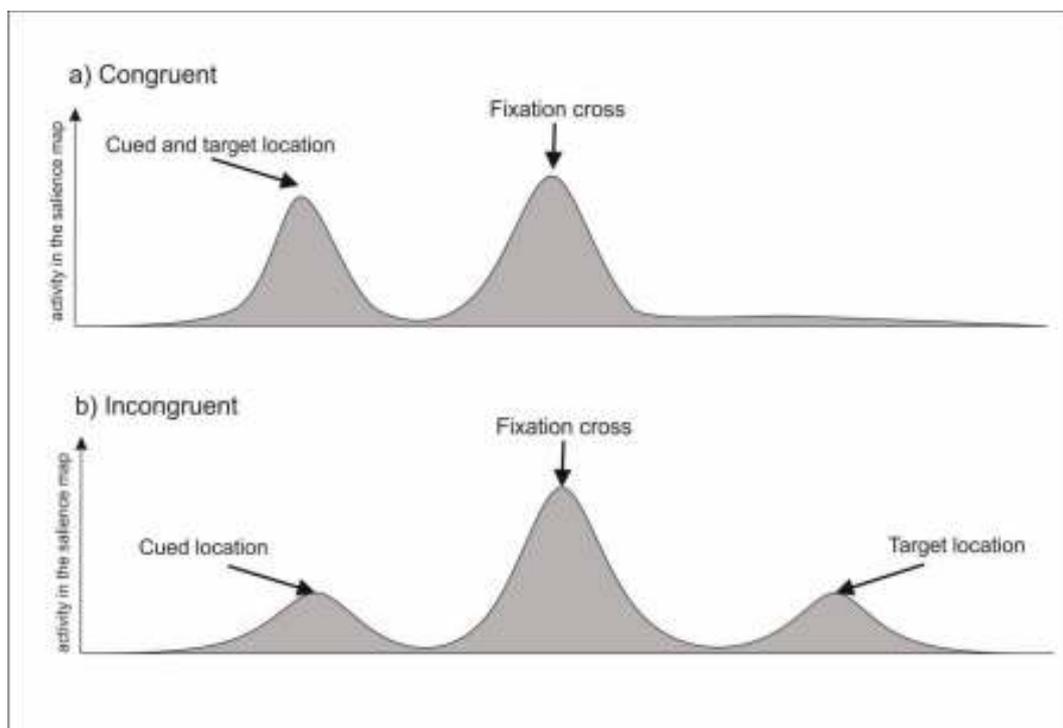


Figure 3.5: The peaks in the hypothesised salience map of Findlay and Walker's (1998) model on congruent and incongruent overlap trials. The y axis represents activity on the salience map, whereas the x axis represents two dimensional space. On congruent trials, the central fixation cross activates one location on the map, whilst the target and the cue activate the same peripheral location, generating a large peak. On incongruent trials, as well as the fixation activation, the target and cue activate two separate locations on the map with smaller peaks. With three locations activated, the competition between peaks takes longer to resolve, increasing SRTs on incongruent trials.

Very few overt errors were executed in Experiment 3, despite the inclusion of the gap condition. However, a new measure in Experiment 3 which looked at overt motor responses was the rate of anticipatory saccades made during the period after the onset of the cue, up until 80ms after the target onset. Saccades made in this interest period could not be target elicited and therefore could have been potentially influenced by the cue. Indeed, it was found that when looking at both small and large saccades, participants made significantly more anticipations in the direction of the cue, than in the opposite direction. This provides the first evidence in this thesis of spontaneous and “involuntary” overt orienting in the direction of the cues. However this effect was seen for both gaze and arrow cues and so does not support the gaze imitation hypothesis. The fact that the majority of these large amplitude anticipations occurred in the gap condition is evidence that the removal of the fixation stimulus was disengaging the oculomotor system, thereby making spontaneous saccades more likely. Although at a lower frequency, more large amplitude anticipations were made in the same direction as the cue compared with the opposite direction, in both the simultaneous and overlap conditions, in similar numbers. This latter observation reflects the fact that as far as this interest period was concerned, simultaneous and overlap conditions were identical except for the last 80ms of the simultaneous condition where the fixation stimulus was removed.

That participants executed many more large anticipatory saccades than they did overt errors after the appearance of the target reflects the interplay between the cues’ effects and that of the sudden onset peripheral target. In the absence of a sudden onset stimulus, the cues appear to exert an automatic effect on participants’ eye movements. However, once the peripheral stimulus is introduced into the display, the cues’ effects are apparently

over-ridden by the powerful reflexive orienting inducing properties of the abrupt visual onset, with very few erroneous saccades in the opposite direction to the target occurring.

As with large anticipatory saccades, more small anticipations were made in the same direction as the cue than in the opposite direction. Further, it was found that more small saccades were made in the presence of gaze cues than arrows, and that the difference between the numbers made in the same and the opposite direction was greater for gaze cues than for arrows.

A study by Engbert & Kliegl (2003) found that in a covert spatial cueing paradigm, using predictive central “arrow” cues (< and >), orientations of micro-saccades were congruent with the direction of attentional orienting. In the current experiment, more small saccades were made in the direction of the cues, than in the opposite direction, particularly for gaze cues. This finding may reflect a stronger influence of gaze cues on covert attention which may be somewhat independent from the large anticipatory saccades observed with gaze and arrow cues, perhaps reflecting two separate processes.

The production of small saccades in the direction of gaze cues cannot however provide an explanation for the congruency advantage observed with SRT, for the congruency effect was of equivalent magnitude for gaze and arrow cues. By the same rationale, the results from analyses of pre-saccadic fixation position further reject the notion that participants’ oculomotor behaviour may have been influenced by the cues prior to target onset. If participants had been fixating an area of the screen in the direction of the cue, the fovea would have been brought closer to the target on congruent trials, facilitating target detection, thereby contributing to the congruency effect seen with SRT. However, there was no evidence for a bias in fixation towards the cued location for either gaze or arrows. It is interesting to note that although participants seemed able to fixate in the centre

of the screen without influence of the cues at the time of the target onset, before this point some participants were unable to suppress the production of anticipatory saccades in the direction of the cues.

The gap pro-saccade task used in Experiment 3 set out to investigate whether a temporal gap between fixation offset and target onset would have the effect of disengaging the oculomotor system from all three cue congruencies. However, the gap procedure did not significantly affect neutral cues more than directional cues, as was suggested it might. It was further anticipated that more overt errors might be produced in the gap condition, relative to the simultaneous and overlap conditions. However, overall very few overt errors were executed. However, as was predicted, participants made large anticipatory saccades in the direction of both gaze and arrow cues, suggesting the cues have direct access to the oculomotor programming system. The predicted gap effect on SRT was observed, and the gap manipulation also influenced the congruency advantage for both cue types, with the largest effect occurring in the overlap condition. It was suggested that a bias in fixation position in the direction of the cues prior to the onset of the target might account for the congruency advantages observed, but the results demonstrate that participants do not tend to look towards the direction of the cue at the start of each trial. Similarly, although there was evidence that people made more small anticipatory saccades in response to gaze cues, this was not responsible for the SRT congruency advantage and therefore argues against “spatial compatibility” accounts of spatial cueing. There were virtually no differences between the cue types in any regard except in this latter respect.

The validity of the use of neutral cues has been further questioned by the results of the current experiment, where once again they failed to provide a baseline with which to

compare the effects of congruent and incongruent cues. In the following experiment, neutral trials were not included in the procedure, to aid clarity when interpreting the results.

In the following experiment, the anti-saccade task used in Experiment 2 was modified to include the gap procedure used in the current experiment. Experiment 2 revealed that when the oculomotor task becomes more complex, arrow cues appear to have no effect on SRTs where as with gaze cues a congruency advantage remains. However, the current experiment has demonstrated that varying the gap between fixation offset and target onset also influences the magnitude of the congruency effect for both gaze and arrow cues in the pro-saccade task. Using this procedure in the anti-saccade task may also similarly influence congruency advantages which may reveal effects of responses to which were absent in Experiment 2. Furthermore, it has been demonstrated in the current experiment that the oculomotor disengagement thought to occur with the offset of a fixation stimulus acts to make saccadic activity more likely during the gap, providing additional measures (error rates and anticipations) of the cues' influence on saccades which were not available in Experiment 2.

Experiment 4: Anti-saccades

3.5 Introduction

The results from Experiment 3 demonstrated that the use of a variable fixation offset procedure did not cause different magnitude congruency effects for gaze and arrow cues to emerge in a pro-saccade task. The use of gap and overlap conditions did however result in larger congruency advantages to emerge overall, when compared to the simultaneous condition which had been used in the first two experiments (i.e. the gap effect interacted with congruency). The anti-saccade task used in Experiment 2 showed that gaze cues but not arrows, resulted in a facilitation of correct responses in the direction opposite to the cue. If congruency advantages in a pro-saccade task are modulated by fixation offset, then it follows that they may also be affected by such a manipulation in an anti-saccade task due to the differential levels of oculomotor engagement thought to occur over the three conditions. Experiment 2 (anti-saccades) used a simultaneous fixation offset/target onset procedure and it is interesting that in Experiment 3, of the three fixation conditions, the smallest overall congruency effect was observed in the simultaneous condition. Therefore, varying the gap between fixation offset and target onset in the anti-saccade task may result in a congruency advantage emerging for arrow cues as well as gaze. Therefore, Experiment 4 aimed to investigate whether a congruency advantage for arrow cues might emerge in a gap anti-saccade task. A further aim of Experiment 4 was to facilitate the production of erroneous saccades, an expected finding when using a gap procedure. In Experiment 2, a trend for more errors on incongruent trials was suggested, but was not statistically significant. A higher rate of errors might therefore lead to a statistically significant difference between error rates with congruent and incongruent cues. Experiment 3 demonstrated that,

particularly during a gap between fixation offset and target onset, participants make more anticipatory saccades in the direction of the cue, than in the opposite. The finding from Experiment 2, which ran contrary to the gaze imitation hypothesis, was that peoples' responses were facilitated in the opposite direction to the cue. The direction of the anticipations in the current experiment is therefore of interest. Do people make anticipatory saccades in the same direction as the cue, as in Experiment 3, or in the opposite direction, as may be suggested by the findings of Experiment 2? Analyses of this measure may go some way to further explaining the mechanism underlying responses to cues in an anti-saccade task.

The anti-saccade task, as has already been discussed, is a more complex task than the pro-saccade task, in terms of the underlying cognitive mechanisms involved. One difference is that in the anti-saccade task, a saccadic response must be suppressed, and fixation maintained instead. The mechanism thought to underlie this response inhibition is an increase in activity of fixation neurons of the SC (Everling, Dorris, Klein, & Munoz, 1999; Munoz & Wurtz, 1992). However, the gap procedure is thought to release the oculomotor system from fixation (Dorris & Munoz, 1995; Kingstone & Klein, 1993a; Kingstone & Klein, 1993b; Reuter-Lorenz, Hughes, & Fendrich, 1991). Some researchers have observed that the gap effect is reduced or even absent in anti-saccade experiments, which has been proposed to be due to the increase in fixation activity required to successfully complete the task (Forbes & Klein, 1996; Reuter-Lorenz et al., 1991; Van Koningsbruggen & Rafal, 2009). However, this finding is not universal, with other studies reporting gap effects with anti-saccades (Fischer & Weber, 1992, 1997; Weber et al., 1998). It is therefore possible that the already stated aims of Experiment 4 may not be achieved, due to a reduced gap effect in comparison to the pro-saccade version of Experiment 3.

Finally Experiment 4, in addition to the anti-saccade task, encompassed a brief and preliminary investigation of the relationship between autistic traits and automatic cue-elicited orienting. Autism is a neurodevelopment condition which encompasses deficits in several cognitive domains, one of which is social intelligence (Baron-Cohen et al., 2000). A lack of interest in social interaction is a common observation in autistic individuals, and this includes a reduced tendency to look towards faces (Osterling et al., 2002) and reduced engagement in joint attention (including gaze following (e.g. Baron-Cohen et al., 1996)). It has been suggested that even in typically developed adults, autistic traits might be related to gaze cueing in spatial cueing-type tasks (Bayliss et al., 2005), with greater presence of autistic traits associated with smaller gaze cueing effects. Therefore, a further aim of Experiment 4 was to conduct a preliminary investigation into the relationship between gaze and arrow cueing in the anti-saccade task and participants' levels of autistic traits. This was achieved by participants completing the Autism Spectrum Quotient (AQ; Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001) after the eye tracking element of the experiment. Although only a relatively small number of participants will be examined here, it may be sufficient to yield results worthy of further investigation with a larger sample size.

3.6 Method

3.6.1 Design

This experiment had a 3 way, repeated measures design, with 2 levels on the factor Cue type (arrow or eye gaze), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Congruency (congruent, incongruent). The dependent measures were

saccadic reaction time (SRT), directional errors, frequency of anticipatory saccades and pre-saccadic fixation position.

3.6.2 Participants

Sixteen Psychology undergraduates from the University of Exeter (13 female) aged between 18 and 20 years ($M = 18.69$ years; $SD = .07$) took part in this experiment in exchange for course credit or £5. All participants had either normal or correct to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

3.6.3 Apparatus and Materials

The apparatus and materials were identical to those of Experiment 3.

3.6.4 Procedure

There was an additional feature to the procedure of Experiment 4, in that participants completed 10 practice trials comprised of 5 arrow and 5 gaze cues trials in various Congruency and Fixation offset conditions with the aim of providing as broad a range of condition combinations as possible. There were no neutral trials in Experiment 4 but the experiment was blocked by the factor Cue type as in previous experiments, so that participants completed 2 blocks of 60 trials each with gaze cues, and 2 blocks of 60 trials each with arrow cues, with the order of cue type presentation counterbalanced across participants.

The task itself was identical to Experiment 3, except that participants were this time instructed to look in the opposite direction to the “target” as quickly as possible.

In addition to completing the anti-saccade task, before the debrief, participants completed a paper version of the Autism Spectrum Quotient (AQ) (Baron-Cohen, Wheelwright, Skinner, et al., 2001). The resulting score gives an indication of the level of autistic-type traits in the participant, with higher scores indicating greater presence of such traits.

3.6.5 Data preparation and analysis

Completed trials were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in the previous experiments, but as practice trials were included in the current experiment, data from these were excluded at this stage. This procedure removed 589 trials representing 15.60% of completed trials.

In addition to the experimental data, participants' AQ scores were calculated according to the scoring system for this test detailed in Baron-Cohen et al. (2001).

3.7 Results

3.7.1 Saccadic reaction time

The mean correct SRT for each participant in each condition was calculated. A 3-way repeated measures ANOVA was performed on correct SRTs, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Congruency (congruent, incongruent). There was a significant main effect of Cue type, $F(1, 15) = 9.22, p = .008$, with responses on gaze trials quicker than those on arrow trials (arrows: $M = 264.65\text{ms}, SD = 8.35$; gaze: $M = 248.17\text{ms}, SD = 7.62$). There was also a significant main effect of Fixation, $F(2, 30) = 29.46, p < .001$, which appears to be the result of longer response times on overlap trials, relative to gap and

simultaneous trials. In addition, there was a main effect of Congruency, $F(1, 15) = 27.89$, $p < .001$, with congruent trials ($M = 246.85\text{ms}$, $SD = 7.90$) quicker than incongruent trials ($M = 265.97\text{ms}$, $SD = 7.57$). There was also a significant interaction between Cue type and Congruency, $F(1, 15) = 9.60$, $p = .007$. Paired samples t -tests showed that for gaze cues, the 27.87ms difference between SRTs on congruent and incongruent trials was highly significant, $t(15) = 6.25$, $p < .001$, whereas with arrow cues, the 10.36ms difference between congruent and incongruent was only just statistically significant, $t(15) = 2.20$, $p < .044$.

Figure 3.6 shows the correct SRTs for congruent and incongruent gaze and arrow cues across the three fixation conditions.

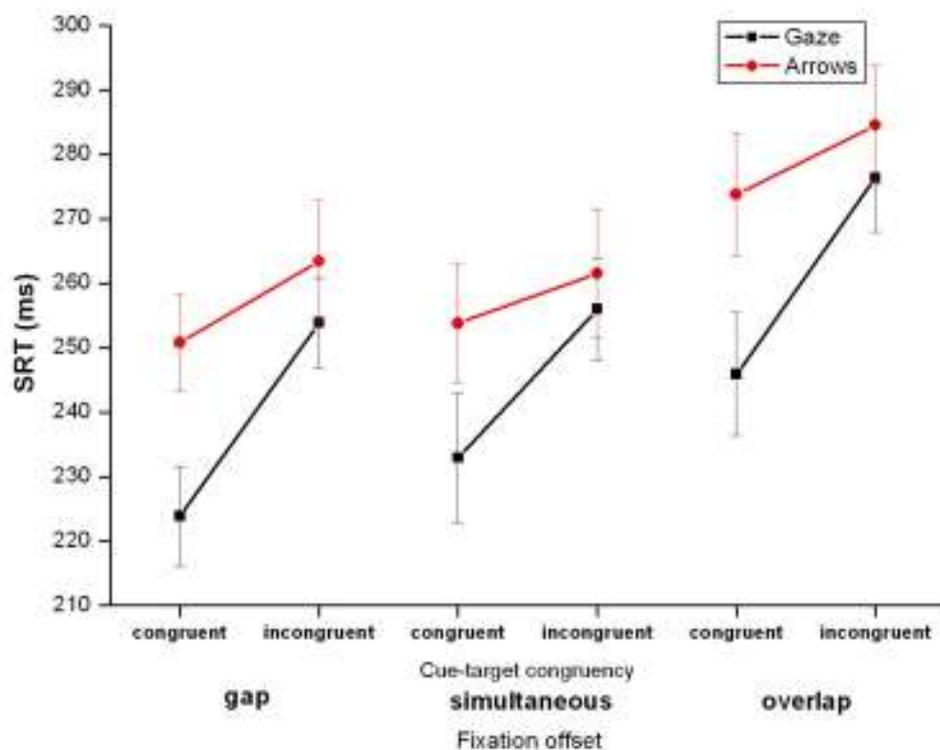


Figure 3.6: Mean SRTs for congruent and incongruent gaze and arrow cues over the three fixation offset conditions. Error bars represent standard error of the mean.

3.7.2 Error rates

In 285 trials (8.94% of the total completed trials), the first response was an error: a saccade incorrectly initiated towards the peripheral target.

The percentage of errors committed in each condition was calculated for each participant by dividing the number of errors committed by the total number of trials for each condition, converted to a percentage.

A 3 way repeated measures ANOVA was conducted on these data with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Congruency (congruent, incongruent).

There was a significant main effect of Congruency, $F(1, 15) = 32.18, p < .001$, with most errors being committed on incongruent trials (congruent: $M = 5.28\%$, $SD = 1.80$; incongruent: $M = 13.13\%$, $SD = 2.50$). The main effect of Fixation approached significance, $F(2, 30) = 2.90, p = .088$ (H-F Criterion). The main effect of Cue type did not approach significance, $F(1, 15) = 1.16, p = .299$. The Cue type by Fixation interaction was not significant, $F(1, 15) = 2.04, p = .148$ and neither were the Fixation by Congruency interaction or the Cue by Congruency interaction, $F_s < 2.00, p_s > .190$. The three way interaction did not reach significance, $F(2, 30) = 2.46, p = .102$, although there appears to be a trend for error rates to vary across Fixation offset and Congruency conditions for arrow cues but less so for gaze cues. Figure 3.7 below shows the error rates of participants for congruent and incongruent gaze and arrow cues over the three Fixation conditions.

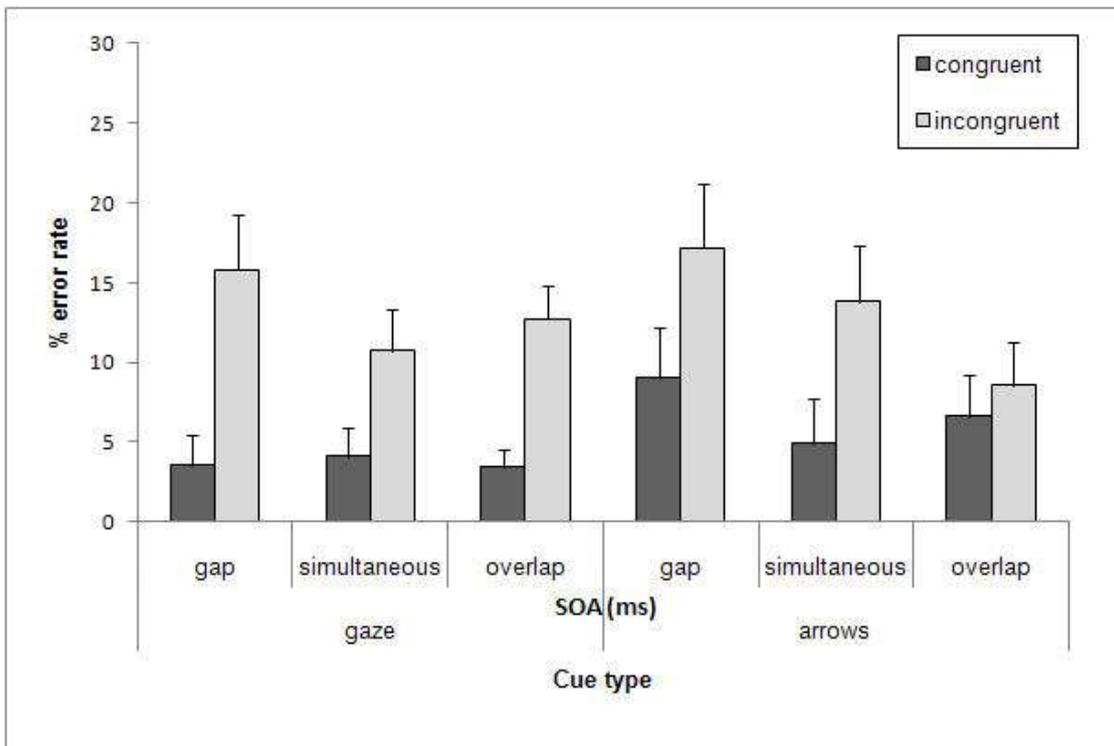


Figure 3.7: The mean percentage of error rates per participant, for congruent and incongruent gaze and arrow cues over the three Fixation conditions. Error bars represent standard error of the mean.

3.7.3 Anticipations

The frequency of small and large anticipatory saccades made during the period after the onset of the cue, but before the onset of the target, were calculated using the procedure detailed in Experiment 3. Anticipations were made on 16.38% of trials.

Large anticipatory saccades

286 large saccades ($> 2.0^\circ$ amplitude) were executed during this period, representing 7.45% of trials. A 3 way repeated measures ANOVA was conducted on these frequency

data, with 2 levels on the factor Cue (arrows, gaze), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Direction (same, opposite). The main effect of Fixation did not reach significance $F(2, 30) = 2.72, p = .082$. The main effect of Direction did not reach significance, $F(1, 15) = 2.22, p = .157$, but there did appear to be a trend for more anticipatory saccades in the opposite direction to the cue, as can be seen in Figure 3.8 below.

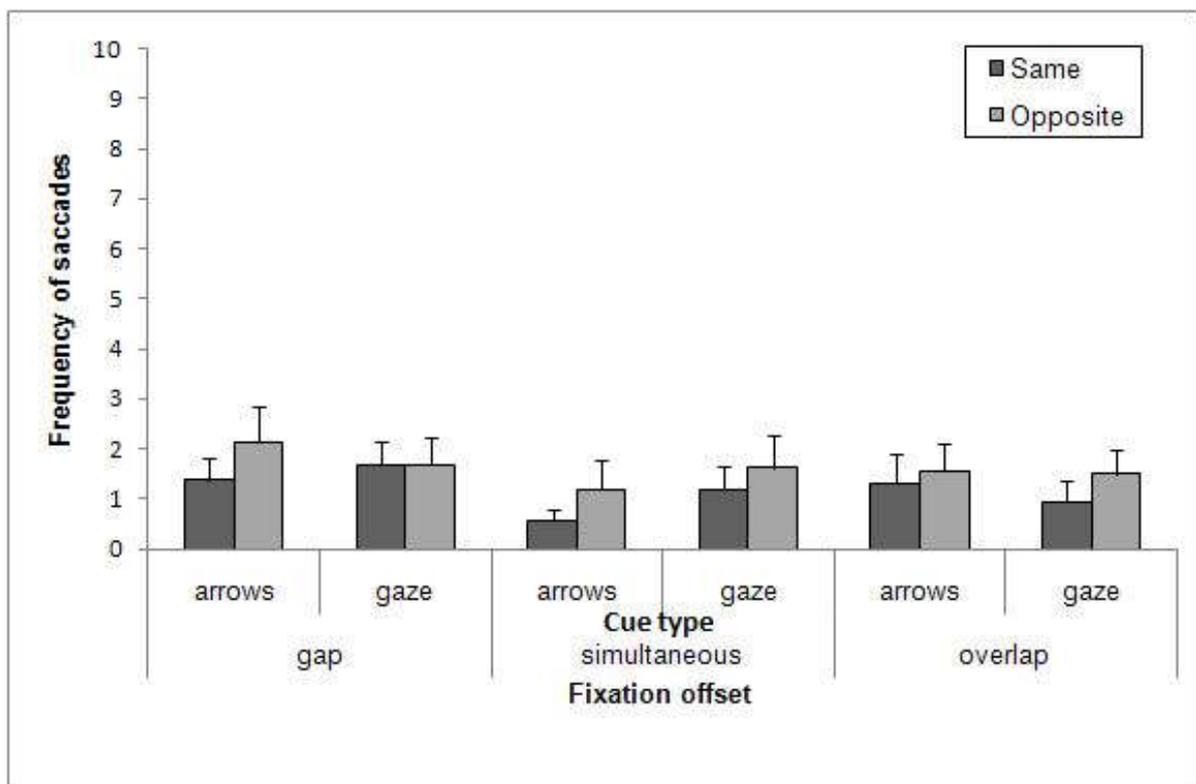


Figure 3.8: Mean frequencies of large anticipatory saccades per participant, made in the same and opposite directions to the cues over the three fixation conditions. Error bars represent standard error of the mean.

Small anticipatory saccades

343 small saccades (0.05 – 1.99° amplitude) were executed during this period, representing 8.93% of trials. A 3 way repeated measures ANOVA was conducted on these frequency data, with 2 levels on the factor Cue (arrows, gaze), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Direction (same, opposite). There was a significant main effect of Cue type, $F(1, 15) = 6.90, p = .019$, with more small saccades produced in the presence of gaze cues (arrows: $M = .66, SD = .37$; gaze: $M = 2.92, SD = 1.02$). No other main effects or interactions reached significance.

3.7.4 Pre-saccadic fixation position

SRT data

As in Experiment 3, the mean fixation position on the x axis, measured in pixels, prior to the response on each completed trial was calculated per condition for each participant. A 3 way, repeated measures ANOVA was conducted on the data, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Cue direction (left, right). Overall, there was a slight bias to the right, with a mean fixation position of 514.46 (the centre of the screen was 510). There was a main effect of Cue direction, $F(1, 15) = 5.12, p = .039$, with participants fixating 1 pixel more to the right when the cue pointed right ($M = 514.84$) compared with when the cue pointed left ($M = 513.60$). There were no other main effects or interactions.

All data

A further analysis was conducted on the mean fixation position at the onset of the target, for all trials. A 3 way, repeated measures ANOVA was conducted on the data, with 2 levels on the factor Cue type (arrows, eyes), 3 levels on the factor Fixation (gap, simultaneous, overlap) and 2 levels on the factor Cue direction (left, right). Again there was a slight fixation bias to the right ($M = 514.41$), which may have been the result of right eye monocular recording. However no main effects or interactions reached significance.

3.7.5 AQ scores

Individual scores on the AQ ranged from 6 to 29 (maximum possible score is 50 , with higher scores representing greater presence of autistic traits). A one way between subjects ANOVA was conducted with 2 levels on the factor Gender (male, female). There was a significant main effect of Gender, with males scoring significantly higher than females (males: $M = 25.67$, $SD = 2.60$; females: $M = 13.39$, $SD = 1.25$).

Six new variables were created in SPSS to represent the congruency advantages with gaze and arrow cues at each of the Fixation conditions, for each participant. Two-tailed bivariate correlational analyses were carried out on the congruency advantage variables and AQ score. Although not significant at the $\alpha = .05$ level, there was a suggestion of a positive correlation between AQ and the congruency advantage for arrow cues in the overlap condition, $r(15) = .48$, $p = .080$, providing a slight indication that higher scores on the AQ may be associated with larger congruency advantages with arrow cues in this condition. The small sample size in this experiment may have been responsible for this correlation not reaching significance. Increasing the statistical power may have resulted in a statistically significant correlation here. There were no other significant correlations.

3.8 General Discussion

Experiment 4 used an anti-saccade task with a variable fixation offset/ target onset and a fixed SOA with the aim of eliciting a higher error rate than the procedure used in Experiment 2, to explore the suggestion of a trend for participants to make errors in the opposite direction to the cue, noted in that experiment. Furthermore, as the variable gap procedure modulated the magnitude of the congruency advantage in the pro-saccade task of Experiment 3, with considerably larger effects in the overlap condition than in the gap and simultaneous conditions, it was anticipated that the same modulation may occur in the anti-saccade version of the task, with the possibility that a congruency advantage might emerge for arrow cues as well as gaze cues. In addition, the rate and direction of anticipatory saccades was of interest. Experiment 3 demonstrated that people made anticipatory saccades in the direction of the cue, but in the anti-saccade task of Experiment 2, there appeared to be a trend for people to make overt errors in the *opposite* direction to the cue, suggesting an influence of task on oculomotor responses to the cues. Therefore it was anticipated that given that the gap condition is likely to produce more anticipatory saccades, the direction of these anticipations might be influenced by task, with more saccades in the opposite direction to the cues a possibility. Finally, Experiment 4 included preliminary investigations into the relationship between cueing effects and autistic traits in the participants.

Varying the temporal gap between the fixation offset and target onset resulted in an overall SRT congruency advantage of 20ms, an effect which was absent from Experiment 2. This finding indicates that arrows as well as gaze cues were causing participants to saccade in the opposite direction to the cues. However although a congruency advantage was present for arrow cues in this experiment, (quicker to saccade in the *opposite* direction

to the cues) the magnitude of the effect was over 17ms larger for gaze cues, adding to the finding from Experiment 2 (anti-saccades) in suggesting that gaze cues have a more pronounced effect on oculomotor programming than arrows. In addition to the effects of cue congruency, there was also an overall effect main effect of cue type on SRTs, with participants quicker to respond on gaze trials. A similar effect was seen at the shortest SOA in Experiment 2, where faster SRTs were also produced with gaze cues than with arrows. The reason for this is not obvious, as the previous experiments have not otherwise demonstrated such an effect. One possible explanation may relate to the engaging properties of the cues interacting with the conditions in this particular paradigm. Taken together these findings suggest that under certain conditions, gaze cues may have a general facilitatory or disengaging effect on the oculomotor system relative to arrow cues.

Participants were slower to respond on overlap trials, which is an expected finding if prolonged duration of a fixation stimulus causes increased activity in fixation neurons, which in turn inhibit the activity of saccade related neurons in the SC (Everling et al., 1999; Munoz & Wurtz, 1992). With reference to Findlay and Walker's (1999) model, activity in the fixate centre will be increased thereby reducing activity in the move centre. However there was no difference in SRTs between gap and simultaneous trials. This was one of the possible outcomes proposed in the introduction of Experiment 4: Some researchers have reported gap effects in anti-saccade tasks (Fischer & Weber, 1992, 1997; Weber et al., 1998) whereas others have reported reduced effects or no gap effect at all, which has been suggested to be the result of the increase in fixation activity required to successfully inhibit the prepotent pro-saccade response, counteracting the disengagement produced by the offset of the fixation stimulus during the gap (Forbes & Klein, 1996; Reuter-Lorenz et al., 1991; Van Koningsbruggen & Rafal, 2009).

The larger magnitude of the overall congruency effect observed here, when compared to Experiment 2, is comparable to that in the overlap condition of Experiment 3. An explanation for the lack of variation in congruency advantage over the three gap conditions in the current experiment might be that the need to voluntarily maintain fixation throughout an anti-saccade task acts as a “cognitive engage mechanism”, whereby participants voluntarily devote more conscious effort to maintaining fixation to avoid making an error, and is similar to having a visually present fixation stimulus, in a sense making all conditions similar to “overlap” trials. The presence of the fixation stimulus in the overlap condition may increase activity of fixation neurons to a greater extent than maintaining fixation without a stimulus present, accounting for the overall increase in SRTs on overlap trials already discussed.

Error rates were anticipated to increase in this experiment in comparison to Experiment 2, due to the gap condition. However, this was not observed: error rates were actually higher in Experiment 2 than in Experiment 4. A possible explanation for this may be that the inclusion of additional practice trials in this experiment. Despite the lower frequency of errors in the current experiment, a significant effect of congruency emerged, with participants making more errors on incongruent trials, i.e. in the opposite direction to the cue, confirming the trend which was apparent in Experiment 2. That people made more errors in the opposite direction to the cues than in the same direction, contradicts the gaze imitation hypothesis on two counts. Firstly, the effect was seen with arrows as well as gaze and secondly, motor responses were being executed in the opposite direction to that predicted. However, it is consistent with the direction of facilitation of SRTs in the anti-saccade task, which are faster in the opposite direction to the cues. With SRT and error

data taken together, it is apparent that oculomotor responses are facilitated in the opposite direction to the cues.

It was suggested in Chapter 2, that the reason for a facilitation of correct saccadic responses in the opposite direction to the cues may be due to enhanced target detection or localisation when the cue points to the target, thereby decreasing the preparation time needed for the execution of eye movements on congruent trials. The increased error rate on incongruent trials observed in Experiment 4 could be explained by the same theory. If the cues cause a shift of covert attention, then on incongruent trials, attention would be allocated to an empty space and the onset of the target on the unattended side could cause attentional capture and the activation of the visual grasp reflex, resulting in an error. Such attentional capture has been demonstrated in visual search-type tasks, where task directed attention can be interrupted by the sudden onset of a stimulus in the display (Theeuwes, Kramer, Hahn, & Irwin, 1998; Theeuwes et al., 1999)

This pattern of facilitation of responses and overt errors in the opposite direction to uninformative cues in an anti-saccade task has been reported elsewhere with peripheral cues. However, Weber et al. (1998) offered an alternative explanation to that proposed above, suggesting that the effect may be the result of the task instruction to produce a saccade in the opposite direction to a visual stimulus: Participants were transposing the instruction onto the first visible stimulus, which is the cue and then making a saccade in the opposite direction. However, one might also expect to see more anticipatory saccades in the opposite direction if this were the case. However, there was no effect of cue direction on anticipatory saccades, but there was a trend for more anticipations in the opposite direction, although the frequencies were lower than in the pro-saccade task. This effect is likely to be due to the increased level of fixation activity needed to suppress the unwanted pro-saccade,

over-riding some of the effects of the cues, with the onset of the target disengaging the oculomotor system before a motor response can be programmed in response to the cues. In addition, the reduced number of anticipatory saccades further suggests that the directional versions of the cues do not “pre-disengage” the oculomotor system.

Although people did not make anticipatory saccades in the direction of the cues (although there was a suggestion of a trend for more saccades in the opposite direction to the cues in the anti-saccade task), they did make more small anticipatory saccades ($< 2.00^\circ$) in the presence of gaze cues, as in the previous experiment suggesting that gaze cues may have been responsible for a general arousal of the oculomotor system. This explanation would tie in with the finding that under some conditions, overall SRTs were faster with gaze cues. However, the increased rate of these small saccades might just reflect participants shifting back and forth between the pupils of the eyes. A further factor which seemed to be influenced equally by gaze and arrow cues was the fixation position prior to the first saccade, with participants fixating an average of 1 pixel from the mean fixation position in the direction of the cues. However, this small bias is unlikely to be responsible for the congruency advantage observed, as there was no effect of cue type on fixation position, whereas there was a larger congruency advantage for gaze than arrow cues. In general there was a tendency for participants to fixate towards the right of centre, but this may simply reflect the fact that right eye monocular recordings were made throughout, and so a slight rightward bias would be expected.

There has been a suggestion in the literature that the influence of gaze and arrow cues may be related to social and emotional abilities or “social intelligence” (Bayliss et al., 2005). The preliminary investigation of the relationship between levels of autistic traits via the AQ and cueing effects suggested that there may be a tendency for people with higher

AQ scores and therefore more autistic traits, to be more influenced by arrow cues than those with lower AQ scores. This finding is interesting, but a larger sample size would be needed to carry out more reliable analyses, and a later chapter will explore this possibility with a larger group of participants.

As in Chapter 2, the results from Experiments 3 and 4 demonstrate that the task instruction can influence oculomotor responses to gaze and arrow cues. Whereas in the pro-saccade task, gaze and arrow cues influenced saccadic responses similarly, in the anti-saccade task gaze cues caused greater facilitation of reaction times in the cued direction, and indeed more generally, than arrow cues. There were also task effects on responses which were not cue specific. There was a reduced gap effect in the anti-saccade task with a congruency advantage which was not modulated by the fixation condition, unlike in the pro-saccade task. Furthermore, there were more large anticipatory saccades made in the cued direction than the uncued direction in the pro-saccade task but not in the anti-saccade task. As in Experiment 2, Experiment 4 demonstrated that the facilitation of responses was in the opposite direction to the cues, rather than in the same direction, as in the pro-saccade tasks. One explanation for the reduced gap effect and lack of spontaneous saccades in the anti-saccade task has already been discussed, specifically that a voluntary increase in fixation activity is needed to inhibit the prepotent pro-saccade response and that this counteracts the effect of an offset of the fixation stimulus. An alternative explanation was offered by Machado & Rafal (2000), who reasoned that if the inhibition of the visual grasp reflex (an increase in fixation activity) is the reason for a reduced gap effect in anti-saccade tasks, then there should be a similar lack of gap effect in go-nogo tasks, where on a proportion of trials, a saccade to a peripheral target must be inhibited and fixation maintained instead. However, these authors found a substantial gap effect in their go-nogo

task, and concluded that another aspect of the anti-saccade task, specifically the voluntary generation of the anti-saccade response, might be the reason for the reduced gap effect reported in several studies of this kind (Forbes & Klein, 1996; Reuter-Lorenz et al., 1991; Van Koningsbruggen & Rafal, 2009). Indeed a further study by the same authors showed that gap effects were reduced when participants received informative cues indicating the correct location for an upcoming pro-saccade compared with when they received uninformative cues (Machado & Rafal, 2004). A more recent study by Van Koningsbruggen & Rafal (2009) suggested independent roles for both oculomotor preparation and inhibition of the visual grasp reflex in reducing gap effects.

Neurophysiological evidence from monkeys suggests that the instruction to make an anti-saccade alone causes increased activity in fixation cells of the SC (Everling et al., 1999) and decreased activity in saccade related neurons of the FEF (Everling & Munoz, 2000) relative to an instruction to make a pro-saccade. The latter study also demonstrated direct descending projections from FEF to SC, suggesting that task set related activity can indeed influence SC activity. In terms of the results of Experiment 4, such an influence of task set may explain the reduced gap effect and lack of spontaneous saccades seen here, in comparison to the pro-saccade task of Experiment 3.

A final observation from the experiments presented in Chapter 3 relates to the susceptibility of the cues' effects to voluntary and reflexive influences. In Experiment 3 (pro-saccades), spontaneous saccade were made in the direction of the cues before the onset of the target, but very few errors were made, suggesting the effect of the cues on oculomotor behaviour was over-ridden by the reflexive response to the sudden onset peripheral stimulus. In Experiment 4, a significant effect of cue-driven anticipatory saccades were absent, reflecting, as has already been proposed, task-related voluntary

mechanisms. These findings suggest that the cues can exert automatic effects on the saccadic system but that these are attenuated when other influences are present concurrently. This places the orienting elicited by arrow and gaze cues in a class which is neither reflexive nor voluntary, but still with some automatic characteristics.

3.9 Conclusions

Chapter 3 has provided evidence that although gaze and arrow cues can both cause automatic orienting of the saccadic system, their effects can be influenced by the task in which they are investigated, with arrow cues appearing to have less robust effects than gaze cues under more cognitively demanding conditions.

Chapter 4 will investigate the possibility that other familiar directional cues may exert automatic effects on oculomotor behaviour and that the preoccupation in the literature with gaze and arrow cues may have caused researchers to overlook a more general influence of directional cues on eye movements and attention.

Chapter 4: *Influence of directional word and finger pointing cues on performance in pro- and anti-saccade tasks*

4.1 Introduction

The preceding experiments have shown that eye gaze cues and to a lesser extent, arrow cues, influence oculomotor behaviour in an apparently automatic manner. It has been argued that these cues may exert their effects on attention and oculomotor programming due to over-learned stimulus-response associations (Brignani, Guzzon, Marzi, & Miniussi, 2008; Guzzon, Brignani, Miniussi, & Marzi, 2010; Vecera & Rizzo, 2006), rather than because of any social and biological significance per se. It has been argued that eye gaze is the first directional cue to be observed from birth and that young infants learn that events and objects of interest occur where other people are looking (Corkum & Moore, 1998; Moore & Corkum, 1994). A similar rationale can account for the effects of arrows: Used continually to direct our attention and actions in the real world, and on the road particularly, the consequences of not directing our attention in their direction can be fatal. However, it is likely that not everyone has had the same degree of exposure to the road signs used as arrow cues in the preceding experiments and this may account for the reduced effects of arrows when compared to eye gaze in the anti-saccade tasks reported in this thesis. Therefore, other directional cues which may be more ubiquitous may exert effects similar to those seen in this thesis with eye gaze cues. In the current chapter, two further forms of directional cue were investigated: One with little social relevance and the other which is arguably just as important as eye gaze as a cue to direction of attention in social interaction.

Experiments 5a and 5b used directional word cues LEFT and RIGHT, whilst Experiment 6a and 6b investigated the influence of photographic finger pointing cues in the same pro and anti-saccade tasks used in Chapters 2 and 3.

Directional word cues have been shown to cause involuntary shifts of attention (Ho & Spence, 2006; Hommel et al., 2001) and automatic programming of eye movements (Hodgson et al., 2009). If eye gaze cues in particular cause the congruency effects seen in the previous experiments predominantly because of their over-learned nature, rather than relevance in social interaction, then similar results should be seen when literate, native English speakers perform the same pro- and anti-saccade tasks with uninformative directional word cues.

However, if the social and biological nature of eye gaze cues is the reason for the larger effects seen with this cue in comparison to arrow cues, then we may expect to a similar influence of other cues which are commonly used to communicate ones' direction of attention in non-verbal, social interactions. Another important behaviour aside from gaze following in the development of joint attention in infants is orienting to pointing gestures of adults (Gliga & Csibra, 2009; Scaife & Bruner, 1975; Woodward & Guajardo, 2002). However, in comparison to work on gaze cues, finger pointing cues have received little interest in the attentional literature. An extant body of studies of covert attention have suggested that finger pointing cues can cause automatic shifts of attention akin to eye gaze cues (Ariga & Watanabe, 2009; Sato et al., 2009, 2010; Tomonaga & Imura, 2009). However, no studies to date have investigated the effects of uninformative pointing cues on performance in oculomotor tasks. Therefore, the aim of Experiments 6a and 6b is to examine the influence of this other form of social cue on performance in pro- and anti-saccade tasks respectively. If similar results are obtained to those with gaze cues then it

might indicate that it is social relevance of the cues which is important in automatically recruiting the saccadic system, of which eye gaze is just one example.

Experiment 5a: Word cues and pro-saccades

4.2 Method

4.2.1 Design

This experiment had a 2 way, repeated measures design with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent). The primary dependent measure was saccadic reaction time (SRT). Directional errors were also measured. As in the preceding chapter, the frequency of anticipations during the period between the onset of the cue and the onset of the target was measured. Finally, the fixation position at the start of the trial was also of interest.

4.2.2 Participants

Sixteen healthy native English speaking undergraduates from the School of Psychology, University of Exeter, (14 female) aged between 18 and 22 years ($M = 19.38$ years; $SD = 1.09$) took part in is experiment in exchange for course credit. All participants had either normal or corrected to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

4.2.3 Apparatus and Materials

Apparatus and materials were identical to those of Experiments 2 - 4 (Chapters 2 and 3) with the exception of the stimuli used as cues.

The directional word cues were prepared in Corel Paint Shop Pro X and were comprised of the letter strings LEFT, RIGHT and XXXX (the neutral condition) written in Arial font, 130 points, in bold. To match the stimuli's perceptual properties as closely as possible to those used in the previous experiments, the colour of the cues matched that of the road signs used in Experiments 1 to 4 and had the RGB value of 0,122,194, a mid blue. The image canvas of the word cues was the same size as the eye gaze cues used in Experiments 1 to 4. Figure 4.1 shows the stimuli used in Experiments 5a and b.

The image displays three distinct text stimuli in a bold, blue, sans-serif font. From left to right, the words are 'LEFT', 'RIGHT', and 'XXXX'. Each word is centered within its own rectangular area, and the three areas are spaced evenly across the horizontal axis.

Figure 4.1: Directional word cue stimuli used in Experiment 5a and b. XXXX represents the neutral condition. Image is not to scale.

4.2.4 Procedure

The experiment consisted of 180 trials, split into three blocks, preceded by 12 practice trials. This resulted in each participant completing a total of 192 trials, with the first 12 trials excluded from the analysis. The same calibration procedure as used in the previous experiments was carried out at the beginning of this experiment. In addition to this calibration, at the beginning of each block of 60 trials and every 10 trials thereafter, a drift correct procedure was carried out.

All trials were presented on a white background. Each trial began with the presentation of a black central fixation cross subtending 1.26° of visual angle, for the duration of 1000ms. Next, one of the word cues was presented, subtending 5.52° of visual

angle (the same diameter as the gaze cues used in Experiments 2-4). The three stimuli, LEFT, RIGHT and XXXX (neutral) written in “road-sign blue”, were presented with equal probability, each being presented 60 times throughout the course of the experimental session, in addition to the preceding practice trials (the order of the 12 practice trials were identical for each participant and consisted of a proportional number of trials from each condition). After a period of 100, 300 or 800ms, the target was presented at the same location and with the same diameter as in Experiments 2-4. The target dot appeared on the left and right sides of the screen with equal probability and for a total of 90 left and 90 right presentations in each experiment. The participants were instructed to maintain fixation on the central cross and ignore the central words until the dot appeared, whereupon they were to make a saccade to the dot as quickly as possible.

4.2.5 Data preparation and analysis

Completed trials were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in the previous experiments. This procedure removed 177 trials representing 6.15% of trials. Practice trials were excluded from the analyses

4.3 Results

4.3.1 Saccadic reaction time

A 2 way repeated measures ANOVA was conducted on the SRT data with 3 levels on the factor SOA (100, 300, 800 ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent). There was a significant main effect of SOA, $F(2, 30) = 7.40, p = .002$ (H-F Criterion), with SRTs decreasing as SOAs increased. There was no significant effect of

Congruency and the interaction did not reach significance ($F_s < 1.00$). The mean SRTs for all conditions are presented in Table 4.1.

A second ANOVA was conducted which excluded the data from neutral trials. There was a similar main effect of SOA, $F(2, 30) = 7.40, p = .016$ (H-F Criterion), but again there was no effect of Congruency ($F < 1.00$) and the interaction did not reach significance.

Cue-target congruency	SOA (ms)		
	100	300	800
Congruent	209.27 (7.36)	205.99 (7.40)	197.78 (5.18)
Neutral	204.54 (6.36)	212.34 (8.85)	193.83 (5.37)
Incongruent	206.75 (7.67)	209.05 (8.08)	195.70 (4.89)

Table 4.1: Mean SRT for congruent, neutral and incongruent word cues over the 3 SOAs.

Figures in parentheses are standard errors of the mean.

4.3.2 Error rates

Only 2 errors were committed, so they were not investigated further.

4.3.3 Anticipations

The frequency of small and large anticipatory saccades made in the same and opposite direction to the cues during the period after the onset of the cue, but before the onset of the target, were calculated for each condition per participant using the procedure detailed in Experiment 3. Anticipations were made on 4.46% of trials.

Large anticipatory saccades

44 large anticipatory saccades ($> 2.0^\circ$ amplitude) were executed during this period, representing 2.16% of trials. A 2 way repeated measures ANOVA was conducted on these frequency data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction (same, opposite).

There was a significant main effect of SOA, $F(2, 30) = 8.68, p = .001$ (H-F Criterion), with the frequency of anticipations increasing as SOA increased (100ms: $M = .03, SE = .03$; 300ms: $M = .53, SE = .19$; 800ms: $M = .81, SE = .19$). The main effect of Direction was not significant however, $F(1, 15) = 2.71, p = .120$. There was a marginally significant interaction between Direction and SOA, $F(2, 15) = 3.36, p = .048$, which appears to be the result of more anticipations being executed in the same direction as the cue than in the opposite direction, at the longest SOA only. Figure 4.2 shows the frequency of large anticipatory saccades over the 3 SOAs.

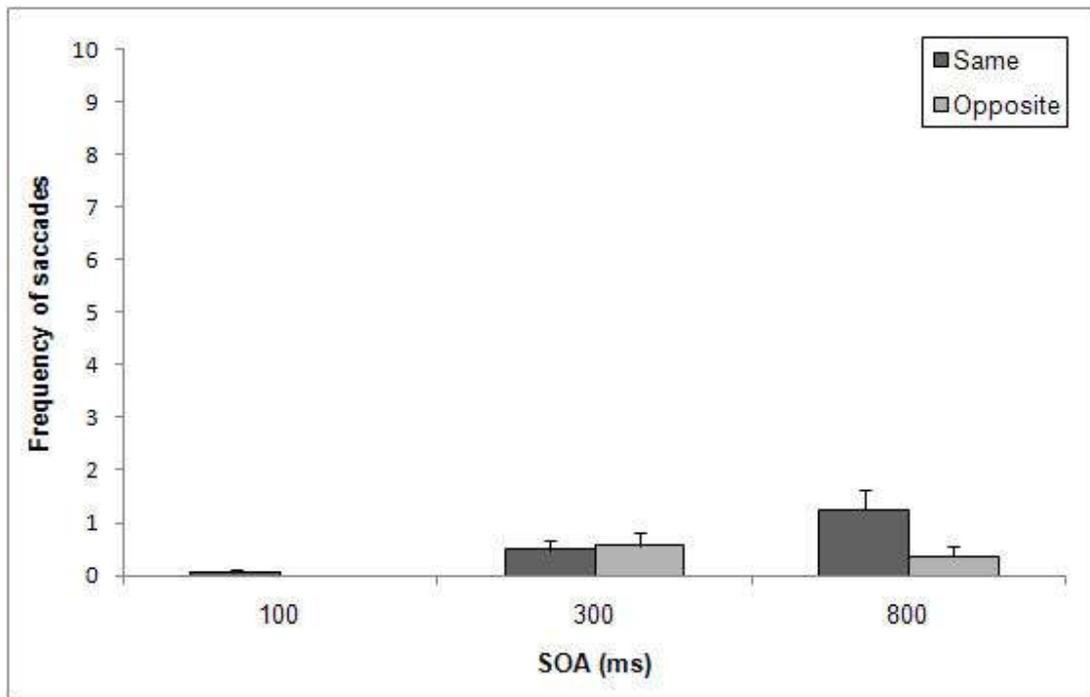


Figure 4.2: Frequency of large anticipatory saccades in the same and the opposite direction to the word cues over the 3 SOAs.

Small anticipatory saccades

47 small anticipatory saccades ($< 2.0^\circ$ amplitude) were executed during this period, representing 2.30% of trials. A 2 way repeated measures ANOVA was conducted on these frequency data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction (same, opposite).

There was a significant main effect of SOA, $F(1.90, 28.23) = 8.63$, $p = .001$ (H-F Criterion), with the frequency of anticipations increasing as SOA increased (100ms: $M = .01$, $SE = .03$; 300ms: $M = .47$, $SE = .17$; 800ms: $M = .97$, $SE = .23$). The main effect of Direction was not significant, $F(1, 15) = 2.38$, $p = .144$. This time the interaction between Direction and SOA was not significant, $F(2, 15) = 2.27$, $p = .121$.

4.3.4 Pre-saccadic fixation position

SRT data

The mean fixation position on the x axis, measured in pixels, prior to the response on each completed trial was calculated per condition for each participant. A 2 way, repeated measures ANOVA was conducted on the data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue direction (left, right). The mean fixation position was 509.96.

There was a significant main effect of SOA, $F(1.58, 23.73) = 4.53, p = .029$ (H-F Criterion), with participants fixating slightly towards the left at 100ms SOA ($M = 508.96, SE = 1.29$) in comparison to 300ms ($M = 510.21, SE = 1.05$) and 800ms ($M = 510.69, SE = .98$) SOAs. The main effect of Cue direction was not significant, $F(1, 15) = 2.31, p = .150$ and neither was the interaction between Cue direction and SOA ($F < 1.00$).

All data

A further analysis was conducted on the mean fixation position at the time of target onset of all trials. A 2 way, repeated measures ANOVA was conducted on the data with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue direction (left, right). The mean fixation position was 513.32. As with the previous analysis, there was a significant main effect of SOA, $F(2, 30) = 4.74, p = .016$ (H-F Criterion), with participants fixating more towards the right as SOA increased (100ms: $M = 509.08, SE = 1.43$; 300ms: $M = 513.98, SE = 2.40$; 800ms: $M = 516.91, SE = 2.88$). There was no effect

of Cue direction and the interaction was not significant ($F_s < 1.0$). These analyses indicate that people did not tend to fixate in the direction of the cue.

Experiment 5b: Word cues and anti-saccades

4.4 Methods

4.4.1 Design

This experiment had the same 2 way, repeated measures design as Experiment 5a with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent). The primary dependent measure was saccadic reaction time (SRT). Directional errors were also measured. As in the preceding chapter and Experiment 5a, the frequency of anticipations during the period between the onset of the cue and the onset of the target was measured, in addition to the fixation position at the start of the trial.

4.4.2 Participants

A further fourteen healthy native English speaking undergraduates from the School of Psychology, University of Exeter, (12 female) aged between 18 and 27 years ($M = 20.00$ years; $SD = 2.77$) took part in this experiment in exchange for course credit. All participants had either normal or corrected to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

4.4.3 Apparatus and Materials

Apparatus and materials were identical to those in Experiment 5a.

4.4.4 Procedure

The procedure was identical to that of Experiment 5a with the exception of task instruction. This time, participants were instructed to look in the opposite direction to the target as quickly and accurately as possible.

4.4.5 Data preparation and analysis

Completed trials were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in the previous experiments. This procedure removed 176 trials representing 6.11% of trials. Practice trials were excluded from the analyses.

4.5 Results

4.5.1 Saccadic reaction time

A 2 way repeated measures ANOVA was conducted on the SRT data with 3 levels on the factor SOA (100, 300, 800 ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent). There was a significant main effect of SOA, $F(1.33, 17.32) = 32.56, p < .001$ (H-F Criterion), with SRTs decreasing as SOAs increased. The main effect of Congruency did not reach significance, $F(2, 26) = 2.89, p = .074$ and the interaction did not approach significance ($F < 1.00$)

A second ANOVA was conducted which excluded the data from neutral trials. There was a similar main effect of SOA, $F(1.44, 18.74) = 20.89, p < .001$ (H-F Criterion), but the effect of Congruency was further from reaching significance than in the analysis with neutrals, $F(1, 13) = 2.81, p = .12$, indicating that the neutral trials were responsible

for the Congruency effect above approaching significance, rather than congruent and incongruent trials. The interaction did not approach significance ($F < 1.00$).

4.5.2 Error rates

A total of 201 errors were committed, accounting for 8.58% of the completed trials.

A 2 way ANOVA was conducted on the percentage of errors per condition per participant, with 3 levels on the factor SOA (100, 300, 800 ms) and 3 levels on the factor Congruency (congruent, neutral, incongruent).

There was a significant main effect of SOA, $F(1.27, 16.52) = 15.82, p < .001$ (H-F Criterion), with the majority of errors being committed at 100ms SOA ($M = 16.82\%$, $SE = 4.04$) with similar percentages executed at 300ms ($M = 5.12\%$, $SE = 1.93$) and 800ms SOA ($M = 3.38\%$, $SE = .98$). The main effect of Congruency did not reach significance and nor did the interaction ($F_s < 1.00$).

A second ANOVA excluding neutrals produced very similar results, with still no effect of Congruency and no significant interaction ($F_s < 1.00$).

4.5.3 Anticipations

The frequency anticipatory saccades made during the period after the onset of the cue, but before the onset of the target, were calculated per condition per participant. Only 31 anticipations were made, accounting for 1.84% of trials. 27 out of the 31 anticipatory saccades were small ($< 2.00^\circ$) and so for the following analysis a distinction was not made between small and large anticipations unlike in the previous experiments, to add statistical power to the analysis.

A 2 way repeated measures ANOVA was conducted on these frequency data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction

(same, opposite). Neither of the main effects nor the interaction approached significance (p s > .200).

4.5.4 Pre-saccadic fixation position

SRT data

The mean fixation position on the x axis, measured in pixels, prior to the response on each completed trial was calculated per condition for each participant. A 2 way, repeated measures ANOVA was conducted on the data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue Direction (left, right). The mean fixation position was 511.54.

Neither of the main effects reached significance, although the interaction between SOA and Cue Direction approached significance, $F(2,26) = 2.68$, $p = .087$, with participants' fixation position seemingly unaffected by the cues at the shorter SOAs (M s = 511, SE s < 1.31) but with a small difference between left and right cues at 800ms SOA, albeit in the opposite direction to the cues (left: $M = 513.17$, $SE = 1.39$; right: $M = 510.54$, $SE = 1.71$).

All data

A further analysis was conducted on the mean fixation position at the time of target onset of all trials. A 2 way, repeated measures ANOVA was conducted on the data with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue Direction (left, right). The mean fixation position was 512.13.

Neither of the main effects or the interaction approached significance ($F_s < 1.2$). As in Experiment 5a, these analyses indicate that people did not tend to fixate in the direction of the cue.

In summary, the cue-target congruency of the directional word cues used in the pro- and anti-saccade tasks had no effect on SRT or error rates. There was a main effect of SOA on SRT in both experiments, with participants quicker to respond as SOA lengthened. There were minimal effects of the cue on direction of anticipatory saccades, with a marginally significant interaction between SOA and direction of large anticipations in the pro-saccade task, with participants making more anticipatory saccades in the direction of the cue than in the opposite direction at 800ms SOA only. There were no effects of cue direction on anticipatory saccades in the anti-saccade task. There were also no effects of cue direction on fixation position at the start of the trials in either experiment.

4.6 Discussion

Experiment 5a investigated the influence of uninformative directional word cues on performance in a pro-saccade task. The preceding experiments have shown that both uninformative arrow and gaze cues can facilitate responses to the cued location in pro-saccade tasks and it was therefore suggested that perhaps any familiar directional cue could elicit this effect. For this reason directional word cues LEFT and RIGHT were compared with a neutral letter string XXXX in the same pro-saccade paradigm used in Experiment 1.

The results from Experiment 5a demonstrate that directional word cues do not influence saccadic responses in the same way as arrow and gaze cues do. There was no SRT facilitation for trials where cue and target were congruent. However, an influence of the cues on anticipatory saccades made in the period before the target appeared, although

small in comparison to those seen with gaze and arrow cues was present. Generally, fewer of these anticipations were made, and there was no influence of the cue direction on the rate of small anticipatory saccades. However there was small effect at 800ms for large anticipations, with participants making more saccades in the direction of the cue than in the opposite direction. The fact that these saccades were made only at 800ms SOA, and not at the earlier SOAs as seen with gaze and arrow cues in the preceding chapter, suggests that they were not occurring automatically. Participants may have been attempting to improve their performance by using the cues to try to predict the location of the upcoming target, despite being instructed to ignore them. In summary, although the word cues had no effects on SRTs, they still appeared to influence saccadic behaviour at some level, evident in the increased rate of anticipatory saccades made in the direction of the cues given a long enough SOA.

Experiment 5b aimed to examine the effects of the directional word cues used in Experiment 5a on performance in the anti-saccade task. As the pro-saccade task in the previous experiment showed much diminished effects of directional word cues on saccadic responses relative to the arrow and gaze cues used in the first two chapters, it was anticipated that the word cues would have similarly reduced effects in the anti-saccade task. In fact, uninformative directional word cues seem to have very little influence on participants' oculomotor responses in an anti-saccade task. Indeed, unlike in Experiment 2 which used the same anti-saccade task with gaze and arrow cues, the word cues used here had no facilitatory effect of SRTs nor did they influence rates of erroneous pro-saccades. Furthermore, the cues did not cause participants to execute any anticipatory saccades in the cued direction during the period between cue and target onset in this anti-saccade task. Fixation position prior to the start of the trial was also unaffected by the cues on the whole,

with a trend at 800ms SOA for participants to fixate slightly in the opposite direction to the cue before the start of the trial.

As in the previous chapter, an effect of task set is suggested by the results of Experiments 5a and b in the current chapter. Just as in the anti-saccade task with gaze and arrow cues of Experiment 4, a reduction in the frequency of anticipatory saccades was observed in the anti-saccade task with words in comparison to the pro-saccade version of the task (4.46% with pro-saccades compared with 1.84% with anti-saccades), with a small influence of cue direction on the direction on anticipatory saccades occurring only in the pro-saccade task. This reduction in saccadic activity further suggests that the increased cognitive involvement required to complete an anti-saccade task may act to inhibit the oculomotor system prior to the onset of the target. It is also noteworthy that the overall rates of anticipatory saccade were lower than in the previous pro- and anti-saccade experiments with gaze and arrow cues. However, it is possible that this may reflect the difference in procedure between Experiments 3 and 4 compared with the current experiment, rather than a difference between the influence of the cues on oculomotor behaviour: The majority of the anticipations were executed in the gap condition in Experiments 3 and 4, a condition which was not used in the current experiment. Furthermore, as different groups of participants were used in each experiment, this result may simply reflect between subject variability.

The findings of Experiments 5a and 5b contradict those of several other investigations of the influence of word cues on attention and eye movements. Recent work by Altman and colleagues (Altman, 2011; Kamide, Altmann, & Haywood, 2003) has demonstrated that words about visual scenes presented auditorily can influence eye movements towards corresponding elements of the scene within 100ms. Furthermore,

neural connectivity between areas of the cortex known to be involved in language and those responsible for action have been identified, particularly for action words (Pulvermüller, 2005), which presumably could extend to words with directional meaning. In terms of attentional orienting, several studies have indicated that directional words are processed automatically and cause automatic orienting of covert attention (Ho & Spence, 2006; Hommel et al., 2001) and saccadic responses (Hodgson et al., 2009). The reason for such contrasting results in the experiments using task-irrelevant words reported here is not clear. However, in Hodgson et al.'s (2009) task, although told to ignore the meaning of the word, participants were required to attend to the word's print colour in order to initiate a saccade to a square of corresponding colour. This contrasts with the instruction in the current experiments which is to ignore the word entirely. The use of task *relevant* cues in Hodgson et al.'s task may have been responsible for the automatic execution of saccades in the direction of the stimulus. It is of note that in Hommel et al.'s (2001) target localisation and detection tasks and in the Ho and Spence (2006) study, although the cues were nonpredictive, participants were not explicitly told to ignore the word cues.

In conclusion, Experiments 5a and 5b demonstrated that not all cues with spatial meaning are able to cause automatic activation of saccadic responses. Task irrelevant word cues LEFT and RIGHT had very little influence on participants' performance in pro and anti-saccade tasks. It is therefore questionable that the reason the gaze cues, and to a lesser extent the arrow cues examined so far in this thesis, appear to automatically facilitate saccadic responses is solely because they are acting via over-learned stimulus responses associations, or similar findings should have been seen with word cues.

The following experiments will investigate the possibility that social and biological relevance is the key to causing the automatic influence on oculomotor behaviour seen with gaze cues. Experiments 6a and 6b will repeat the pro- and anti-saccade tasks carried out with other cues, but this time, with finger pointing cues.

Experiment 6a: Pointing cues and pro-saccades

4.7 Method

4.7.1 Design

This experiment had a 2 way, repeated measures design with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent). The primary dependent measure was saccadic reaction time (SRT). Directional errors were also measured. As with the previous experiments, the frequency of anticipatory saccades and the mean fixation position prior to the onset of the target were also calculated.

4.7.2 Participants

Seventeen healthy undergraduates and postgraduates from the University of Exeter (12 female) aged between 18 and 38 years ($M = 21.76$ years; $SD = 4.92$) took part in this experiment in exchange for £4. All participants had either normal or corrected to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

4.7.3 Apparatus and Materials

Apparatus and materials were identical to those of Experiments 5 with the exception of the stimuli used as cues.

The finger pointing cues were prepared in Corel Paint Shop Pro X and were comprised of photographs of a hand pointing left or right on a white background. The right hand cue was a mirror image of the photograph taken for the left hand cue to control for variations in stimulus properties. The particular hand used for the stimuli was chosen on the basis that it was not obviously either male or a female. To match the stimuli's perceptual

properties as closely as possible to those used in the previous experiments, the colour, contrast and brightness of the cues were closely matched to the eye gaze cues used in Experiments 1 to 4. The image canvas of the pointing cues was the same size as the eye gaze cues used in Experiments 1 to 4. Figure 4.3 shows the stimuli used in Experiments 6a and 6b.

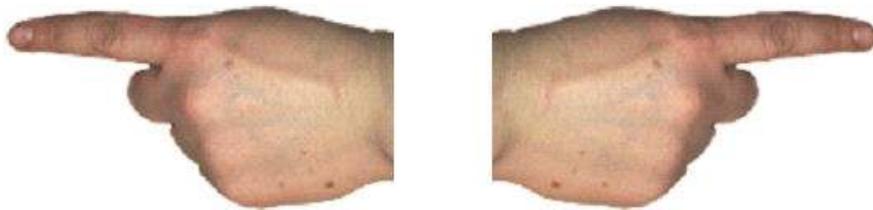


Figure 4.3: Finger pointing cue stimuli used in Experiment 6a and b. Images are not to scale.

4.7.4 Procedure

Participants completed 120 trials split into 2 blocks, following 5 practice trials. As with the preceding experiments, the direction, congruency and SOA conditions were presented randomly with the practice trials excluded from the analysis. The same calibration procedure as used in the previous experiments was carried out at the beginning of this experiment. At the beginning of each block of 60 trials and every 10 trials thereafter, a drift correct procedure was performed. The on screen dimensions of fixation cross, target stimulus diameter and eccentricity were the same as the Experiments 2-5.

4.7.5 Data preparation and analysis

Completed trials were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in the previous experiments. This procedure removed 140 trials representing 6.86% of trials. Practice trials were excluded from the analyses.

4.8 Results

4.8.1 Saccadic reaction time

The mean correct SRT for each participant in each condition was calculated. A 2-way repeated measures ANOVA was performed on correct SRTs, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent).

There was a significant main effect of SOA, $F(1.53, 24.51) = 5.10, p = .021$ (H-F criterion), with SRTs longest at the 300ms SOA ($M = 227.43\text{ms}, SE = 5.80$) and similar SRTs at the shortest and longest SOAs (100ms: $M = 214.71\text{ms}, SE = 6.40$; 800ms: $M = 211.75\text{ms}, SE = 7.99$). There was also a significant main effect of Congruency, $F(1, 16) = 12.72, p = .003$, with participants quicker to correctly respond on congruent trials (congruent: $M = 213.63\text{ms}, SE = 5.94$; incongruent: $M = 222.30\text{ms}, SE = 6.46$). There was also a significant interaction between the two factors, $F(2, 32) = 8.06, p = .001$. Table 4.2 below displays the means, standard errors and p and t values for t tests conducted on congruent/incongruent pairs at each of the SOAs. The congruency advantage was significant at both the 100 and 300ms SOAs, but not at 800ms SOA. Figure 4.7 on page 167 shows SRTs on congruent and incongruent trials across the 3 SOAs.

SOA (ms)	Mean Congruency advantage (ms)	Standard Error	<i>t</i>	Significance (2 tailed)
100	16.47	5.41	3.05	.008
300	17.38	4.42	3.93	.001
800	7.83	4.44	1.76	.097

Table 4.2: Mean congruency advantage, *t* values and significance values at the 3 SOAs for pointing cues in the anti-saccade task of Experiment 6a.

4.8.2 Error rates

Only 1 error was committed.

4.8.3 Anticipations

The frequency of small and large anticipatory saccades made in the same and opposite direction to the cues, during the period after the onset of the cue but before the onset of the target, were calculated using the procedure detailed in Experiment 3. Anticipations were made on 12.11% of trials.

Large anticipatory saccades

111 large saccades (> 2.0° amplitude) were executed during this period, representing 5.44% of trials. A 2 way repeated measures ANOVA was conducted on these frequency data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction (same, opposite).

There was a significant main effect of SOA, $F(1.94, 31.09) = 13.75, p < .001$ (H-F criterion), with the rate of anticipations increasing as SOA increased. There was also a main effect of Direction, $F(1, 16) = 17.17, p = .001$, with more anticipations in the same direction as the cue ($M = 2.00, SE = .45$) than in the opposite direction ($M = .18, SE = .12$). The interaction between SOA and Direction was also significant, $F(2, 32) = 9.11, p = .001$, which appears to be the result of a greater difference between the frequency of large anticipatory saccades as the SOA lengthens. Figure 4.4 shows the interaction between SOA and Direction.

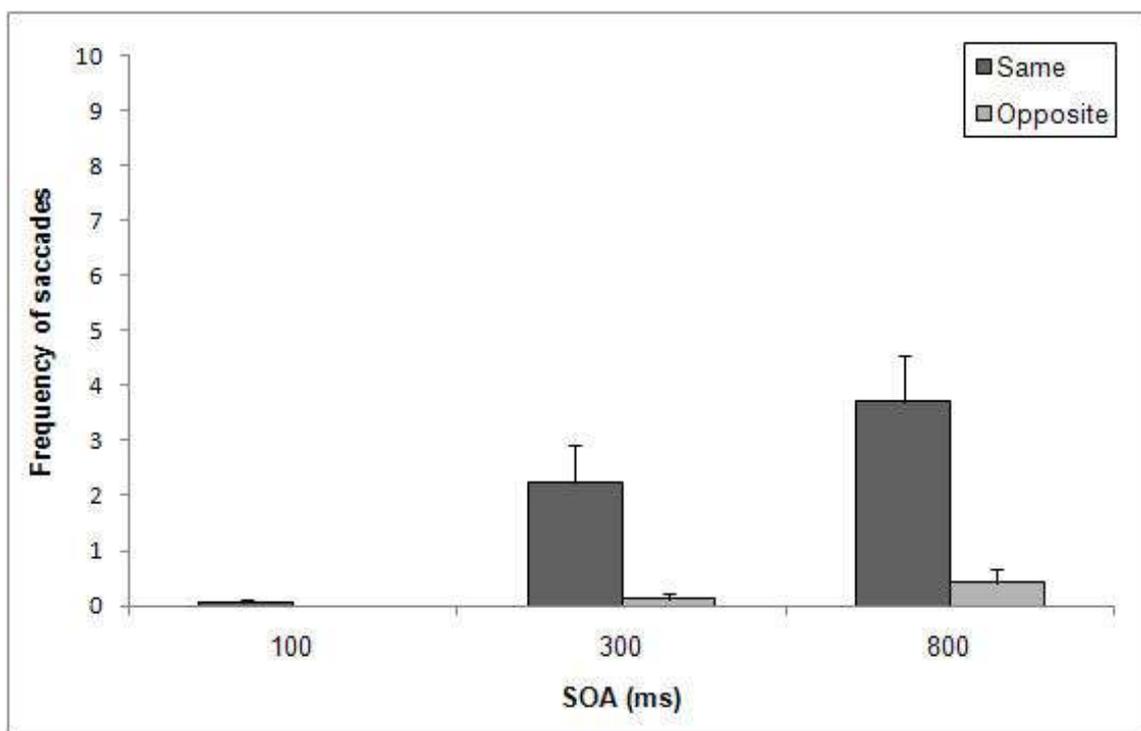


Figure 4.4: The frequency of large anticipatory saccades made in the same and opposite directions to the pointing cues over the 3 SOAs, (pro-saccades). Error bars represent standard error of the mean.

Small anticipatory saccades

136 small saccades ($0.05 - 1.99^\circ$ amplitude) were executed during this period, representing 6.67% of trials. A 2 way repeated measures ANOVA was conducted on these frequency data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue Direction (same, opposite). There was a significant main effect of SOA, $F(1.22, 19.51) = 5.75, p = .021$ (H-F criterion), with the rate of small anticipations increasing as SOA increased (100ms: $M = .03, SE = .03$; 300ms: $M = 1.38, SE = .50$; 800ms: $M = 2.50, SE = .98$). However there was no effect of Direction, $F(1, 16) = 2.16, p = .161$, and the interaction was also not significant.

4.8.4 Pre-saccadic fixation position

SRT data

As in Experiment 3 and 4, the mean fixation position on the x axis, measured in pixels, prior to the response on each completed trial was calculated per condition for each participant. A 2 way, repeated measures ANOVA was conducted on the data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue direction (left, right). Overall, there was a slight bias to the right, with a mean fixation position of 511.16 (the centre of the screen was 510). There was a main effect of Cue direction, $F(1, 16) = 6.44, p = .022$, with participants fixating 1 pixel towards the right of the mean with rightwards cues ($M = 512.0, SD = 1.23$) and 1 pixel towards the left of mean with leftward cues ($M = 510.47, SE = 1.21$). There was also a marginally significant interaction between Cue direction and SOA, $F(2, 32) = 3.42, p = .045$, which seems to be due to a greater

difference between fixation position with left and right cues occurring at the 800ms SOA.

Figure 4.5 shows the interaction between SOA and Cue direction.

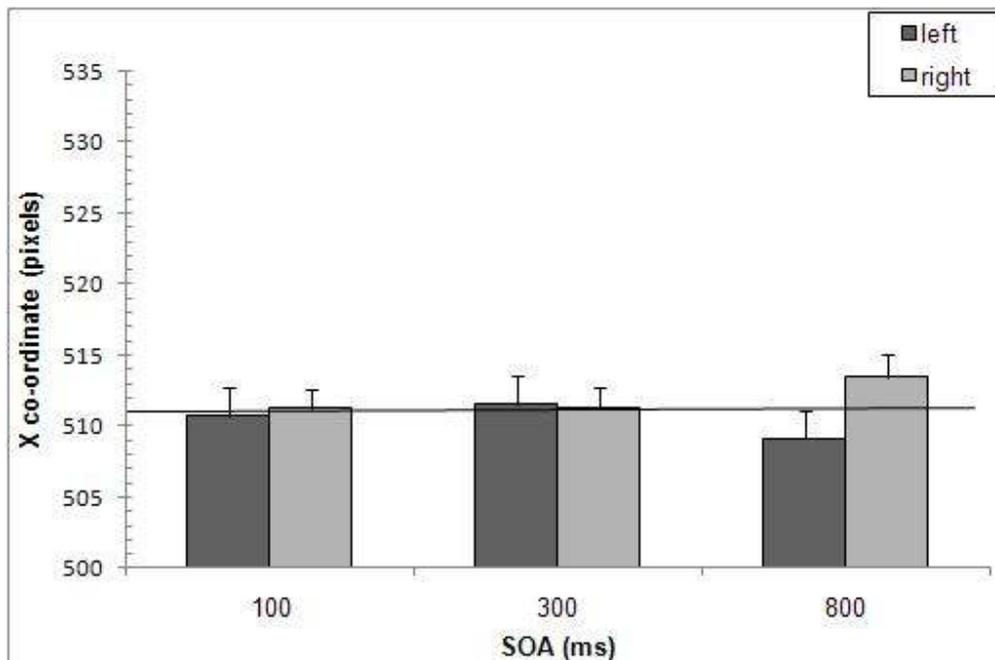


Figure 4.5: Mean fixation positions on the X axis with left and right pointing cues prior to trials entered into the SRT analysis. The horizontal line represents the mean overall fixation position. The error bars represent standard error of the mean.

All data

A further analysis was conducted on the mean fixation position at the onset of the target, for all trials. A 2 way, repeated measures ANOVA was conducted on the data with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue direction (left, right). Again there was a slight fixation bias to the right ($M = 512.66$). There was a significant main effect of Cue direction, $F(1, 16) = 7.40$, $p = .015$ with participants fixating towards the right with rightward cues ($M = 517.14$, $SE = 2.79$) and towards the left with

leftward cues ($M = 508.45$, $SE = 1.59$). There was also a significant interaction between SOA and Cue direction, which seemed to reflect a greater difference between left and right cue fixation position in the 800ms SOA, as with the analysis of SRT fixation position.

Figure 4.6 shows this interaction.

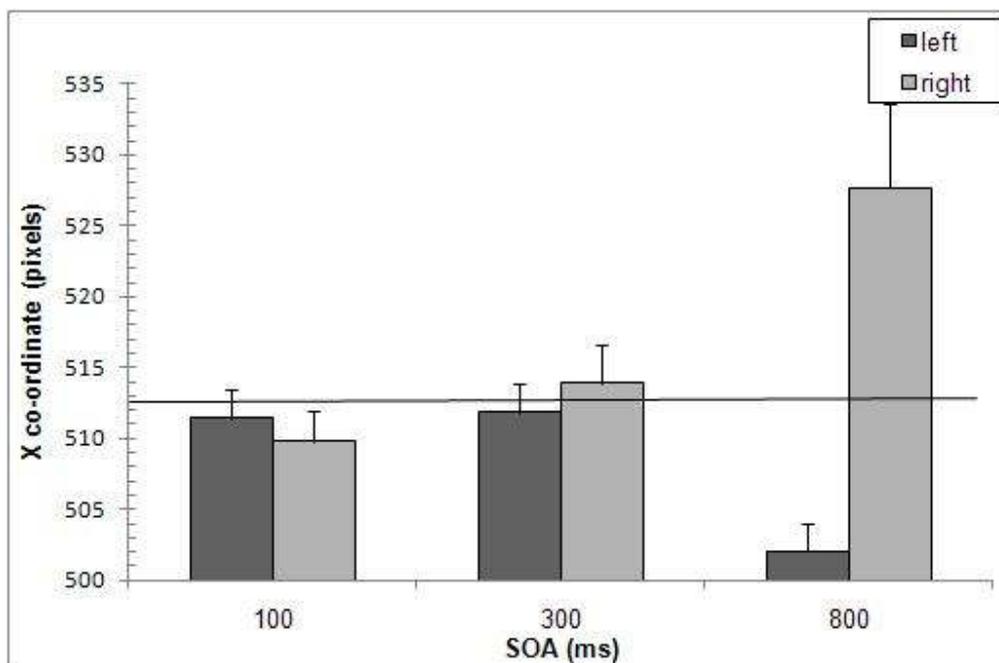


Figure 4.6: Mean fixation positions on the X axis with left and right pointing cues prior to all trials. The horizontal line represents the mean overall fixation position. The error bars represent standard error of the mean.

In summary, the pointing cues used in Experiments 6a caused a congruency advantage at 100 and 300 ms SOAs. People made more large anticipatory saccades in the direction of the cue than in the opposite direction, particularly at the longer SOAs. In addition, people tended to fixate in the direction of the cue at the start of the trial at the longer SOAs.

Experiment 6b: Pointing cues and anti-saccades

4.9 Methods

4.9.1 Design

This experiment had a 2 way, repeated measures design with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent).

The primary dependent measure was saccadic reaction time (SRT). Directional errors were also measured. Again, the frequency of anticipatory saccades and the mean fixation position prior to the onset of the target were also calculated.

4.9.2 Participants

A different group of seventeen healthy undergraduates and postgraduates from the University of Exeter (12 female) aged between 18 and 38 years ($M = 21.35$ years; $SD = 3.61$) took part in is experiment in exchange for £4. All participants had either normal or correct to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

4.9.3 Apparatus and Materials

Apparatus and materials were identical to those of Experiments 6a.

4.9.4 Procedure

The procedure was identical to Experiment 6a, with the exception of task instruction. This time, participants were asked to look in the opposite direction to the target as quickly and as accurately as possible.

4.9.5 Data preparation and analysis

Completed trials were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in the previous experiments. This procedure removed 127 trials representing 6.23% of the total number of trials. Data from practice trials were excluded from the analyses.

4.10 Results

4.10.1 Saccadic reaction time

The mean correct SRT for each participant in each condition was calculated. A 2-way repeated measures ANOVA was performed on correct SRTs, with 2 levels on the factor 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent).

There was a significant main effect of SOA, $F(2, 32) = 44.04, p < .001$ (H-F Criterion), with responses getting faster as SOA increased. There was also a main effect of Congruency, $F(1, 16) = 56.75, p < .001$, with congruent trials significantly faster than incongruent (congruent: $M = 259.79\text{ms}, SE = 5.86$; incongruent: $M = 275.62\text{ms}, SE = 6.72$). The interaction between SOA and Congruency was also significant, $F(2, 32) = 9.92, p < .001$. Table 4.3 displays the means, standard errors and p and t values for t tests conducted

on congruent/incongruent pairs at each of the SOAs. Although significant at both the 100 and 300ms SOAs, the congruency effect is considerably larger at 100ms.

Figure 4.7 shows the mean correct SRTs for congruent and incongruent pointing cues over the 3 SOAs, for both Experiment 6a (pro-saccades) and Experiment 6b (anti-saccades).

SOA (ms)	Mean Congruency advantage (ms)	Standard Error	<i>t</i>	Significance (2 tailed)
100	30.92	4.31	7.18	<.001
300	11.22	4.44	2.53	.022
800	5.35	3.34	1.60	.129

Table 4.3: Mean congruency advantage, *t* values and significance values at the 3 SOAs for pointing cues in the anti-saccade task of Experiment 6b.

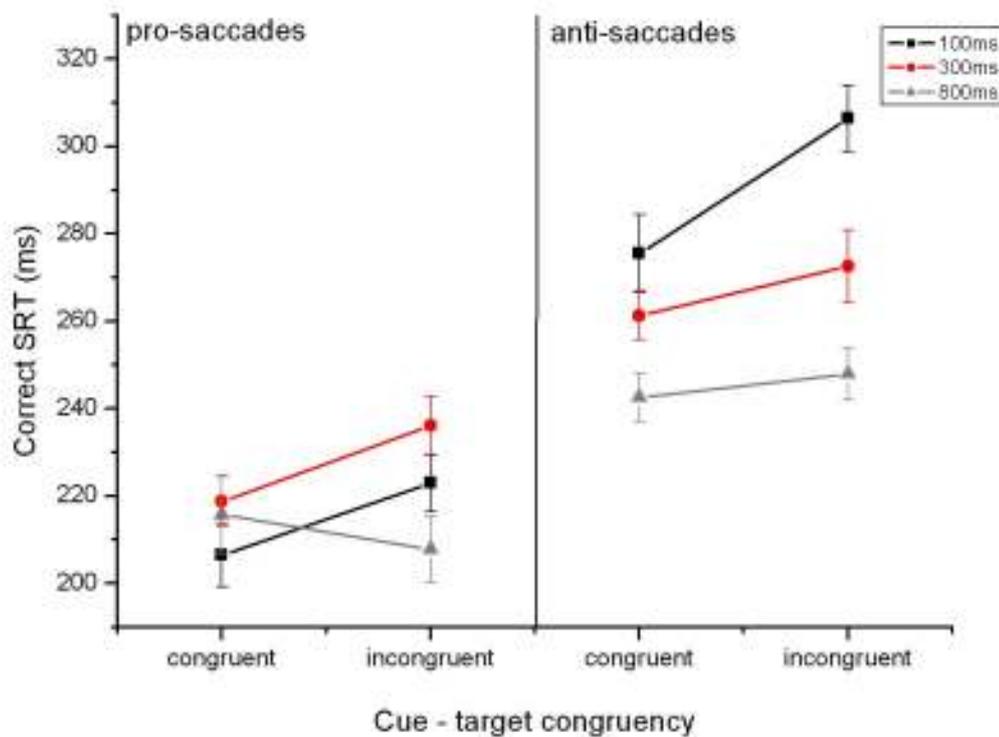


Figure 4.7: Mean correct SRT for congruent and incongruent pointing cues over the 3 SOAs for pro-saccades (Experiment 6a) and anti-saccades (Experiment 6b). Error bars represent standard error of the mean.

4.10.2 Error rates

A total of 96 errors were committed, accounting for 4.70% of the completed trials.

A 2 way ANOVA was conducted on the percentage of errors per condition per participants, with 3 levels on the factor SOA (100ms, 300ms, 800 ms) and 2 levels on the factor Congruency (congruent, incongruent).

There was a main effect of SOA, $F(1.45, 23.16) = 5.41, p = .019$ (H-F Criterion), with error rates decreasing as SOA increased. There was no significant effect of Congruency however, $F(1, 16) = 2.14, p = .163$, although there was a trend for more errors

on incongruent trials than on congruent (congruent: $M = 4.26$, $SE = 1.49$; incongruent: $M = 5.95$, $SE = 2.21$). The interaction was not significant.

4.10.3 Anticipations

The frequency of large ($> 2.0^\circ$ amplitude) and small ($< 2.0^\circ$ amplitude) anticipatory saccades were calculated per participant per condition. 154 anticipations were made in total, occurring on 7.55% of trials.

Large anticipatory saccades

72 large anticipatory saccades were made. A 2 way repeated measures ANOVA was conducted on these frequency data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction (same, opposite). There was a significant main effect of SOA, $F(1.41, 22.62) = 8.55$, $p = .004$ (H-F Criterion), with frequency of anticipations increasing as SOA increased. There was no effect of Direction on frequency of large anticipatory saccades ($F = 1.07$), and the interaction was also not significant ($F = 1.03$).

Small anticipatory saccades

80 small anticipatory saccades were executed. A further 2 way repeated measures ANOVA was conducted on these frequency data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction (same, opposite). As with large anticipatory saccades, there was a significant main effect of SOA, $F(1.58, 25.29) = 19.83$, $p < .001$ (H-

F Criterion), with frequency of anticipations increasing as SOA increased. Also as with large anticipatory saccades, there was no effect of Direction ($F < 1.00$) and the interaction was again not significant ($F < 1.00$).

4.10.4 Pre-saccadic fixation position

SRT data

The mean fixation position on the x axis, measured in pixels, prior to the response on each completed trial was calculated per condition for each participant. A 2 way, repeated measures ANOVA was conducted on the data, with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue direction (left, right). The mean fixation position was 510.27. There was a significant main effect of SOA, $F(1.88, 30.01) = 4.32, p = .025$ (H-F Criterion), with participants fixating towards the left at 100ms ($M = 509.30, SE = .95$) and 300ms SOA ($M = 509.75, SE = .89$), and towards the right at 800ms SOA ($M = 511.77, SE = 1.02$). There was no effect of Cue direction on fixation position, $F(1, 16) = 1.14, p = .301$ and the interaction was not significant ($F < 1.00$).

All data

A further analysis was conducted on the mean fixation position at the onset of the target, regardless of whether the subsequent saccade met the SRT criteria of amplitude, SRT and direction. A 2 way, repeated measures ANOVA was conducted on the data with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue direction (left, right). The mean fixation position was 511.42. None of the main effects or interactions reached significance, and taken together with the analysis of fixation position prior to completed trials only, these results demonstrate that people did not tend to fixate in the direction of the cues prior to the start of the trial.

To summarise, the pointing cues used in Experiment 6b caused a congruency advantage at 100 and 300 ms SOAs. There was no significant effect of the direction of the cues on error rates although there was a trend for more errors on incongruent trials. The cues had no effects on the rates of anticipatory saccades in this anti-saccade task nor did they affect the fixation position at the start of each trial.

4.11 General Discussion

Experiment 6a investigated the influence of uninformative hand pointing cues on performance in a pro-saccade task. It was found that as with the gaze and arrow cues in Experiment 1, pointing cues resulted in a facilitation of saccadic responses in the cued direction. Moreover, the facilitation occurred at short, but not long SOAs. In addition, people made large anticipatory saccades in the direction of the cues at 300 and 800ms SOAs, and there was a tendency for participants to fixate in the direction of the cue at the longest SOA.

That the congruency advantage emerged at the shortest SOAs indicated that the cues were being processed automatically, despite the explicit instruction to ignore them. This contrasts with the findings from Experiment 1, where there was no change in the congruency advantage over the 3 SOAs. The cueing effect found here with pointing cues was substantially larger than in Experiment 1 and the effect seen here at 300ms is also larger than that for gaze and arrow cues in the simultaneous condition of Experiment 3 (which has the same stimulus presentation parameters as the 300ms SOA in the current experiment). However, some caution must be exercised in comparing the magnitude of the congruency effects across experiments which differ in both participants making up the

sample and procedure (the current experiment not employing neutral cues). Nevertheless, the results from SRTs in Experiment 6a show that finger pointing cues produced a rapidly emerging congruency advantage despite the instruction to ignore them.

The pointing cues also caused large spontaneous saccadic movements to be initiated in their direction before the onset of the target. This further suggests an activation of a saccadic programme in response to viewing pointing cues. The fact that these saccades did not occur exclusively at the longest SOAs suggests that they may have been produced automatically in response to the cue, rather than as a strategic attempt to pre-empt the location of the target. Regardless of the time period required to initiate these anticipatory saccades, the participants had been instructed to ignore the cues, but it is apparent that this was not possible in all cases. However, an alternative interpretation of this effect of cue direction on anticipatory saccades may be that participants were looking towards the end of the finger of the pointing cue whilst they were supposed to be fixation on the central cross. The cues subtended 5.52° of visual angle, meaning that either side of the fixation cross the cue subtended 2.26° of visual angle, with saccades greater than 2.00° considered large anticipatory saccades. If this was the reason for the greater frequency of saccades in the direction of the cues, the mean amplitude of the saccades would be expected to be in the region of 2.26° . However, post-hoc analysis of the data revealed that the the mean saccade amplitude of large anticipatory saccades made in the direction of the pointing cues was 8.98° , considerably outside of the cue stimulus region, meaning this possibility can be confidently rejected.

A further finding demonstrating that the cues influenced oculomotor programming was that there was a tendency for participants to fixate an area of the screen in the direction of the cues at the start of the trial. This was particularly evident when all trials, correctly

completed or not, were considered. The reason some of these trials would have been excluded from the SRT analysis is precisely because the participant was fixating an area outside the central region of the screen at the start of the trial. However this effect was only statistically significant at the 800ms SOA, which was the only condition not to show a SRT advantage for congruent over incongruent trials. It is therefore not possible that the observed fixation bias in the cued direction is responsible for the congruency advantage observed at the shorter SOAs.

Experiment 6b examined the effects of hand pointing cues on anti-saccade task performance. Participants were quicker to make correct anti-saccades in the opposite direction to the cues (when cue and target were congruent). This effect is qualitatively analogous to those found with gaze cues in Experiment 2 (anti-saccades) and both gaze and arrow cues in Experiment 4 (gap anti-saccades). The cueing effect seen here was present at both shorter SOAs, but was substantially larger at 100ms, indicating that the cues were acting automatically given such a short cue-target interval. There was no significant effect of cue congruency on error rates, although there was a suggestion of a trend for more errors on congruent trials. Unlike in the pro-saccade task with pointing cues, there were no effects of cue direction on the rate of either small or large anticipatory saccades made during the period after the onset of the cue but before the onset of the target. In addition, there was no fixation bias apparent in this anti-saccade task. To summarise, despite the congruency effect on SRT, the pointing cues had little effect on spontaneous oculomotor behaviour in the anti-saccade task.

The finding that the pointing cues used in the current chapter produced markedly different results in the pro and anti-saccade tasks, suggests, as in Experiments 3 and 4 (gap pro- and anti-saccade tasks) that task set may have a profound influence of the degree to

which uninformative cues can influence saccadic behaviour. Whereas in the pro-saccade task, the participant is prepared to make a saccade towards a sudden onset stimulus as soon as it appears, in the anti-saccade task, this reflexive saccade must be suppressed in favour of a reprogramming of an anti-saccade to the mirror image location. This suppression of the reflexive saccade is thought to occur via cognitively modulated increase in activity of fixation neurons in the SC (Everling, Dorris, Klein, & Munoz, 1999; Munoz & Wurtz, 1992), and this mechanism is also a likely candidate for the reduced rate of spontaneous saccadic activity seen in anti-saccade tasks relative to pro-saccade tasks, observed thus far in this thesis.

The finding that pointing cues can influence attentional mechanisms is not without precedent. Uninformative pointing cues have been shown to cause an automatic congruency advantage at short SOAs in covert target detection tasks (Ariga & Watanabe, 2009; Sato et al., 2009, 2010; Tomonaga & Imura, 2009) and were shown to cause Stroop-like interference when presented together with auditory directional cues (Langton, O'Malley, & Bruce, 1996) and head/gaze cues (Langton & Bruce, 2000). Furthermore, the STS has been shown to be activated by social cues other than eyes gaze such as head and body orientation (Puce & Perrett, 2003) but also finger pointing (Materna, Dicke, & Thier, 2008; Sato et al., 2009). As already discussed, orienting to the pointing of adults is an important ability in the development of joint attention in infants (Gliga & Csibra, 2009; Scaife & Bruner, 1975; Woodward & Guajardo, 2002) and may also be a predictor of language development (Mundy & Gomes, 1998). Indeed, it has been suggested that the reason arrows are used to direct action and attention in the real world is precisely because they look like pointing hands (Eco, 1979; McNeill, 2000) and perhaps this is why they have the qualitatively similar, albeit muted, effect on the oculomotor system to gaze cues reported in this thesis.

It may not be surprising therefore, that the pointing cues in the current experiments exerted automatic influence on oculomotor behaviour in pro and anti-saccade tasks, when they are so clearly a critical communicative medium in the real world. What is surprising however is given the demonstrable importance of pointing, why it has received so little attention in comparison to eye gaze as a social cue, particularly in studies of overt attentional orienting.

4.12 Conclusions

Experiments 5 and 6 have provided evidence for the mechanisms underlying orienting to eye gaze. The results presented here indicate that an arbitrary stimulus-response associative account cannot alone explain the finding that gaze cues and to a lesser extent arrow cues, cause the automatic programming of saccadic eye movements, as directional word cues do not have these automatic effects on oculomotor responses. Rather, it appears that cues require a degree of social-relevance to cause this effect, as finger-pointing cues have the same influence on saccadic responses as eye gaze cues.

Chapter 5: *The role of ecological validity of gaze and arrow cues on automatic orienting in the anti-saccade task*

Experiment 7

5.1 Introduction

Achieving greater ecological validity in the study of symbolic cues was one of the primary aims of this thesis. A challenge for the study of a real-world phenomenon such as spontaneous gaze following in the laboratory is the difficulty in generalising the results obtained in controlled settings to naturalistic behaviour outside the laboratory. As has been noted by Kingstone (2009), the laboratory does not involve the usual complex array of extraneous stimuli one would encounter in a genuine social situation and nor does the participant possess the same motivational factors one would experience if engaging in social interaction with another individual in the real world. It is therefore important that the properties of the experiment which can be increased in ecological validity without impinging on the reliability or validity of the paradigm, are manipulated to maximise their likeness to everyday stimuli and this thesis has strived to achieve this goal.

Contrary to this rationale, several authors have argued that ecological validity, particularly of eye gaze cues, is of little importance in producing automatic orienting of attention and saccades in cueing paradigms. The majority of the oculomotor studies of gaze and arrow cueing to date have used schematic images made of rudimentary black lines and circles (Kuhn & Benson, 2007; Kuhn & Kingstone, 2009; Kuhn et al., 2010) but have claimed that these stimuli are as effective as more naturalistic cues in producing cueing

effects (Kuhn et al., 2010). One study investigated this issue by comparing photographic and schematic gaze cues and found that the schematic cues were as influential in producing congruency effects in a covert spatial cueing paradigm as the more naturalistic cues (Hietanen & Leppänen, 2003). A further study investigating the influence of gaze and arrow cues on saccade trajectories found that photographic and schematic gaze cues had comparable effects on eye movements (Hermens & Walker, 2010).

With the extant literature on oculomotor effects in response to gaze and arrow cues predominantly using schematic cues, the finding in this thesis that in an anti-saccade task, arrow cues have significantly less effect on oculomotor performance than gaze cues, could therefore be attributed to the increased ecological validity of the stimuli used here. However, the only previous study to use anti-saccades used photographic gaze cues only (Koval, Thomas, & Everling (2005). It is therefore not clear whether the findings from the gaze and arrow anti-saccade experiments reported here can convincingly challenge those in the literature which state that people are automatically primed to make saccades in the direction of both averted eye gaze and arrow cues, when both the task and the cue stimuli used here are novel relative to the wider literature. In addition, the rationale that ecological validity is crucial to effectively studying the influence of directional cues may be undermined if schematic cues cause equivalent effects to their real world counterparts.

For these reasons, Experiment 7 assessed the influence of the same schematic eye gaze and arrow cues used in Kuhn and Kingstone (2009) in the anti-saccade task detailed in Experiment 2 of Chapter 2. A repetition of the pro-saccade task with schematic cues was not necessary, as previous research has shown that such cues do cause automatic orienting of attention in both covert (Friesen & Kingstone, 1998; Ristic et al., 2002) and overt versions of this task (e.g. Friesen & Kingstone, 2003). If ecological validity is critical to

effectively studying real-world directional cues in the laboratory, then quantitatively or qualitatively distinct results may be obtained when using schematic cues, in comparison to the anti-saccade tasks with gaze and arrow cues already reported in this thesis. If a similar pattern of results emerges with schematic cues, then the degree to which ecological validity is of importance may be seriously questioned. A qualitatively similar pattern of results to those obtained with the ecologically valid cues would add weight to the findings of this thesis, that imitative saccades in response to gaze or even arrow cues is not an obligatory response, but rather can be modulated by task set.

5.2 Method

5.2.1 Design

This experiment had the a 2 way, repeated measures design with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent). The primary dependent measure was saccadic reaction time (SRT). Directional errors were also measured. The frequency of anticipations during the period between the onset of the cue and the onset of the target was measured, in addition to the fixation position at the start of the trial.

5.2.2 Participants

Seventeen healthy undergraduates and postgraduates from the University of Exeter, (11 female) aged between 18 and 26 years ($M = 20.18$ years; $SD = 1.94$) took part in is experiment in exchange for £4. All participants had either normal or corrected to normal vision. Written informed consent was given by all participants and ethical approval for this

experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

5.2.3 Apparatus and Materials

Apparatus and materials were identical to those of Chapters 2- 4 with the exception of the stimuli used as cues. The schematic cues were created from the descriptions given in Kuhn and Kingstone (2009). Both arrow and gaze cues were drawn using Microsoft Publisher 2007 using black lines and circles on a white background. The arrow cues subtended 4.76° of visual angle, which was also the distance between the pupils of the gaze cues. The whole gaze cue, including surrounding “face” subtended 8.57° of visual angle. The “mouth” of the gaze cue subtended 3.81° of visual angle, the same length as the line of the arrow. The stimuli used in the current experiment can be seen in Figure 5.1

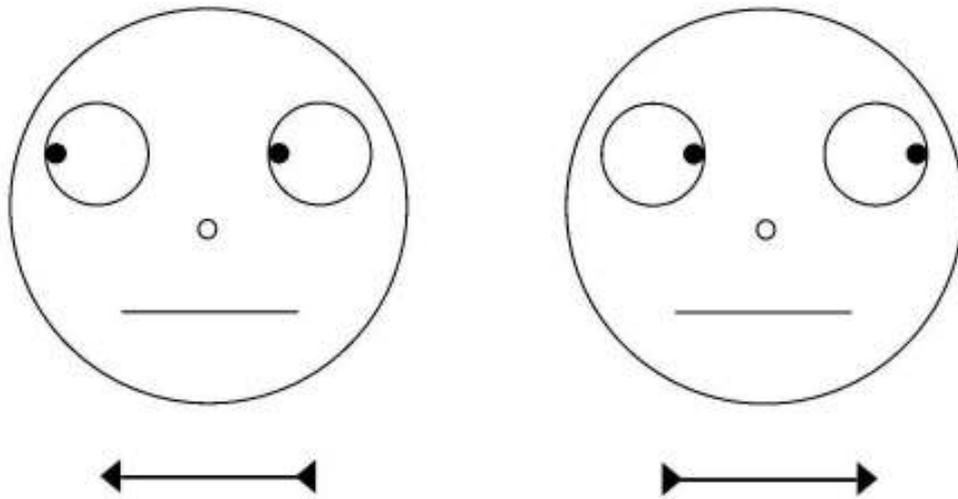


Figure 5.1: Schematic gaze and arrow cues used in Experiment 8, based on Kuhn & Kingstone, 2009. Figures are drawn to scale relative to each other only.

5.2.4 Procedure

The procedure of the current experiment was similar to that of Experiment 2, Chapter 2, with some additions. As in the previous experiments, prior to the start of the experiment, a calibration procedure was performed in order to map raw data into eye gaze position, as in the previous experiments. In addition to this, at the start of each block and every 10 trials thereafter, a drift correct calculation was performed in order to account for any headband slippage in the preceding trials.

The experiment began with 10 practice trials, comprised of selection of the gaze and arrow cue conditions. The experiment was then blocked by the factor cue type (arrow or eye gaze) with one block of 60 trials for each cue type. The order in which the cue types were presented was counterbalanced between subjects to prevent any order effects from

emerging. The SOA and congruency conditions were randomly presented within each block.

All trials were presented on a white background. Each trial began with the presentation of a black central fixation cross subtending 1.26° of visual angle, for the duration of 1000 ms. Following this, the schematic cue was presented on the screen. The arrow cues were presented in the centre of the screen. For the gaze block, the cues were aligned on screen so that the fixation point was located equidistant between the two eyes. After a period of 100, 300 or 800 ms, the target, a black dot with a diameter of approximately $.95^\circ$ of visual angle, was presented. As in the previous experiments, the dot could appear vertically centred at either the left or right of the screen at an eccentricity of 14.75° of visual angle, where it remained for 2000 ms. The target dot appeared on the left and right sides of the screen with equal probability. As with all previous experiments, the participants were instructed to maintain fixation on the central cross and ignore the arrow and gaze cues until the dot appeared, whereupon they were to make a saccade in the opposite direction to the dot as quickly as possible. Participants were informed that the direction to which the arrows or eyes pointed in no way predicted the likely position of the target dot. An interval of 1000 ms separated each trial.

5.2.5 Data preparation and analysis

Completed trials were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in the previous experiments. This procedure removed 178 trials representing 8.73% of trials. Practice trials were excluded from the analyses

5.3 Results

5.3.1 Saccadic reaction time

A 3 way repeated measures ANOVA was conducted on the SRT data with 2 levels on the factor Cue type (arrows, gaze), 3 levels on the factor SOA (100, 300, 800 ms) and 2 levels on the factor Congruency (congruent, incongruent). There was a significant main effect of SOA, $F(1.74, 27.81) = 8.75, p = .002$ (H-F Criterion), with SRTs decreasing as SOAs increased. The main effect of Congruency was also significant, $F(1, 16) = 11.71, p = .003$. There was no main effect of Cue type however ($F < 1.00$). The only interaction to reach significance was the 3 way interaction between Cue type, SOA and Congruency, $F(2, 32) = 3.96, p = .029$. *T*-tests between incongruent and congruent pairs of arrow and gaze cues at each SOA showed that the difference was not significant for any of the gaze cues pairs, but that for arrow cues, the difference was only significant at 100ms SOA, although the difference approached significance at 300ms SOA. Table 5.2 displays the means, standard errors and *p* and *t* values for *t*-tests conducted on congruent/incongruent pairs at each of the SOAs for each cue type. Figure 5.2 shows the mean SRTs with congruent and incongruent arrow and gaze cues over the 3 SOAs.

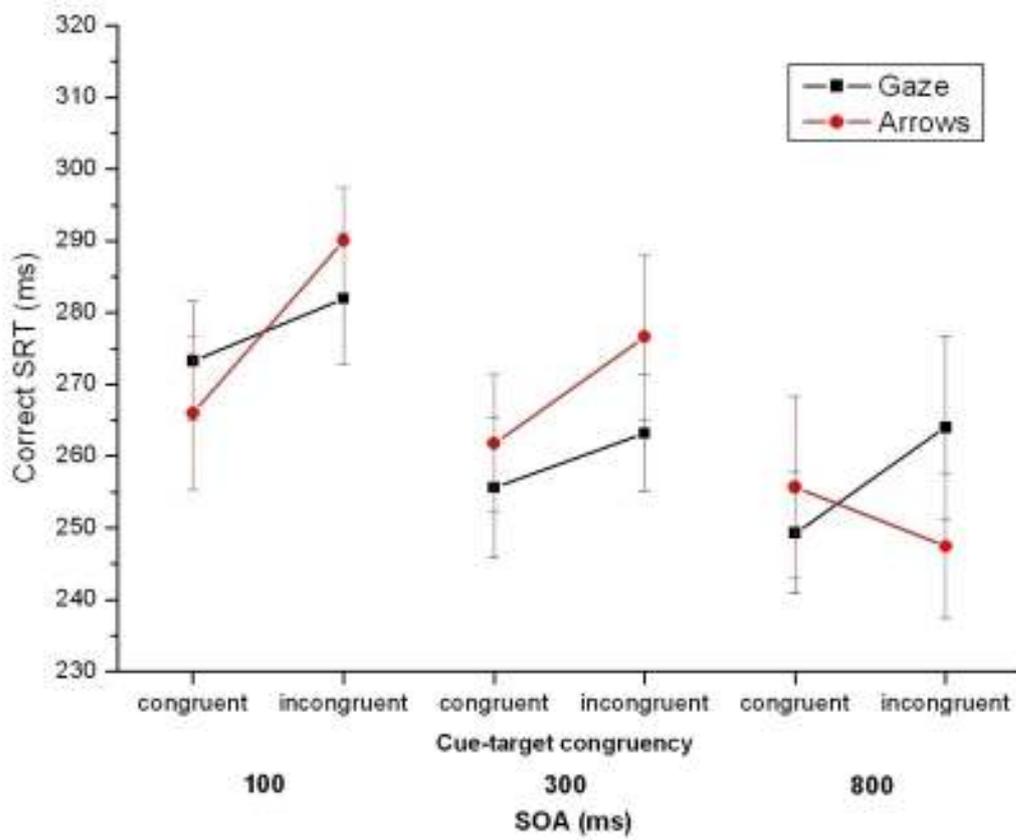


Figure 5.2: Mean correct SRT for congruent and incongruent schematic gaze and arrow cues over the 3 SOAs. Error bars represent standard error of the mean.

Cue type	SOA	Mean Congruency advantage (ms)	Standard Error	<i>t</i>	Significance (2 tailed)
Arrows	100	24.07	9.24	2.60	.019
	300	14.83	7.25	2.05	.058
	800	8.22	7.60	1.08	.295
Gaze	100	8.71	5.08	1.72	.106
	300	7.57	7.76	.98	.344
	800	14.72	8.56	1.72	.105

Table 5.1: Mean congruency advantages, *t* and significance values for schematic gaze and arrow cues over the 3 SOAs.

5.3.2 Error rates

A total of 179 errors were committed, accounting for 9.61% of the completed trials.

A 3 way ANOVA was conducted on the percentage of errors per condition per participant, with 2 levels on the factor Cue type (arrows, gaze), 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent).

There was a significant main effect of SOA, $F(1.70, 27.15) = 12.16, p < .001$ (H-F Criterion), with the majority of errors being committed at 100ms SOA ($M = 14.87\%$, $SE = 2.77$) with similar percentages executed at 300ms ($M = 7.20\%$, $SE = 2.14$) and 800ms SOA ($M = 7.44\%$, $SE = .1.82$). The main effect of Congruency was also significant, $F(1, 16) = 5.37, p = .034$, with more errors produced on incongruent trials ($M = 12.10\%$, $SE = 2.51$) than on congruent trials ($M = 7.60\%$, $SE = 1.96$). There was also a significant interaction

between Cue type and Congruency, $F(1, 16) = 5.12, p = .038$. *T*-tests showed that there was a significant difference between the error rates on congruent and incongruent trials for arrow cues, $t(16) = 2.63, p = .018$, but not gaze cues, $t(16) = .98, p = .341$. Figure 5.3 shows the error rates for congruent and incongruent arrow and gaze cues over the 3 SOAs.

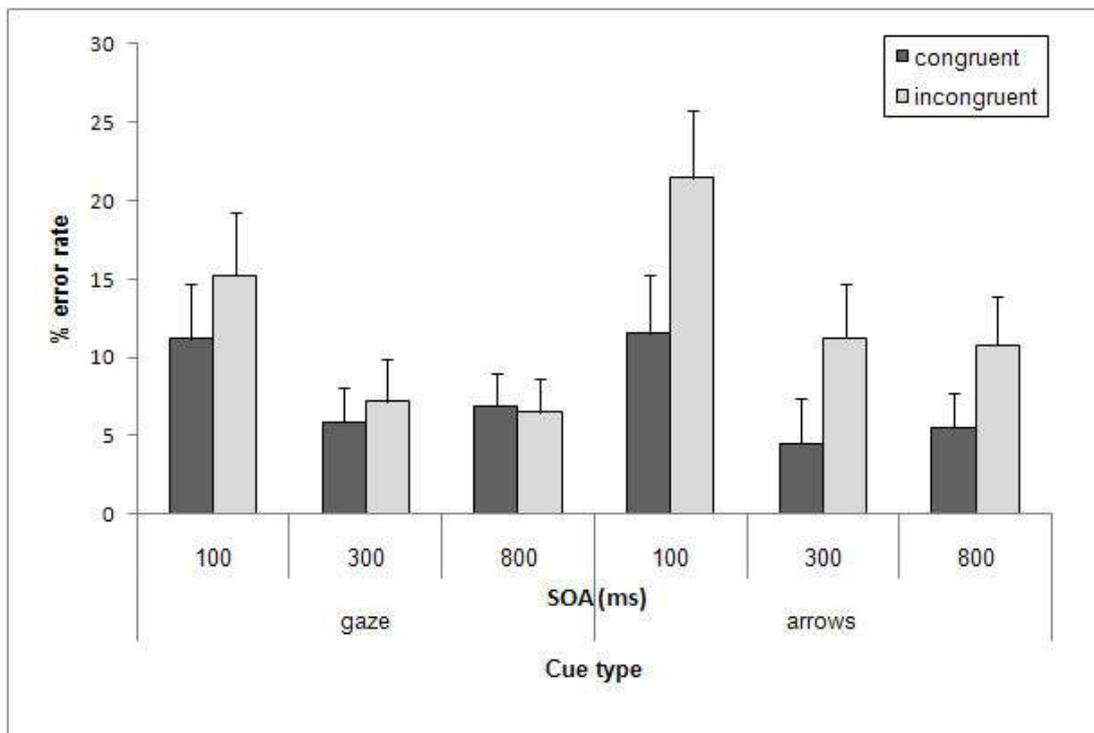


Figure 5.3: Mean error rate per condition, per participant with congruent and incongruent schematic gaze and arrow cues over the 3 SOAs. Error bars represent standard error of the mean.

5.3.3 Anticipations

As with the previous experiments, the frequency of small and large anticipatory saccades made during the period after the onset of the cue, but before the onset of the target, were calculated. 148 anticipations were made in total, accounting for 7.25% of trials.

Large anticipations

83 large anticipatory saccades ($> 2.00^\circ$ amplitude) were made, occurring on 4.07% of trials. A 3 way repeated measures ANOVA was conducted on these frequency data, with 2 levels on the factor Cue type (arrows, gaze), 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction (same, opposite). There was a significant main effect of SOA, $F(1.13, 18.03) = 10.51, p = .004$ (H-F Criterion), which was the result of participants making more anticipatory saccades as the SOA increased. There was also a significant main effect of Direction, $F(1, 16) = 9.57, p = .007$, with more anticipations in the opposite direction to the cue ($M = .60, SE = .15$) than in the same direction ($M = .22, SE = .08$). There was also a significant interaction between SOA and Direction, $F(2, 32) = 4.58, p = .018$. This appears to be the result of a greater difference between the frequency of anticipatory saccades in the same and the opposite direction occurring at 800ms SOA. There were no significant effects of Cue type, indicating that people made no more anticipatory saccades with arrows than gaze cues.

Figure 5.4 shows the rates of large anticipatory saccades in the same and opposite direction to the cues, over the three SOAs.

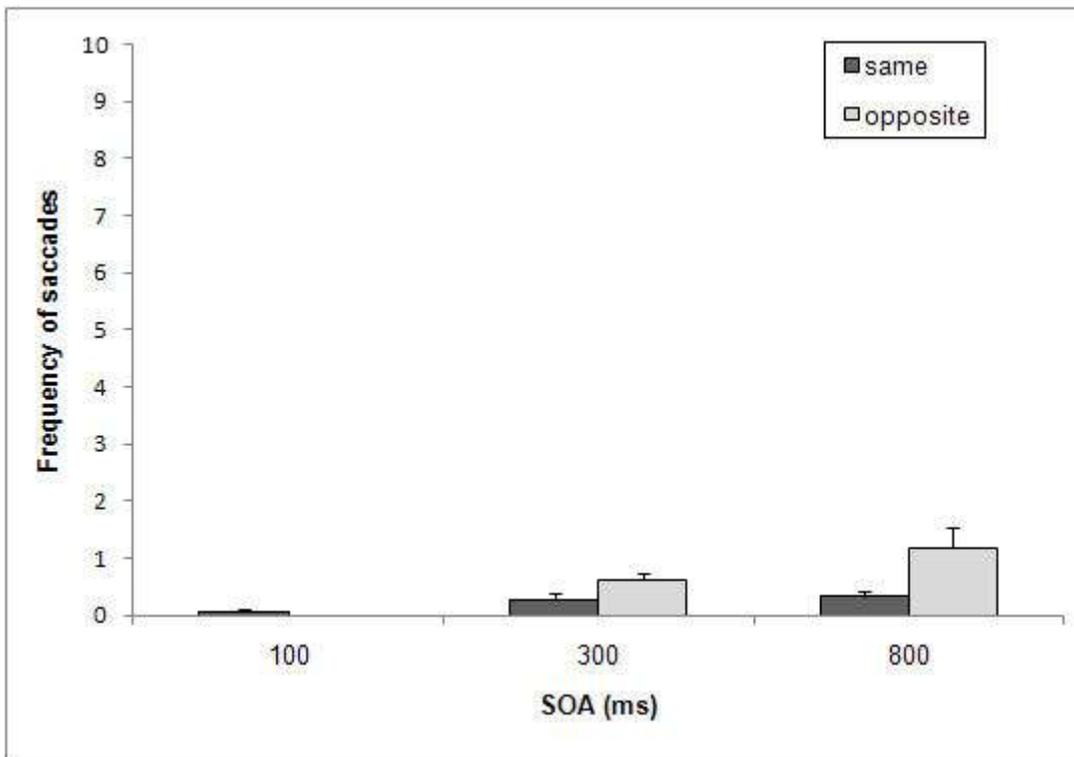


Figure 5.4: Frequency of large anticipatory saccades per participant, in the same and opposite direction to the cues, over the 3 SOAs. Error bars represent standard error of the mean.

Small anticipations

65 small anticipatory saccades (< 2.00 amplitude) were made, occurring on 3.19% of trials. As with the analysis of large anticipatory saccades above, a further 3 way repeated measures ANOVA was conducted on these frequency data, with 2 levels on the factor Cue type (arrows, gaze), 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Direction (same, opposite). There was a significant main effect of SOA, $F(1.21, 19.32) = 7.48, p = .010$ (H-F Criterion), which was the result on participants making more anticipatory saccades as the SOA increased (100ms: $M = .03, SE = .02$; 300ms: $M = .29, SE$

= .08; 800ms: $M = .63$, $SE = .20$). None of the other main effects or interactions reached significance.

5.3.4 Pre-saccadic fixation position

SRT data

The mean fixation position on the x axis, measured in pixels, prior to the response on each completed trial was calculated per condition for each participant. A 3 way, repeated measures ANOVA was conducted on the data, with 2 levels on the factor Cue type (arrows, gaze), 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue Direction (left, right). The mean fixation position was 509.23

The only effect to approach significance was that of Cue type, $F(1, 16) = 4.40$, $p = .052$, with participants tending to fixate more towards the left with gaze cues ($M = 507.91$, $SE = 1.50$), but in the centre with arrow cues ($M = 510.54$, $SE = 1.71$). None of the other main effects or interactions approached significance.

All data

A further analysis was conducted on the mean fixation position at the time of target onset of all trials. A 2 way, repeated measures ANOVA was conducted on the data with 3 levels on the factor SOA (100ms, 300ms, 800ms) and 2 levels on the factor Cue Direction (left, right). The mean fixation position was 506.91.

The main effect of SOA approached significance, $F(1.21, 19.43) = 3.94$, $p = .055$, with participants seeming to fixate towards the left of the screen at the shorter SOAs (100ms: $M = 504.71$, $SE = 3.09$; 300ms: $M = 504.79$, $SE = 4.05$) but more in the centre at 800ms SOA ($M = 511.24$, $SE = 3.49$). There was a main effect of Cue direction, $F(1, 16) = 6.17$, $p = .024$, with people fixating approximately in the centre when the cues pointed left

($M = 509.82$, $SE = 3.30$) but towards the left when the cues pointed right ($M = 504.00$, $SE = 3.54$). There was also a marginally significant interaction between SOA and Cue direction, $F(2, 32) = 3.21$, $p = .053$. This appears to be the result a large difference between the mean fixation positions in the presence of left and rightward cues at the 800ms SOA. Figure 5.5 shows this marginal interaction.

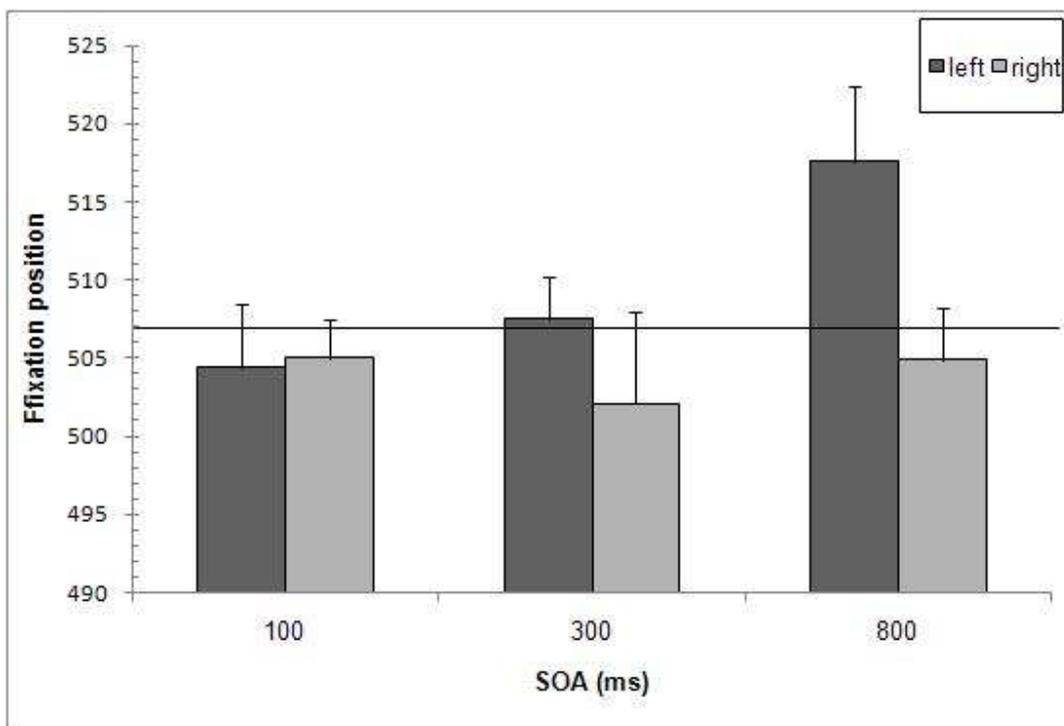


Figure 5.5: Mean fixation position for all trials, with left and rightward cues over the 3 SOAs. The horizontal black line represents the overall mean fixation position. Error bars represent standard error of the mean.

In summary, there was a significant SRT congruency advantage at 100ms which approached significance at 300ms SOA for arrow cues only, with SRTs in the presence of congruent gaze cues no quicker than when they were incongruent. Most errors were committed at 100ms SOA, with significantly more produced on incongruent trials than congruent for arrow cues only. Overall, participants made more large anticipatory saccades

in the opposite direction to the cues, particularly at the longest SOA, but there was no difference in the rates made in the presence of gaze and arrow cues. Participants made more small anticipatory saccades as the SOA increased but the frequencies were not influenced by cue type or direction. In addition, direction of the cues biased the pre-saccadic fixation position in the opposite direction of the cues equally for gaze and arrows.

5.4 Discussion

Experiment 7 sought to ascertain the role of ecological validity of cues in producing automatic orienting, particularly in response to gaze cues. By using the same schematic cues as previous studies investigating oculomotor responses to gaze and arrow cues, the experiment aimed to determine whether the finding that in anti-saccade tasks, participants' responses are generally facilitated in the opposite direction to real-world gaze and to a lesser extent arrow cues also occurs with the schematic versions of the stimuli.

The results from this experiment suggest that ecological validity is an important factor in the production of saccadic responses to gaze cues. Whereas Experiment 2 demonstrated that participants' responses are facilitated in the opposite direction to real-world gaze cues but not arrow cues, in an anti-saccade task, Experiment 7 showed a different pattern of results. The schematic gaze cues had little effect on either participants' correct SRTs or rate of erroneous pro-saccades, whilst the schematic arrow cues influenced SRTs at the shortest SOA only (but approached significance in their effects at 300ms SOA) and error rates at the longer SOAs, facilitating responses in the opposite direction to the cues. In comparison to Experiment 2 then, responses to schematic arrow cues are greater than to real-world arrow cues, whilst responses to schematic gaze cues are reduced when compared to those made in the presence of their more ecologically valid counterparts.

Although the congruency effects were not significant for the schematic gaze cues, they were qualitatively similar to those seen in previous chapters with the photographic gaze cues, with correct SRTs executed when cue and target were congruent being slightly quicker than when incongruent. This indicates that it may be the magnitude of the effect which is influenced by the ecological validity of gaze cues, suggesting that schematic and photographic cues may be influencing the same saccadic generating processes, just to a different degree.

The greater influence of the less naturalistic arrow cues in the current experiment in comparison to the real-world arrow cues used in Experiment 2, requires explanation. A possible interpretation is that as the width of the arrow cues in the current experiment were slightly greater than the road sign cues used in earlier experiments (4.57° of visual angle in Experiment 2; 4.76° Experiment 7), they were more salient and participants were less able to ignore them. A further possibility that as the arrow contained a “head” and a “tail” at exactly the same eccentricities as the pupils of the gaze cues, it may have resembled a pair of eyes more closely than the road sign arrow cues used in previous experiments. It also suggests that ecological validity may only be a critical property of gaze cues. This may not be surprising when one considers the relative improvement in ecological validity for gaze and arrow cues when moving from schematic to real-world versions. The difference between the real-world and schematic gaze cues is clearly evident, but between the two versions of the arrow cues, is less so. Indeed, “real” arrows are inherently schematic, whereas real gaze cues are parts of complex human anatomy. It therefore seems reasonable to expect that a reduction in ecological validity might differentially influence responses to gaze cues.

Participants made large anticipatory saccades in the opposite direction to both gaze and arrow cues during the period prior to target onset. In addition, there was a tendency for people to fixate an area of the screen at the start of the trial which was in the opposite direction to the cues. Taken together, these findings further suggest that the anti-saccade preparatory set (“preparatory set” is used to refer to a pre-adopted readiness to perform a particular action in response to a sensory stimulus: (Connolly, Goodale, Menon, & Munoz, 2002; Everling & Munoz, 2000) may have influenced the saccadic system even before the instruction to make an anti-saccade (i.e. the appearance of the target) had been given. Participants may have been transposing the instruction to “go opposite” onto the first stimulus they saw: The cue. That statistically at least, the preparatory set did not appear to influence responses to the schematic gaze cues during the trial period indicates that the cues were easily ignored during the task itself, in comparison to the more ecologically valid cues in the previous experiments.

In the current experiment, schematic versions of gaze and arrow cues were examined within the same anti-saccade task used in Experiment 2 with the real-world versions of the cue. However, it could be argued that the photographic cues used in the previous experiments themselves lack in ecological validity. After all, not only are the gaze cues comprised of just the eye region of a face but both cue types have been taken out of the “real world” and introduced into controlled experimental paradigms which therefore, it could be argued, lack the extraneous and competing influences experienced during natural, every day behaviour. Indeed, this is an inherent problem in experimental psychology paradigms. Whilst on one side, researchers must attempt to prevent any confounding influences impinging on the isolated process or behaviour under investigation by controlling factors known to do so, on the other side the ultimate goal is to try to study and

understand natural behaviour. Some recent work has attempted to study social attention in real-world settings (Kuhn, Tatler, Findlay, & Cole, 2008) and this is sure to be an avenue of psychological research which is likely to provide advances in our understanding of how humans process and respond to social cues in natural settings.

5.5 Conclusions

In the anti-saccade tasks reported in this thesis in preceding chapters, it has been repeatedly found that participants' responses are facilitated in the opposite direction to gaze cues, and also, but to a smaller degree to arrow cues. Experiment 7 has demonstrated that the reason for this contradiction to the gaze imitation hypothesis can't simply be due to the different stimuli used to most studies in the literature: Schematic arrows have a qualitatively similar effect to the real-world versions and the schematic gaze cues produce facilitation in the same direction as the photographic gaze cues, albeit not to a statistically significant magnitude. Rather, these findings support the suggestion that the task set can influence responses to cues. In addition, they demonstrate that the ecological validity (or biological plausibility) of eye gaze cues is a modulating factor in the magnitude of the automatic saccadic response observed in the anti-saccade task used in previous chapters, but that this property may be less important for arrow cues.

Chapter 6: *The relationship between autistic traits and influence of gaze and arrow cues in males*

Experiment 8

6.1 Introduction

One of the hallmarks of the Autism Spectrum Disorders (ASD) is an impairment in social functioning. One of the earliest manifestations of the disorders in infants is as an inability to engage in joint attention with adults, one aspect of which is spontaneous gaze following (Leekam, Baron-Cohen, Perrett, Milders, & Brown, 1997; Leekam, Hunnisett, & Moore, 1998). The disorders are much more common in men than women, but even in the normal population there is a greater presence of autistic-traits in males. The gender bias has been accounted for by The Extreme Male Brain Theory of autism (Baron-Cohen, 2002), which proposes that ASD lies at the extremity of a continuum of a cognitive style which is typically male.

The Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, et al., 2001) was developed as a method of measuring the presence of autistic traits in the normal population. The AQ is a self report questionnaire consisting of 50 questions relating to social and communication skills, imagination and attention abilities. Participants respond by selecting their answer from a likert-type scale, rating the degree to which they agree with each statement. In their original trial of the AQ, Baron-Cohen et al. (2001) found that 80% of participants with high functioning autism (HFA) or Asperger's Syndrome (AS) scored over 32 out of a possible 50 on the AQ, whereas only 2% of the control group did

so. Typically developed men scored more highly on the AQ than women, but there was also a greater variation in scores in men. Although the authors stressed that the AQ was not intended as a definitive test for ASD, they argued that their findings demonstrated that it was sensitive to the presence of autistic traits and that its brevity and self-report administration made it a useful tool in the diagnosis of ASD, but also in identifying autistic traits in normal populations.

If ASD is an extreme expression of a typically male cognitive style which is impaired in empathising, it might be expected that men would be less influenced by the eye gaze of other people than women. Indeed, Bayliss, Pellegrino, & Tipper (2005) demonstrated that in a covert spatial cueing task, male participants were less affected by gaze cues than females, showing smaller RT congruency advantages. However, males displayed similarly small cueing effects for arrow as well as gaze cues. Men also scored significantly higher than women on the AQ, replicating the gender difference observed in Baron-Cohen et al. (2001) and as is predicted by the Extreme Male Brain theory of autism (Baron-Cohen, 2002). Importantly, Bayliss et al. (2005) found a negative correlation between the congruency advantage caused by gaze cues but not arrow cues, and participants' scores on the AQ, suggesting that the more autistic traits people exhibit, the less affected by the cues they were.

Kuhn et al. (2010) conducted their voluntary saccade task (see (Kuhn & Benson, 2007; Kuhn & Kingstone, 2009) with schematic gaze and arrow cues with both typically developed adults and those with AS and HFA. However, Kuhn et al. (2010) did not enter gender as a variable in their analyses nor even state the relative number of males and females in their control group. Surprisingly, they found equal cueing effects for eye gaze and arrows in both the typically developed group and the ASD group, but found no

correlations between scores on the AQ and cueing by gaze or arrows in either group. However, Kuhn et al. used a small sample size for a correlational analyses, each group (typically developed and ASD) containing only 12 participants. Although Chapter 5 of this thesis demonstrated that the ecological validity of gaze cues was important in determining the magnitude of the cueing effects, it is not clear why this should be the case. There is a possibility that the reduction in magnitude might be because of a change in “status” in the cues, from social to non-social (or perhaps just less social), so that they are processed more like arrows by the brain. It makes sense therefore to use ecologically valid cues wherever possible. For this reason, and for the fact that they found cueing effects in the ASD group, it is possible that Kuhn et al. may have been measuring something other than social attention per se with their schematic cues, and if so, their lack of a significant relationship to AQ scores may be less surprising.

Furthermore, the schematic nature of the cues may have negated the efforts of the authors in their aims of studying social attention, when the cues were so lacking in ecological validity, a possibility proposed but firmly dismissed by the authors.

The participants who have taken part in the previous experiments in this thesis have been predominantly female (approximately 75%). This gender imbalance may have implications for the generalisability of the results of this thesis to both sexes. Therefore, the first aim of Experiment 8 was to determine whether males are influenced in the same way as women by real-world gaze and arrow cues in a shortened anti-saccade task. A preliminary investigation into the relationship between autistic traits and cueing by gaze and arrow cues was conducted in Chapter 3, with a small sample size. As these initial data suggested the possibility of a relationship between cueing effects and AQ score, the second aim of the current experiment was to further investigate this relationship, with a larger,

male only sample with the potential for more variability in autistic traits, by correlating participants' scores on the AQ with the congruency effects elicited by gaze and arrow cues in the anti-saccade task.

6.2 Method

6.2.1 Design

The anti-saccade experiment had a 2 way, repeated measures design with 2 on the factor Cue type (arrows, gaze) and 2 levels on the factor Congruency (congruent, incongruent). The primary dependent measures were saccadic reaction time (SRT) and directional errors.

6.2.2 Participants

39 healthy male undergraduates and postgraduates from the University of Exeter aged between 18 and 36 years ($M = 22.74$ years; $SD = 5.07$) took part in this experiment in exchange for £4. All participants had either normal or corrected to normal vision. Written informed consent was given by all participants and ethical approval for this experiment was granted by the Ethics Committee of the School of Psychology, University of Exeter.

6.2.3 Apparatus and Materials

Apparatus and materials of the anti-saccade task were the same as those of Chapters 2- 4, with just the left and right versions of the cues used (i.e. neutral cues were not used). In addition, an online version of the AQ was constructed using open source software PHP Surveyor, which was hosted on a server housed in the Psychology department, University of Exeter.

6.2.4 Procedure

Prior to the start of the experiment, the same calibration procedure as in the previous experiments was performed. In addition to this, at the start of each block and every 10 trials thereafter, a drift correct calculation was performed in order to account for any headband slippage in the preceding trials.

The experiment began with 10 practice trials, comprised of selection of the gaze and arrow cue conditions. The experiment contained only one block, comprised of 40 trials, with gaze and arrow trials randomly presented, as were the congruency conditions and target location.

The trial procedure was the same as in Experiment 2, except that the cues were always presented with the same SOA of 300ms. Only one SOA was used to keep the length of the testing session brief. This SOA was chosen because voluntary processes were unlikely to be acting, whilst enough time existed between the onset of the cue and the target to allow for the emergence of pro-saccade errors.

After completion of the anti-saccade task, the participants carried out the AQ. The first 8 participants completed it on paper, whilst the remainder completed the PHP surveyor version online, with their answers being saved to a database housed on the same server as the questionnaire. Participants were informed that the questionnaire asked 50 questions about their social skills, imagination abilities and their attention. Responses were chosen from a Likert scale of options which were “definitely agree”, “slightly agree”, “slightly disagree”, “definitely disagree”. They were instructed to answer the questions with their initial response and not to spend too long contemplating their answer. The questionnaires took approximately 5 minutes to complete. The 50 questions that comprise the AQ are included in Appendix A.

At the end of the questionnaire, participants were debriefed as to the purpose of the study.

6.2.5 Data preparation and analysis

Completed trials from the anti-saccade task were isolated by using the same criteria in respect of SRT, saccade direction, amplitude and start position as in the previous experiments. This procedure removed 125 trials representing 8.01% of trials. Practice trials were excluded from the analyses.

Individual SRT Congruency effect

The mean congruency effect for gaze cues and arrow cues for each participant was calculated, by subtracting the mean SRT with congruent gaze cues from the mean SRT with incongruent gaze cues, and repeating the process with the mean SRTs for congruent and incongruent arrow cues, creating four new variables in SPSS.

Individual Efficiency scores

After Kuhn et al. (2010), efficiency scores were created to incorporate a measure of speed and accuracy of responses. The mean SRT for each condition was divided by the proportion of correct saccades in that condition. Lower scores represented greater efficiency. The efficiency scores of congruent gaze and arrow cues were then subtracted from the efficiency score for incongruent trials for the relevant cue type. This resulted in overall cueing effects for gaze cues and for arrow cues which took account of error rates as well as SRT.

AQ scores

With the exception of the first 8 participants (who completed paper versions of the AQ), the answers given by the participants in the AQ were recorded in a MySQL database automatically at the end of the questionnaire and downloaded as a file. The total score for each participant was then calculated by adding up all the points for the 50 questions, giving a score out of 50.

6.3 Results

6.3.1 Saccadic reaction time

A 2 way repeated measures ANOVA was conducted on the SRT data with 2 levels on the factor Cue type (arrows, gaze) and 2 levels on the factor Congruency (congruent, incongruent). The main effect of Congruency was highly significant, $F(1, 38) = 27.49, p < .001$, with participants quicker to correctly respond on congruent trials. There was also a main effect of Cue type, $F(1, 38) = 4.69, p = .037$, with participants quicker to respond in the presence of arrow cues than gaze cues (arrows: $M = 237.51\text{ms}, SE = 4.86$; gaze: $M = 242.27\text{ms}, SE = 4.55$). The Cue type by Congruency interaction was not significant, however, $F < 1.00$. Figure 6.1 below shows the mean SRTs for congruent and incongruent gaze and arrow cues.

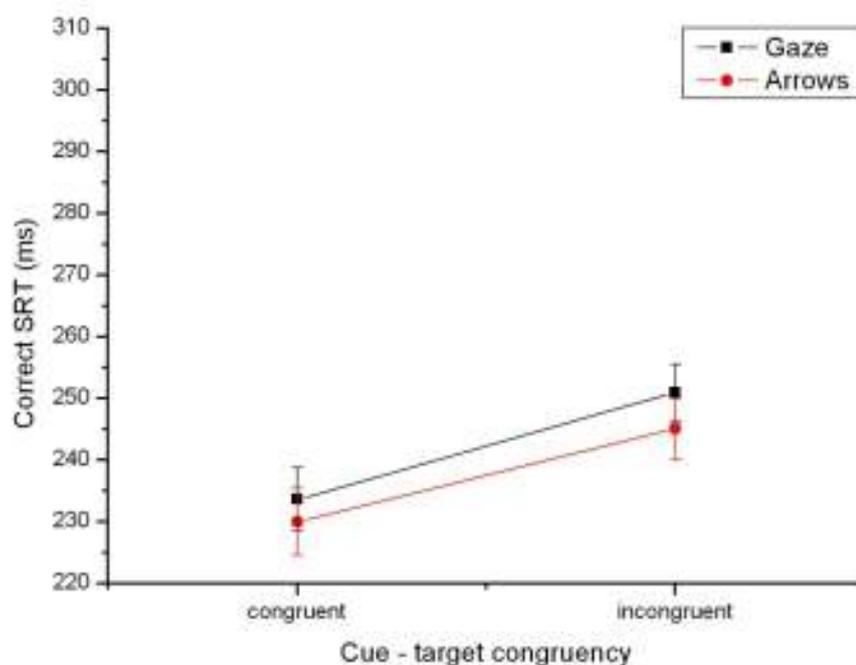


Figure 6.1: Mean correct SRTs for congruent and incongruent gaze and arrow cues used in Experiment 8. Error bars represent standard error of the mean.

6.3.2 Error rates

Sixty nine erroneous pro-saccades were committed.

A 2 way ANOVA was conducted on the percentage of errors per condition per participant, with 2 levels on the factor Cue type (arrows, gaze) and 2 levels on the factor Congruency (congruent, incongruent). There was a significant main effect of Congruency, $F(1, 38) = 7.25, p = .010$, with participants making more errors on incongruent trials ($M = 7.22\%, SE = 1.18$) than on congruent trials ($M = 2.28\%, SE = 0.63$). The main effect of Cue type was also significant, $F(1, 38) = 18.70, p < .001$, with participants making more errors in the presence of arrow cues ($M = 6.20\%, SE = 1.12$) than gaze cues ($M = 3.29\%, SE = 0.68$). The interaction between Congruency and Cue type was not significant however, $F < 1.00$.

6.3.3 AQ scores

The mean AQ score was calculated per participant. The mean score was 17.03, $SD = 4.90$ (maximum possible score = 50), with individual scores ranging from 7 to 28.

6.3.4 Correlations

Several correlational analyses were conducted between AQ scores and behavioural measures. An α level of .05 was set throughout the following analyses.

Two-tailed correlational analyses were conducted between individual SRT congruency effects for gaze and arrow cues and scores on the AQ. There was no significant correlation between gaze cues and AQ score ($r = -.07, p = .666$) or arrow cues and AQ score ($r = .04, p = .822$). Figure 6.2 shows scatterplots of gaze and arrow congruency advantage against AQ scores.

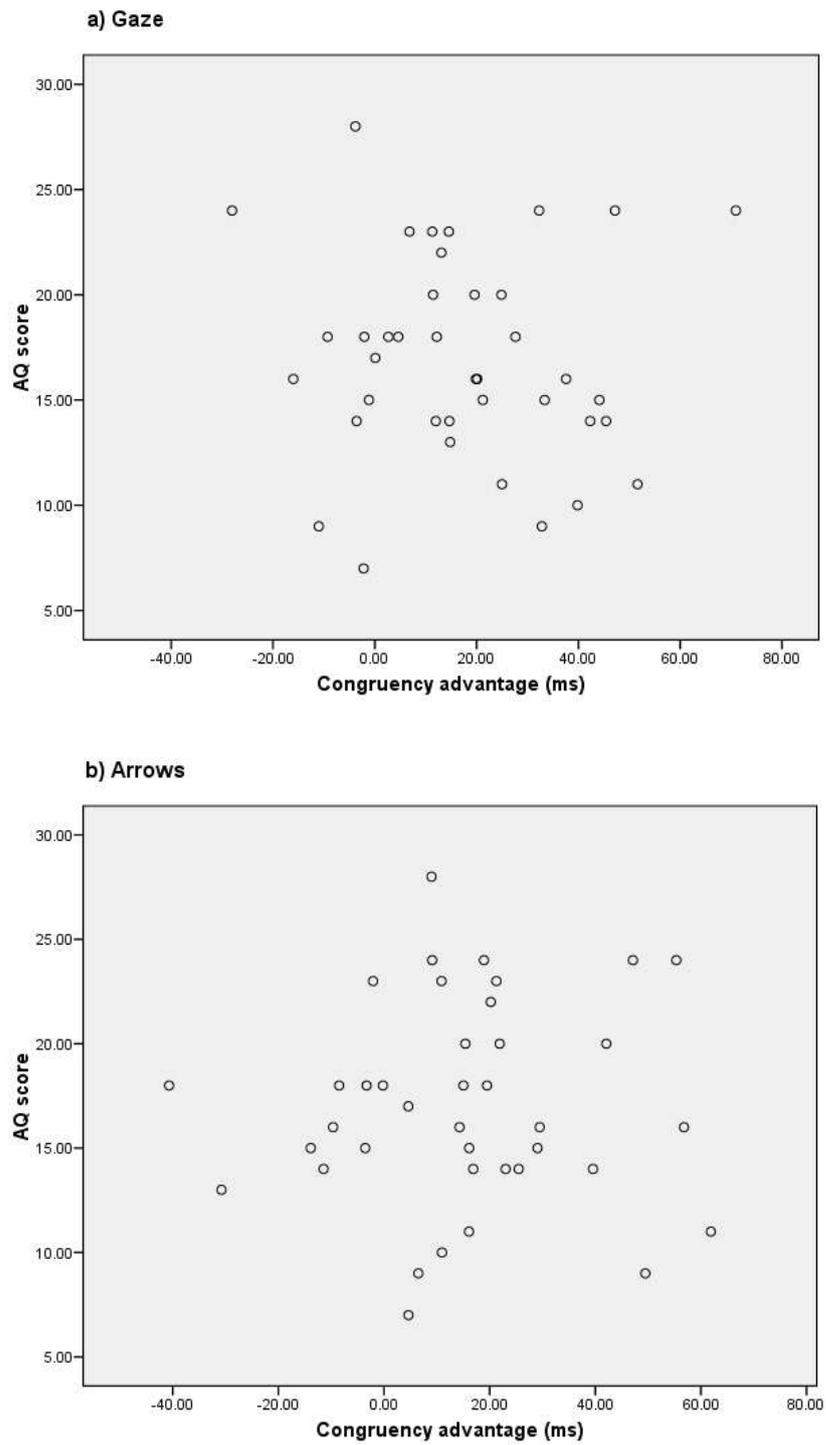


Figure 6.2: Scatterplots of a) gaze cue congruency advantage and b) arrow cue congruency advantage against AQ score.

Additional 2-tailed correlational analyses were conducted between individual absolute mean SRT scores in each condition and AQ score. None of the correlations reached significance. Table 6.1 displays the correlation statistics between mean congruent and incongruent gaze and arrow SRTs and AQ score.

Cue type	Congruency	<i>r</i>	Significance (2 tailed)
Arrows	Congruent	-.05	.748
	Incongruent	-.03	.852
Gaze	Congruent	.01	.940
	Incongruent	-.04	.817

Table 6.1: Correlation statistics and significance values of correlations between mean congruent and incongruent gaze and arrow SRTs and AQ score.

Further 2-tailed correlational analyses were carried out between AQ scores and overall cueing effects for gaze and arrow cues, outlined in the methods section, which encompass both speed and accuracy of responses.

There was no significant correlation between AQ and either the overall gaze cueing effect, $r = -.10$, $p = .552$, or the overall arrow cueing effect, $r = -.16$, $p = .339$.

In summary, in the anti-saccade task, there was an overall congruency effect which was the same for gaze and arrow cues, with participants quicker to correctly respond when the cue and target were congruent. Participants were quicker to respond and made more errors in the presence of arrow cues than gaze cues, but in general made more errors on

incongruent trials. The mean AQ score was 17.03, but individual AQ scores did not correlate with any cueing measures or absolute SRTs in any condition.

6.4 Discussion

Experiment 8 set out to examine whether any differences exist in the way men respond to gaze and arrow cues when compared to the previous experiments, of which the majority of participants have been female. In addition, Experiment 8 sought to identify the existence of a relationship between autistic traits as measured by the AQ and cueing effects of gaze and arrows.

The shortened anti-saccade task in the current experiment used just one SOA of 300ms. The mean congruency advantage for arrow cues was 15ms and for gaze, 17ms. The results of the current experiment can be compared with the 300ms SOA condition in Experiment 2 (Chapter 2) and the simultaneous fixation offset condition in Experiment 4 (Chapter 3), both of which were anti-saccade tasks including the same experimental conditions and a similar procedure as the current experiment. In both these experiments, at the same SOA of 300ms, arrow cues had very little effect on participants' SRTs. In Experiment 2 there was less than 2ms difference between SRTs on congruent and incongruent trials (with incongruent trials actually the slightly quicker of the two) and in Experiment 4, there was only a 7ms congruency advantage in the equivalent condition for arrow cues. In contrast, gaze cues have consistently produced cueing effects larger than arrows, with 10ms and 23ms in equivalent conditions in Experiments 2 and 4 respectively. Not only were the cueing effects larger than for arrows than in previous experiments, but overall SRT was shorter for arrows than gaze cues in the current experiment, indicating that arrows had a generally facilitatory effect on oculomotor responses in this male sample. As

well as influencing SRT, arrow cues also influenced the rate of erroneous pro-saccades more than gaze cues in current experiment. No such effect of cue type on error rates has been observed in the previous experiments.

As earlier experiments in this thesis have mainly included female participants, it may be possible to draw the tentative conclusion that sex may play a role in the degree to which arrows cues can influence oculomotor responses. Male participants appear to show a greater susceptibility to these task-irrelevant arrows than perhaps do females. These findings are in stark contrast to those of Bayliss et al. (2005) who showed reduced cueing effects for males to both gaze and arrow cues in comparison with females in their covert attention task. The reason for this very different outcome may lie in dissimilarities in the task, modality of response, sample size and stimuli, between the two experiments. Furthermore, the equivalent cueing effects of gaze and arrow cues was not predicted by the Extreme Male Brain theory of autism (Baron-Cohen, 2002) as, according to this view, males should show reduced influence of gaze cues in comparison to women. However, an alternative explanation may be that the inter-mixed gaze and arrow cues in this experiment may have caused the equal effects between the two cue types.

The mean score on the AQ of 17.03 is similar to that reported in Baron-Cohen et al. (2001) for male students ($M = 18.6$), although the variation in scores was larger in their study than observed here ($SD = 4.90$ vs. 6.60). It is also comparable to the findings of Bayliss et al. (2005). However, unlike the latter study, the results from Experiment 8 provide no evidence of any relationship between cueing effects caused by gaze and arrow cues and participants' levels of autistic like traits. Although at odds with the findings of Bayliss et al. (2005), these findings concur with those of Kuhn et al. (2010), who similarly were unable to find any suggestion of a correlation between AQ scores and cueing effects.

However, the use of schematic rather than real world cues by Kuhn et al. leaves open the possibility that the mechanism of cueing they observed had little to do with social processing per se. Nevertheless, the fact remains that even with the real-world cues used in the current experiment, there was still no apparent relationship between AQ scores and cueing by gaze or arrows. ASD is a multifaceted condition, encompassing deficits and impairments in domains outside of social ability. The AQ reflects this, and asks questions pertaining to all areas of atypical functioning in ASD, such as attention switching and attention to detail. Specific examples of statements from the AQ which are unrelated to the social and communication domains of ASD include “I like to plan any activities I participate in carefully” and “I am fascinated by dates.” It is not immediately obvious why such qualities *should* relate to processing of directional cues, social or otherwise. It may be that a tool more specifically gauged at assessing social abilities per se might produce evidence of a relationship between gaze cueing and social or communicative abilities.

An alternative explanation is that gaze cueing in the laboratory has less to do with social processing than researchers of social attention like to believe. Several studies, including that by Kuhn et al. (2010), already discussed, have shown that individuals with autism orient attention in the direction of both non-predictive schematic and real-world gaze cues in the laboratory (Chawarska et al., 2003; Kylliainen & Hietanen, 2004; Senju, Tojo, Dairoku, & Hasegawa, 2004; Swettenham et al., 2003), whilst deficits in spontaneous gaze following are considered a hallmark of autism. One study even showed that the same individuals who produced cueing effects in response to non-predictive gaze cues in the lab, did not spontaneously gaze follow in more naturalistic settings (Chawarska et al., 2003). These findings fundamentally challenge the validity of cueing-type paradigms in studying real-world behaviour, if individuals with profound social and communicative deficits are

able to perform normally on such tasks. It is possible that such tasks do not tap social processing even in typically developed individuals and that a more general, non-social attentional mechanism might be responsible for the cueing effects repeatedly observed. However, Kuhn et al. (2010) argue that the apparently automatic orienting to eye gaze cues in autism may reflect an atypical processing strategy which is perhaps learned, whereby gaze cues are processed via the same mechanism as arrow cues without regard for the social relevance of the cues.

6.5 Conclusions

In conclusion, the results from Experiment 8 suggest that men may be more influenced by arrow cues than females, but that they show the same magnitude SRT cueing effects for arrows and gaze cues, a finding not supported by the Extreme Male Brain theory of autism. There was no evidence for a relationship between autistic traits as measured by the AQ and cueing effects caused by either eye gaze or arrow cues, suggesting that either the AQ may not be adequately sensitive to social behaviour per se or alternatively that the gaze cueing in an anti-saccade task may be less related to social processing and more the result of a more general attentional process. In the final experimental chapter of this thesis, the relationship between social processing and gaze and arrow cueing will be further explored in a patient with damage to the orbitofrontal cortex, an area thought to be critical to the effective processing of emotionally and socially significant information.

Chapter 7: *Orienting to gaze and arrow cues in patients with frontal cortical damage*

7.1 Introduction

Evidence has been presented in the introduction to this thesis for the involvement of the prefrontal cortex in processing of both eye gaze and arrow cues. However, some researchers suggest that this area might have a particular function in interpreting and responding to eye gaze in particular, perhaps via a mirror neuron system (Grosbras et al., 2005; Hooker et al., 2003). The orbitofrontal cortex (OFC) in particular has been implicated in processing of and responding to social information. Patients with lesions to this area of the brain often manifest difficulties in social interaction and reduced sensitivity to others' emotions and intentions (Hornak et al., 2003, 1996; Mah et al., 2004; Rolls et al., 1994; Stone et al., 1998), whilst displaying largely intact cognitive functioning in other areas (Cicerone & Tanenbaum, 1997; Damasio et al., 1990; Nies, 1999).

If the OFC is critical in mediating responses to social and emotional stimuli, it might be anticipated that patients with damage to the OFC might not be influenced by eye gaze cues in the same way as controls whilst displaying typical responses to non-social cues. Vecera and Rizzo (2004; 2006) investigated this possibility with neurological patient EVR, who had sustained a bilateral lesion to the OFC after removal of a meningioma. EVR's behaviour post-surgery manifested as "acquired sociopathy" (p. 86, Damasio, Tranel, & Damasio, 1990) in that he was inept in his interactions with others and showed little regard for the usual social norms and conventions. Vecera and Rizzo performed

spatial cueing type tasks with EVR using schematic gaze cues. EVR showed no cueing effect with non-predictive gaze cues (Vecera & Rizzo, 2006), nor even when the cues were predictive of target location (Vecera & Rizzo, 2004) although he demonstrated typical responses to traditional exogenous cues (sudden onset peripheral cues). However, EVR also did not orient in the direction of predictive word cues, which the authors proposed is suggestive of a more general impairment in the mechanisms responsible for learning about stimulus-response associations rather than a specifically social deficit.

In an attempt to replicate and expand upon the findings of Vecera and Rizzo, Experiments 9a and 9b presented pro-saccade and anti-saccade tasks using real-world gaze and arrow cues to three neurological patients with lesions to the frontal lobes along with an age matched control group. Of the neurological patients, one, patient LG, had a circumscribed lesion to the OFC, very similar to that of patient EVR, whilst the others, BE and JW, had fronto-lateral cortical lesions. If social processing is differentially disrupted by damage to the OFC then it would be anticipated that LG would show atypically attenuated responses to gaze but not arrow cues, relative to controls and perhaps also the other patients. However, if the OFC mediates the formation and implementation of stimulus-response associations more generally, then reduced influence of arrow cues as well as gaze cues might be expected when LG performs the tasks, relative to controls and the other patients. A further possible outcome would be that frontal lobe damage not specific to the OFC might disrupt cueing to gaze and/or arrow cues with all the patients showing atypical cueing effects relative to controls. Accounts of the frontal lobes' contribution to inhibitory control, including that of eye movements predict that the frontal patients may have difficulty in performing the tasks at all. The frontal eye fields (FEF) of the frontal lobes appear to have an important role in the voluntary control of saccades. For example, in pro-

saccade tasks, patients with lesions to the FEF have been shown make reflexive saccades with particularly short latencies towards the contralesional hemifield and voluntary saccades with particularly long latencies to the ipsilesional hemifield (Henik, Rafal, & Rhodes, 1994) although reports of a greater rate of express saccades (those with latencies less than 90ms) towards the ipsilesional field have also to be found (Braun, Weber, Mergner, & Schulte-Monting, 1992). The FEF also seem to have a role in the disengagement of the saccadic system from visual stimuli, with damage to this area resulting in deficits in voluntary gaze shifts (Rivaud et al., 1994). Specifically in the anti-saccade task, elevated rates of pro-saccade errors towards the peripheral target are commonly reported in patients with lesions to both the ventrolateral (VLPC) and dorsolateral prefrontal cortex (DLPC) (Guitton et al., 1985; Hodgson et al., 2007; Pierrot-Deseilligny, Ploner, Muri, Gaymard, & Rivaud-Pechoux, 2002; Walker et al., 1998). In short, it is possible that the frontal patients examined here may have difficulty in performing the anti-saccade task in particular, regardless of the specific influence of the gaze and arrow cues. In this regard, in addition to examining the influence of social and non-social cues in frontal lobe damage, Experiment 9 represents a feasibility study of the use of these oculomotor tasks with neurological patients.

7.2 Patient case descriptions

7.2.1 Patient LG

Patient LG was a right handed woman, who was 61 year old at time of testing and who 20 years previously (1990) had a bi-frontal craniotomy to remove a benign meningioma. Although she made a good physical recovery following the surgery she developed epileptic seizures which are currently controlled via medication (1 x400mg of carbamazepine and 2 x

500mg levetiracetam daily). She had not reported a seizure in the 6 months period prior to testing. Thorough assessment was carried out by a clinical neuropsychologist in 2007 as part of clinical investigations into her self-reported long term memory problems (extras from their report are given in quotations in what follows). Whilst “fully oriented for person, place and time of testing” she reported having “no memory of her previous marriage or the birth of her daughters” although knowledge of “factual details from her personal past” appeared preserved relative to details of past events and experiences. She performed normally on tests of immediate and working memory and in learning items from a word list. Performance on some tests of executive function was “moderately reduced including mental flexibility (Trails B test: (Reitan & Wolfson, 1985), verbal fluency (FAS of the COWA: Spreen & Strauss, 1998) and response inhibition. She scored 38 on the National Adult Reading Test (NART: (Nelson, 1982) equating to an estimated pre-morbid performance IQ score of 98. Mood inventory scores showed moderately increased levels of anxiety and depression. LG was not examined for visual impairment or neglect. At the time of these assessments, no tests of social or emotional processing were carried out with LG.

For the purposes of this thesis, in 2011 LG was tested for performance of two tasks of social and emotional processing to identify any dysfunction in these domains: Reading the Mind in the Eyes test (revised) (Baron-Cohen, Wheelwright, Hill, Raste, & Plumb, 2001) and The Faux Pas Recognition Test (Baron-Cohen et al., 1999; Stone et al., 1998). Impairments in these tasks alongside a attenuated influence of gaze cues but not arrow cues in LG might provide evidence that gaze cueing is related to social functioning and Theory of Mind in the real-world and is mediated by the OFC.

The Reading the Mind in the Eyes test contains 36 pages, each comprised of a greyscale photograph of the eye area of a male or female adult. LG was asked to select one of 4 words written on the page to describe what the person in the photograph was thinking or feeling. Figure 7.1 shows an example of one of the questions from the task.

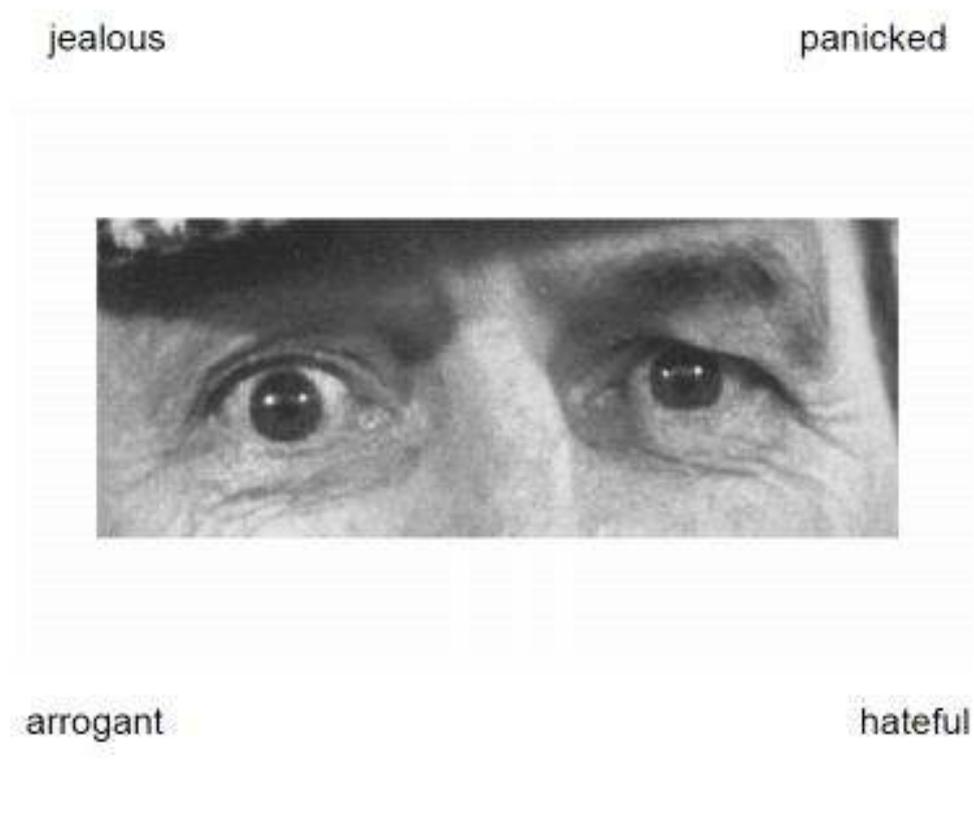


Figure 7.1: Example of a page from the Reading the Mind in the Eyes task (revised) (Baron-Cohen et al., 2001).

LG scored 22 out of a potential 36. The mean score for females in the original pilot study was 26.4, whereas LG's score is the same as seen in individuals with high functioning autism and Asperger's syndrome (Baron-Cohen et al., 2001). In short, LG's score on the Mind in the Eyes test was atypically low.

The Faux Pas Recognition Test (Baron-Cohen et al., 1999; Stone et al., 1998) consists of twenty vignettes detailing brief social interactions. In half of the vignettes one of the protagonists (the speaker) makes a faux pas – they say something which may upset or offend the other protagonist (the listener) without realising that they have done so. Several questions are then asked about the content of the story. Firstly participants are asked whether anyone has said anything they shouldn't have said. Following this, several further questions are asked relating to the intentions and emotions of the protagonists. Control questions are also asked to identify any comprehension difficulties. The vignettes were read aloud to LG but she had in front of her a paper copy that she could refer to at any time. This was particularly important for LG, due to her memory problems. It was stressed that she was not being tested on her memory of what happened in the vignettes. Participants can score a total of 60 points in the faux pas questions and a further 20 points on the non-faux pas questions.

On the faux pas vignettes, LG scored 47 out of 60. On the non-faux pas vignettes she scored 14 out of 20. She answered all the factual control questions correctly. LG correctly detected all the faux pas stories and correctly answered all the empathy questions.

However, on several occasions she attributed the faux pas to lack of tact or plain malice on the part of the speaker, rather than because they harboured a false belief about the situation. LG also answered “yes” to several of the non-faux pas stories, indicating that someone had made a faux pas when none had occurred.

Structural MRI scanning was carried out on all 3 patients at the Peninsula Magnetic Resonance Imaging centre as part of an earlier research project into inhibitory oculomotor control in frontal patients (Hodgson et al., 2007). Whole brain T1 weighted structural scan

was acquired with a voxel resolution of $2 \times 2 \times 2 \text{ mm}^2$. DWI/DTI anisometry images were also acquired but not reported here. The structural scan image revealed a clearly demarcated lesion caused by surgical excision of the tumour (Figure 7.2). The affected area was the bilateral orbitofrontal cortex, with the lesion almost entirely residing within Brodmann Area BA10, but with its most posterior-lateral extent encroaching into BA47 and most ventral extent including parts of BA 11 and 12. The area affected was manually circumscribed using the Region of Interest drawing tool within MRIcro software (Chris Rorden, University of South Carolina). The structural scan was normalised to a standardised template (Talairach coordinates; Talairach & Tournoux, 1988) using the cost function masking technique (Brett, Leff, Rorden, & Ashburner, 2001). Within this normalised space the total lesion volume was calculated as 60.8ccs.

7.2.2 Patient JW

Patient JW was a right handed 82 year old man who suffered a right hemisphere MCA stroke in 2005. He participated in a research study in 2007 at which time his Minimal state (Folstein, Folstein, & McHugh, 1975) score was recorded as 28/30 indicating normal orientation in time and space and basic working memory function. He scored 35 out of 50 on NART test (Nelson, 1982) which equates to a premorbid performance IQ score of 99.

His forward digit span was recorded as 6 and his backward digit span score was 5 (i.e. within normal performance range). His spatial span was assessed by the Corsi block tapping task (Corsi, 1972). For this test his forward memory span was recorded as 3, i.e. in the low to abnormal range, however on the more demanding backward digit span task he scored 4 which would be considered normal. There was no detectable left sided weakness or hemiparesis apparent on examination at the time of testing. Given the right parietal

locus of his lesion a Mesulam cancellation test (Mesulam, 2000) was given to assess symptoms of neglect. In this test the patient has to cross out a series of target shapes printed on a piece of paper embedded within a field of distracting non-target shapes. Although he cancelled all the specified target shapes in this task, it was noted that he commenced cancelling shapes from the right and proceeded in an organised search pattern from top to bottom and right to cancelling all target shapes after 4 minutes of search, suggestive of the presence of a mild degree of exploratory neglect. The fact that only one task of attentional neglect was conducted means the presence of hemispatial neglect in JW cannot be ruled out. JW's visual function was not examined.

Structural MRI scanning and lesion reconstruction was carried out as described for patient LG above. T1 weighted MRI scans revealed an area of infarction in the right parietal-temporal-frontal region (See Figure 7.2). The lesion included large areas of the temporal lobe (BA 21 and BA 22) as well as the superior parietal lobule (BA 39) but also encroached into the ventrolateral frontal cortex (BA 44) and spread dorsally and medially to include part of the anterior cingulate gyrus (BA 24). The volume of the normalised lesion was calculated as 67.1 cc.

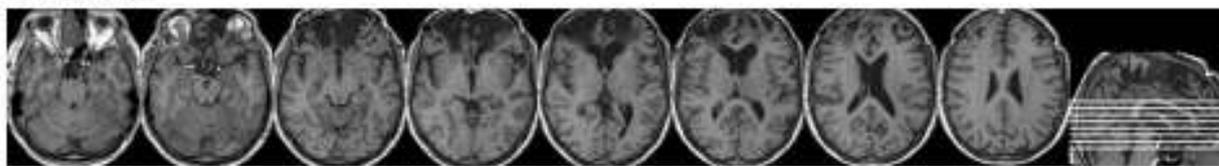
7.2.3 Patient BE

Patient BE was a right handed 71 year old man who suffered a left Middle Cerebral Artery (MCA) stroke 8 prior to the testing session. At the time of testing he had measurable signs of unilateral motor rigidity and weakness in his upper limb on the contralesional (right) side along with marked slowing of finger movement and dexterity. In the period initially following his stroke he was found to be profoundly aphasic but 6 years following his stroke

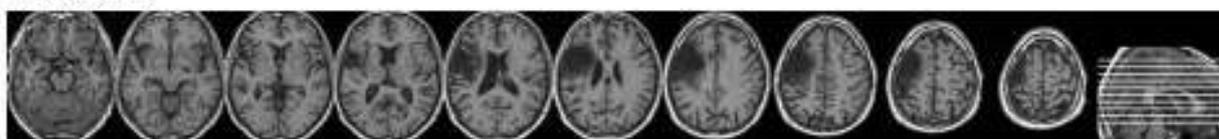
his score on the Western Aphasia Battery (Kertesz, 1982) naming score was 61 and FAS (Spreen & Strauss, 1998) was 26, both in the low range indicative of only a marginal impairment in language production on these test. However, in person he showed a clear poverty in language production and only produced short sentences of 2 or 3 words together. These aphasic symptoms therefore made it difficult to carry out a number of other standardised tests (e.g. National Adult Reading Test, digit span etc.). BE's visual function was not assessed.

Structural MRI scanning and lesion reconstruction was carried out as described for patient LG above. The scan revealed an area of infarction which spared the anterior temporal and parietal lobes and only partially encroached into the ventrolateral frontal cerebral cortex BA44 (i.e. the MCA "water shed" region most commonly affected in stroke was spared in this patient). Instead the lesion was largely confined to the left dorsolateral prefrontal cortex (BA9 / 46 see Figure 7.2). Normalised lesion volume was calculated as 86.1cc.

PATIENT LG



PATIENT BE



PATIENT JW



LESION ROI OVERLAY



Figure 7.2: Multi-slice axial views of normalised T1 MRI structural scans for the 3 patients. The coronal section shows the level at which each of the slices displayed corresponds to. Bottom panel shows an overlay plot of all 3 patients regions of interest (ROI) onto a standardised T1 scan template image (for comparison Patient BE's ROI is displayed on the right hemisphere. Purple = non-overlapping regions and Green = areas that overlapped in patients BE and JW).

Experiment 9a: Pro-saccades

7.3 Method

7.3.1 Design

The experiment had a 3 way, repeated measures design with 2 levels on the factor Cue type (arrows, gaze), 2 levels on the factor SOA (300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent). The primary dependent measures were saccadic reaction time (SRT) and directional errors.

7.3.2 Participants

Patients

LG, BE and JW all completed the pro-saccade task. The experiment took place within the School of Psychology, University of Exeter and the patients provided written informed consent. Ethical approval for the experiment to be carried out specifically with patients was granted via Track B of the School of Psychology, University of Exeter's Ethics Committee.

Control group

Eleven neurologically healthy participants between the ages of 51 and 77 years old ($M = 61.27$ years, $SD = 8.47$), who were naïve to the purposes of the experiment, volunteered to take part in this experiment. Participants reported normal, or corrected to normal vision. All participants gave written informed consent and ethical approval was granted by the Ethics Committee of the School of Psychology, University of Exeter.

7.3.3 Apparatus and Materials

Apparatus and materials were the same as those of Chapters 2- 4, with just the left and right versions of the cues used (i.e. no neutral cues were used).

7.3.4 Procedure

Cue discrimination task

It has been suggested that gaze perception abilities decline with age (Slessor, Phillips, & Bull, 2008). Therefore, to determine that all participants, patients and controls, could discriminate between the left and right versions of the cues, prior to the start of the experiment, 10 images of the gaze and arrow cues (5 of each) were presented to the participants via a Microsoft Office PowerPoint presentation. Participants were asked to say aloud whether the eyes or the arrows were pointing left or right. In the case of patient BE, his aphasia prevented him from verbalising the direction of the cues, so he tapped on the relevant side of the desk to indicate his answer. All participants, patients and controls, completed this task flawlessly.

Pro-saccade task.

The procedure for the pro-saccade task was closely based on that used in younger control participants (Chapter 2). The experiment began with 10 practice trials, comprising a selection of the gaze and arrow cue trials. This was followed by 4 blocks, which comprised 20 trials each, with alternating blocks of gaze and arrow cues. Half the trials of each condition were assigned to each of the two blocks of each cue type with the trials then presented randomly within that block. The stimuli were presented on the same monitor as

in Experiments 2-8 and therefore possessed the same dimensions and locations as in previous experiments.

7.3.5 Data preparation and analysis

Eye movements were analysed and processed using an identical procedure and criteria in respect of SRT, saccade direction, amplitude and start position as in previous experiments with the exception that upper limit was placed on SRT in the present experiments (due to the long latency of response observed in some patients). BE's data had to be filtered more generously relative to controls, as he appeared to have difficulty in returning to the fixation cross between each trial. For BE saccades which started anywhere within the central 50% of the screen (as opposed to the central 10% for controls) were included in the analyses. Despite this, only 24 trials remained, equating to 70.00% of BE's trials being excluded from analysis. In respect of the control group, the filtering criteria removed 171 trials, representing 17.81% of trials. For LG, this removed 4 trials (5%) and for JW, 5 trials were removed (6.25%).

7.4 Results

7.4.1 Control group performance

Saccadic Reaction Times

The overall mean SRT across all conditions for the control group was 247.16ms ($SE = 11.23$). The lower bound for the 95% confidence interval for the overall mean SRT was 222.13ms and the upper bound was 272.18ms.

A 3 way repeated measures ANOVA was conducted on the SRT data from the control group, with 2 levels on the factor Cue type (arrows, gaze), 2 levels on the factor SOA (300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent). The main effect of SOA was significant, $F(1, 10) = 25.23, p = .001$. The main effect of Congruency approached significance, $F(1, 10) = 3.89, p = .077$, with participants quicker to correctly respond on congruent trials. The mean correct SRT, standard errors and upper and lower bounds for the 95% confidence intervals for each condition for the control group can be seen in Table 7.1. The magnitude of the congruency effect across conditions, along with the 95% confidence intervals of the effect size is shown in Table 7.2. The main effect of Cue type did not approach significance, and nor did any of the interactions, $F < 1.20$. Only 3 directional errors were committed by the control group overall.

Cue type	SOA (ms)	Congruency	Mean SRT (ms)	Standard error	95% confidence intervals	
					Lower	Upper
Arrows	300	Congruent	251.10	14.74	218.26	283.94
		Incongruent	269.45	17.76	229.88	309.03
	800	Congruent	224.73	14.67	192.05	257.42
		Incongruent	226.01	10.93	201.65	250.37
Gaze	300	Congruent	260.63	12.27	233.30	287.96
		Incongruent	273.98	15.37	239.74	308.23
	800	Congruent	229.25	8.49	210.33	248.17
		Incongruent	242.08	13.21	212.66	271.51

Table 7.7.1: Mean correct SRTs, standard errors and 95% confidence intervals for congruent and incongruent arrow and gaze cues at both SOAs for the control group.

Cue type	SOA (ms)	Mean congruency effect (ms)	95% confidence intervals	
			Lower	Upper
Arrows	300	18.35	-8.62	45.33
	800	1.28	-19.89	22.44
Gaze	300	13.35	-2.28	28.98
	800	12.83	-11.21	36.88

Table.7.2: Mean congruency effects and 95% confidence intervals for gaze and arrow cues at 300 and 800ms SOA for the control group.

Anticipatory saccades

The frequency of anticipatory saccades made at least 80ms after the onset of the cue and until 80ms after the onset of the target was determined. 234 anticipatory saccades were made by the control group during this period, equating to a mean frequency per participant of 21.27 saccades, with individual participant frequencies ranging from 3 to 54. The 95% confidence interval for total number of anticipatory saccades per participant ranged from 9.48 to 33.06. Unlike previous experiments, no distinction was made between small and large anticipatory saccades to increase the power of the analysis

A 3 way repeated measures ANOVA was conducted on the frequency data, with 2 levels on the factor Cue type (arrows, gaze), 2 levels on the factor SOA (300ms, 800ms) and 2 levels on the factor Cue direction (same, opposite). The main effect of SOA was significant, $F(1,10) = 13.13, p = .005$ with more anticipations made at the 800ms SOA ($M = 3.77, SE = .92$) than the 300ms SOA ($M = 1.55, SE = .47$). The main effect of Cue direction was also significant, $F(1,10) = 13.63, p = .004$, with participants making more anticipatory saccades in the same direction as the cue ($M = 3.71, SE = .86$) than in the opposite direction ($M = 1.61, SE = .55$). The main effect of Cue type was not significant however, $F < 1.40$ although the interaction between Cue type and Cue direction was significant, $F(1,10) = 8.15, p = .017$, which appears to be the result of a greater discrepancy between the frequency of anticipatory saccades made in the same and opposite direction to arrow cues than to gaze cues. The mean frequencies of anticipatory saccades and 95% confidence intervals for the Cue type x Cue direction interaction can be seen in Table 7.3 below. The frequency of anticipatory saccades in all conditions is graphically presented in

the next section in Figure 7.3, alongside that of the patients. None of the other interactions reached significance, $F_s < 1.45$, $p_s > .25$.

Cue type	Cue Direction	Mean frequency of saccades	95% confidence intervals	
			Lower	Upper
Arrows	Same	4.32	2.21	6.42
	Opposite	1.46	.22	2.69
Gaze	Same	3.10	1.16	5.03
	Opposite	1.77	.47	3.08

Table 7.3: Mean frequency of anticipatory saccades per participant and 95% confidence intervals for gaze and arrow cues made in the same and opposite directions as the cue for the control group

7.4.2 Patients

Patient LG

LG appeared to perform the task with ease, although her mean SRT was 279.70ms (SD = 36.18), slightly outside the upper bound of the 95% confidence interval for controls. However, some of LG's SRTs in individual conditions were within the 95% confidence interval for controls, with the exception of congruent arrow cues at 300ms, both congruent and incongruent arrows at 800ms as well as congruent gaze cues at 800ms, where LG was slower to respond than controls (Figure 7.3: Table 7.1).

For LG, the congruency effects for arrow cues at 300ms SOA and gaze cues at 800ms SOA were outside the normal range with both showing *incongruency* advantages

(i.e. responses on incongruent trials were quicker than on congruent; Table 7.2; Table 7.4).

Although her congruency effects for arrow cues at 800ms SOA and gaze cues at 300ms SOA were within the 95% confidence interval for controls, they were very close to zero, indicating very little effect of the cues on SRT.

LG made no errors in the pro-saccade task or anticipatory saccades in the pro-saccade task, which was atypical when compared to the 95% confidence intervals for anticipatory saccades made by controls.

Cue type	SOA (ms)	Mean congruency effect (ms)	
		LG	JW
Arrows	300	- 14.58 *	36.80
	800	2.25	-26.62 *
Gaze	300	1.68	13.77
	800	-16.40 *	-67.65 *

Table 7.4: Mean congruency effects for gaze and arrow cues in the pro-saccade task at 300ms and 800ms SOA for the patients. * indicates effect which is outside of the 95% confidence intervals for the control group, presented in Table 7.1

Patient JW

JW also appeared to perform the pro-saccade task well, with only 5 trials removed in the data preparation procedure outlined in Section 7.3.5. However, his mean SRT was

327.30ms, much slower than the controls. Due to the lateralised nature of JW's lesion, SRT of left and right saccades were determined and it was discovered that JW was slower to saccade to the contralesional (left) side of the screen (left: $M = 440.39\text{ms}$; right: $M = 207.56\text{ms}$), which accounted for his slower SRTs overall. However despite this lateralisation effect on SRTs, JW made approximately the same number of saccades to the left (36) as he did to the right (34) and they were of similar amplitudes in both directions (left: $M = 9.80^\circ$; right: $M = 10.44^\circ$). In a number of individual conditions, JW's SRTs were longer than controls: incongruent arrow cues at 300ms SOA and both congruencies for arrows at 800ms SOA, as well as both congruencies for gaze cues at 800ms SOA were all outside the upper bound of the controls' 95% confidence intervals.

As can be seen in Table 7.4, JW's cue congruency effects were also atypical for both cue types at 800ms SOA, for which he showed large incongruency advantages. However, he displayed normal congruency advantages for both cues at 300ms.

JW made only 2 directional errors and he made 14 anticipatory saccades, within the normal range for controls, with equal numbers occurring to the left and right hemifields, with similar numbers with gaze and arrow cues (6 and 8 respectively). JW made substantially more anticipations in the same direction as the cue (11) than in the opposite direction (3).

Patient BE

Interestingly, BE appeared to have great difficulty in performing the pro-saccade task correctly. It was apparent that he understood the instruction, but despite many reminders to return his gaze to the centre of the screen and look at the cross at the start of each trial, he failed to do so as often as he was able to do so correctly. The result of this difficulty is that

BE correctly completed only 22 trials out of a potential 80. For this reason, an analysis of the correct trials is not appropriate.

Delayed return to fixation in Patient BE

BE had difficulty in returning to the central fixation cross at the start of each trial, despite several reminders. Consequently on a high proportion of trials his first saccade emanated from an area towards the left or right of the screen. From visual inspection of the data, it appeared that on a large proportion of these “delayed return to fixation” trials, BE was maintaining fixation in the area of screen where the target had been positioned on the previous trial. 36 delayed return to fixation trials were identified (equal numbers in the presence of gaze and arrow cues) and were classified as starting on the left or right of the screen (outside the central 50% of the screen horizontally). As can be seen from Figure 7.5, BE started more trials on the side of the screen where the target had appeared on the previous trial, particularly with arrow cues.

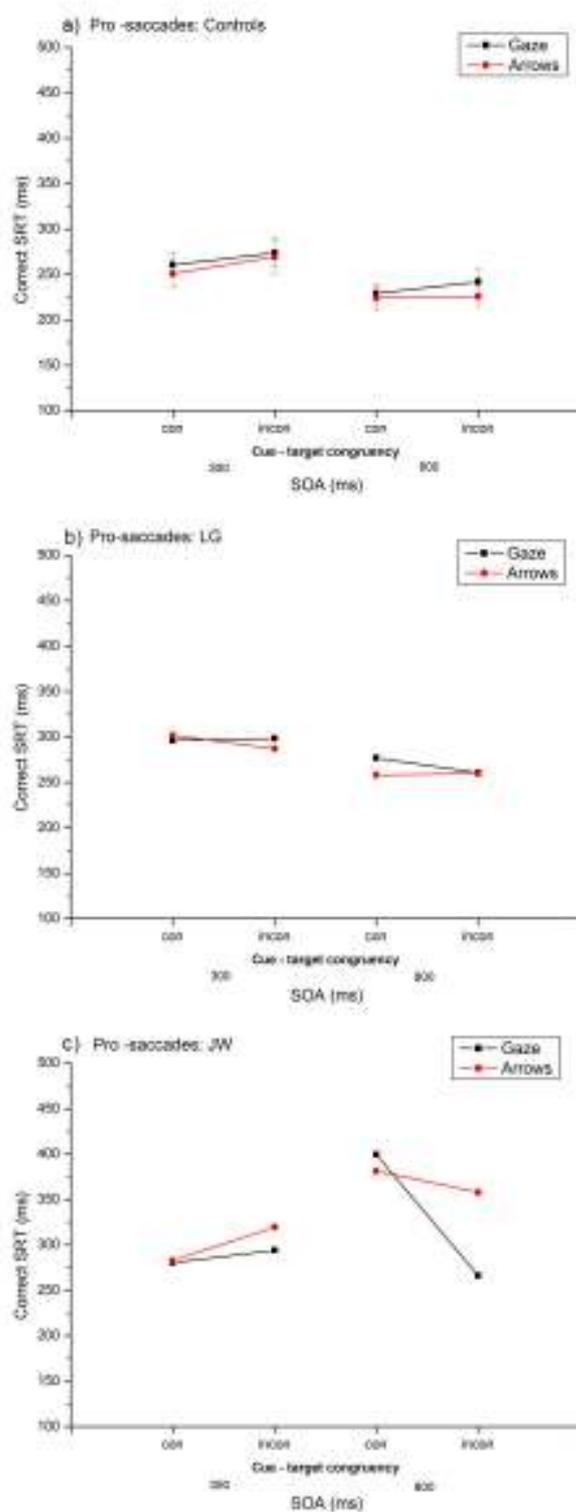


Figure 7.3: Mean correct SRTs in the pro-saccade task for a) the control group and (b – c) the patients for congruent and incongruent gaze and arrow cues over the two SOAs. In panel a), error bars represent standard error of the mean.

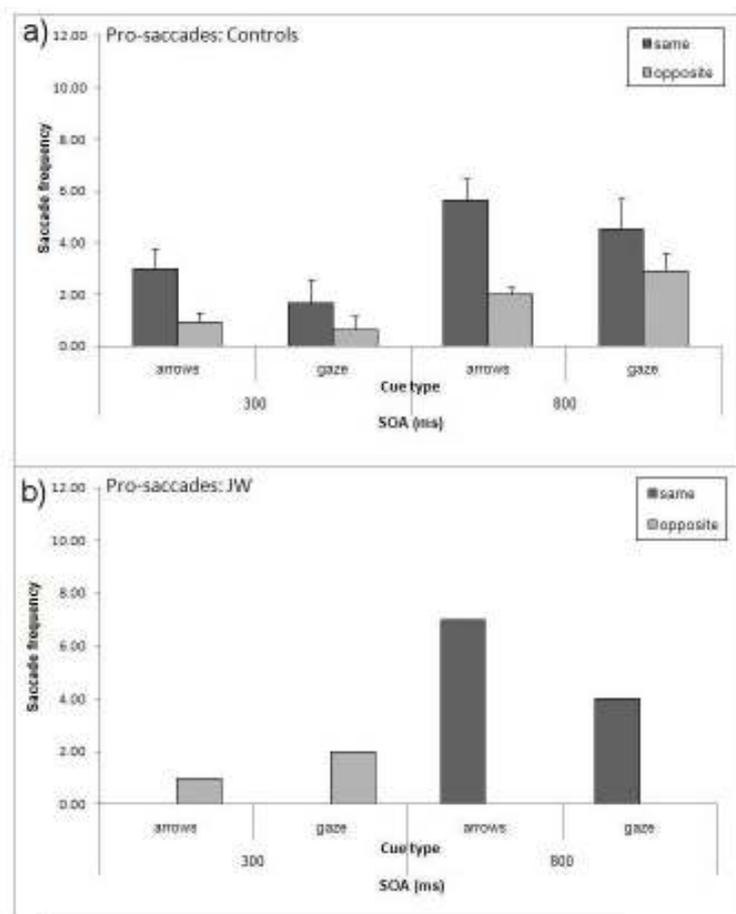


Figure 7.4: Mean frequency of anticipatory saccades in the pro-saccade task made in the same and opposite direction of gaze and arrow cues at both 300ms and 800ms SOA for a) controls and b) JW. Error bars in a) represent standard error of the mean. Patient LG did not make any anticipatory saccades.

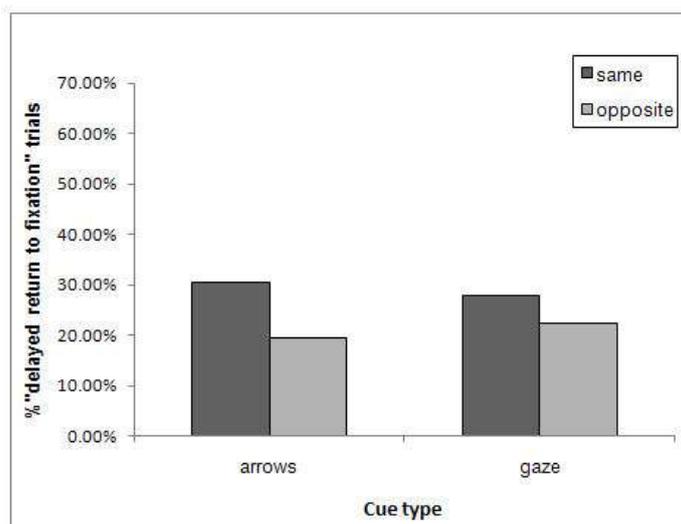


Figure 7.5: Trials in the pro-saccade task where patient BE's first saccade began on the left or right of the screen and the percentages of those trials that started on the same or opposite side to the target in the preceding trial.

Experiment 9b: Anti-saccades

7.5 Method

Experiment 9b had the same design, participants and apparatus as Experiment 9a. The procedure was identical to that of Experiment 9a with the exception of task instruction. This time, participants were instructed to look in the opposite direction to the peripheral “target” as accurately and as quickly as possible.

For the control group, the data preparation procedure removed 135 trials, equating to 14.06% of all trials. For the patients, the procedure removed 1 trial from LG’s data and 5 trials from JW’s data. Using the same criteria as Experiment 9b with BE’s data left only 18 completed trials. Therefore, as in Experiment 9a, BE’s correctly completed trials were not analysed.

7.6 Results

7.6.1 Control group performance

Saccadic reaction times

The overall mean SRT across all conditions for the control group was 308.55ms ($SE = 14.34$). The lower bound for the 95% confidence interval for the overall mean SRT was 276.61ms and the upper bound was 340.49ms.

A 3 way repeated measures ANOVA was conducted on the SRT data from the control group, with 2 levels on the factor Cue type (arrows, gaze), 2 levels on the factor SOA (300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent). The main effect of SOA was significant, $F(1,10) = 28.51$, $p < .001$. The main effect of

Congruency almost reached significance, $F(1,10) = 4.44$, $p = .061$, with participants quicker to correctly respond on congruent trials. The main effect of Cue type did not approach significance, $F < 1.00$, and neither did the SOA by Congruency or three way interaction ($F_s < 1.00$). Although the Cue by Congruency interaction did not approach significance, $F(1,10) = 1.97$, $p = .191$, there appeared to be a smaller congruency effect with arrows (4.72ms) than with gaze cues (16.56ms), as can be seen in Figure 7.6. The mean correct SRT, standard errors and upper and lower bounds of the 95% confidence intervals for each condition for the control group can be seen in Table 7.5, whilst Table 7.6 displays the mean SRT congruency effects and 95% confidence intervals for the control group.

Cue type	SOA (ms)	Congruency	Mean SRT (ms)	Standard error	95% confidence intervals	
					Lower	Upper
Arrows	300	Congruent	327.60	16.86	290.04	365.17
		Incongruent	334.35	16.19	298.28	370.43
	800	Congruent	282.60	13.37	252.80	312.40
		Incongruent	285.28	16.85	247.73	322.84
Gaze	300	Congruent	317.56	14.74	284.72	350.40
		Incongruent	338.85	15.91	303.40	374.30
	800	Congruent	285.16	15.81	249.92	320.39
		Incongruent	296.99	16.10	261.13	332.85

Table 7.5: Mean correct SRTs, standard errors and 95% confidence intervals for congruent and incongruent arrow and gaze cues at both SOAs for the control group.

Cue type	SOA (ms)	Mean congruency effect (ms)	95% confidence intervals	
			Lower	Upper
Arrows	300	6.75	-12.64	26.15
	800	2.68	-17.75	23.12
Gaze	300	21.29	10.20	32.38
	800	11.83	-6.02	29.68

Table 7.6: Mean congruency effects and 95% confidence intervals for gaze and arrow cues at 300 and 800ms SOA for the control group.

Error rates

68 errors were committed by the control group, representing 8.24% of completed trials. The mean error rate per participant was 9.32 % with a 95% confidence interval ranging from 4.22% to 14.43%. Error rates per condition per participant were calculated and a 3 way repeated measures ANOVA was conducted on the data, with 2 levels on the factor Cue type (arrows, gaze), 2 levels on the factor SOA (300ms, 800ms) and 2 levels on the factor Congruency (congruent, incongruent). None of the main effects or interactions reached significance, but this was not unexpected due to the small number of data points. Despite this, it is apparent from Figure 7.7 which shows the control data alongside that of the patients and Table 7.6, that there was a trend for the controls to make more errors on incongruent trials, particularly at 300ms SOA.

Cue type	SOA (ms)	Congruency	Mean error rate (% per condition)	Standard error	95% confidence intervals	
					Lower	Upper
Arrows	300	Congruent	5.18	2.78	-1.01	11.37
		Incongruent	13.91	6.15	.20	27.62
	800	Congruent	9.20	3.25	1.96	16.45
		Incongruent	12.16	5.17	.64	23.67
Gaze	300	Congruent	5.96	1.72	2.12	9.80
		Incongruent	13.83	5.25	2.13	25.52
	800	Congruent	7.97	2.90	1.51	14.42
		Incongruent	6.39	2.35	1.15	11.63

Table 7.7: Mean percentage of errors per condition per participant, as well as standard errors and 95% confidence intervals for congruent and incongruent arrow and gaze cues at both SOAs for the control group.

Anticipatory saccades

The frequency of anticipatory saccades made at least 80ms after the onset of the cue and until 80ms after the onset of the target was determined. 158 anticipatory saccades were made by the control group during this period, equating to a mean frequency per participant of 14.36 saccades, with 95% confidence intervals ranging from 5.51 to 23.22. As in Experiment 9a, no distinction was made between small and large anticipatory saccades.

A 3 way repeated measures ANOVA was conducted on the frequency data, with 2 levels on the factor Cue type (arrows, gaze), 2 levels on the factor SOA (300ms, 800ms) and 2 levels on the factor Cue direction (same, opposite). The main effect of SOA was significant, $F(1,10) = 7.30, p = .022$ with more anticipations made at the 800ms SOA ($M = 2.59, SE = .77$) than the 300ms SOA ($M = 1.00, SE = .28$). However, none of the other main effects or interactions reached significance ($F_s < 1.00$) although the 3 way interaction between Cue type, SOA and Cue direction was the closest to reaching significance, $F(1,10) = 2.54, p = .142$. The frequency of anticipatory saccades for the control group is displayed alongside that of the patients in Figure 7.8

7.6.2 Patients

Patient LG

As in Experiment 9a, LG performed the anti-saccade task without problem. Her mean SRT across all conditions was 316.21ms ($SD = 45.56$), within the normal range for controls. LG's SRTs in individual conditions were all within the 95% confidence intervals for controls.

Figure 7.6 shows mean SRTs for LG, the other patients and the control group in each of the conditions in Experiment 9b.

As can be seen in Table 7.8, LG showed normal cue congruency effects for arrow cues at both SOAs and atypical congruency effects for gaze cues at both SOAs, as she was outside the lower bound of the 95% confidence intervals. For both cue types at 300ms SOA, LG's congruency effects (albeit in the normal range for arrows) were close to zero.

Finally, LG made only one directional error and one anticipatory error during the anti-saccade task. When compared to the 95% confidence intervals resulting from the

control group error rate data, LG's directional error rate of 1.27% was atypically low, as was her rate of anticipatory saccades.

Cue type	SOA (ms)	Mean congruency effect (ms)	
		LG	JW
Arrows	300	-0.025	-49.64*
	800	8.50	-86.20*
Gaze	300	3.50*	149.50*
	800	-10.40*	-24.25*

Table 7.8: Mean congruency effects for gaze and arrow cues in the anti-saccade task at 300ms and 800ms SOA for the three patients. * indicates effect which is outside of the 95% confidence intervals for the control group, presented in Table 7.6.

Patient JW

JW's mean correct SRT was 528.51ms ($SD = 176.77$), far beyond the normal range for controls. As was found in Experiment 9a, there was a discrepancy between the SRTs of JW's left and right saccades. However, unlike in the pro-saccade task, where JW was found to be slower to saccade to the contralesional left hemifield, in the anti-saccade task, he was considerably slower to correctly saccade to the right hemifield ($M = 603.30$ ms) than to the left ($M = 324.55$ ms). This finding suggests that JW was experiencing attentional neglect in the contralesional (left) hemisphere as is often reported with lesions to this area of the cortex (Butter, Rapcsak, Watson, & Heilman, 1988; Damasio, Damasio, & Chui, 1980). The presence of such neglect would render detection of the peripheral target more difficult

when it appeared on the (contralesional) left of the screen which would have the effect of slowing the generation of the correct anti-saccade response. Despite this, of the 41 correct saccades JW made, 30 of those were made to the right hemifield, which presumably relates to intact saccade generating mechanisms in the unlesioned hemisphere. There appeared to be only a little difference between the amplitudes of left and right saccades however (left: $M = 8.87^\circ$; right: $M = 10.20^\circ$). When compared to the 95% confidence intervals for controls, JW's responses were all outside the upper bound, i.e. they were atypically slow.

JW's congruency effects were atypical in all cases. For arrow cues at both SOAs he showed very large incongruency effects (faster with incongruent cues than congruent cues). At 300ms SOA with gaze cues he showed a very large congruency effect (149.50ms) which reversed at the 800ms SOA to give an incongruency effect, all outside the values predicted by the control group data.

Out of the 75 trials JW completed, almost half (34) were directional errors in which the target was fixated, equating to an overall error rate of 45.33%. Of these errors, 26 were executed towards the target when it appeared on the right (ipsilesional) side of the screen, with only 8 executed to left hemifield targets, suggesting JW experienced attentional neglect to the contralesional side. 19 errors were produced with arrow cues and 15 with gaze cues. When cue and target were congruent, JW produced errors on 15 occasions. When incongruent, he produced 19 errors. There was a bigger difference between the number of errors on congruent versus incongruent trials for arrows (8 vs. 11) than there was for gaze (7 vs. 8). Two thirds of the errors were produced at the 300ms SOA. The number of errors was roughly equal in number when the cues were pointing left and right. When compared to the 95% confidence intervals for controls, JW made more errors than is typical in all conditions with the exception of congruent gaze cues at 800ms SOA. JW's error data can

be seen alongside that of the controls and patients in Figure 7.7 where his elevated error rates are evident.

The frequencies of JW's anticipatory saccades were similar to that of controls, as can be seen in Figure 7.8.

Patient BE

Delayed return to fixation

BE correctly completed only 18 trials, which were not analysed due to their low frequency. The reason that so many trials were excluded related to BE's inability to return to the fixation cross for the start of each trial. BE started 48 trials by fixating an area outside of the central region. Only 15 of these were on gaze cue trials. Figure 7.9 illustrates the number of trials starting on the same or opposite side to the target in the previous trial in the arrow and gaze condition. Unlike in the pro-saccade task, of these delayed return to fixation trials, most started on the side opposite the target in the previous trial.

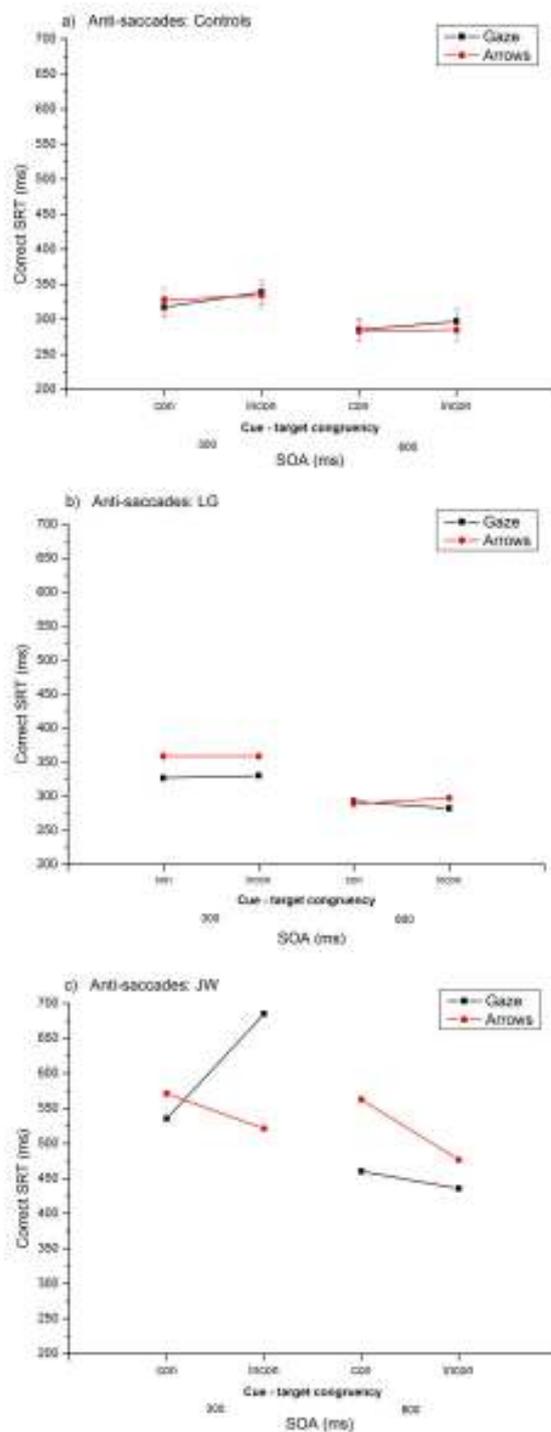


Figure 7.6: Mean correct SRT in the anti-saccade task with congruent and incongruent gaze and arrow cues at 300 and 800ms SOA for a) the control group, b) patient LG and c) patient JW. Error bars in a) represent standard error of the mean.

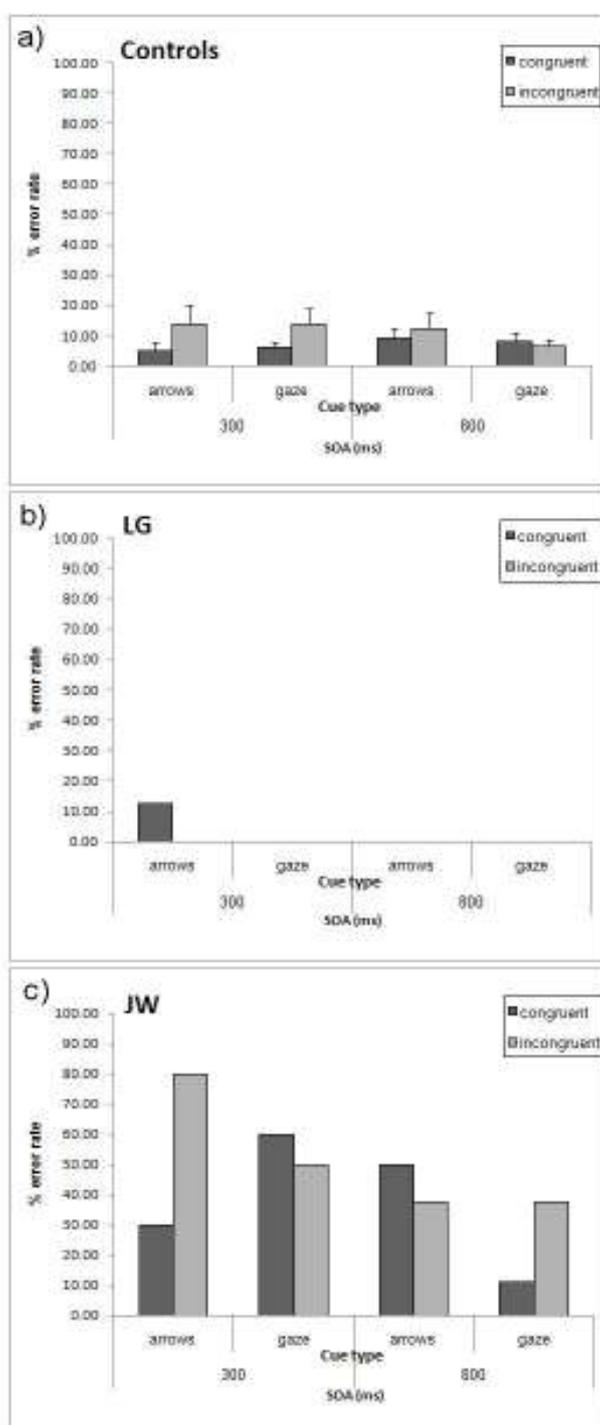


Figure 7.7: Mean percentage of errors per condition in the anti-saccade task for congruent and incongruent gaze and arrow cues at 300 and 800ms SOA in the anti-saccade task for a) controls, b) LG and c) JW. In a) error bars represent standard error of the mean.

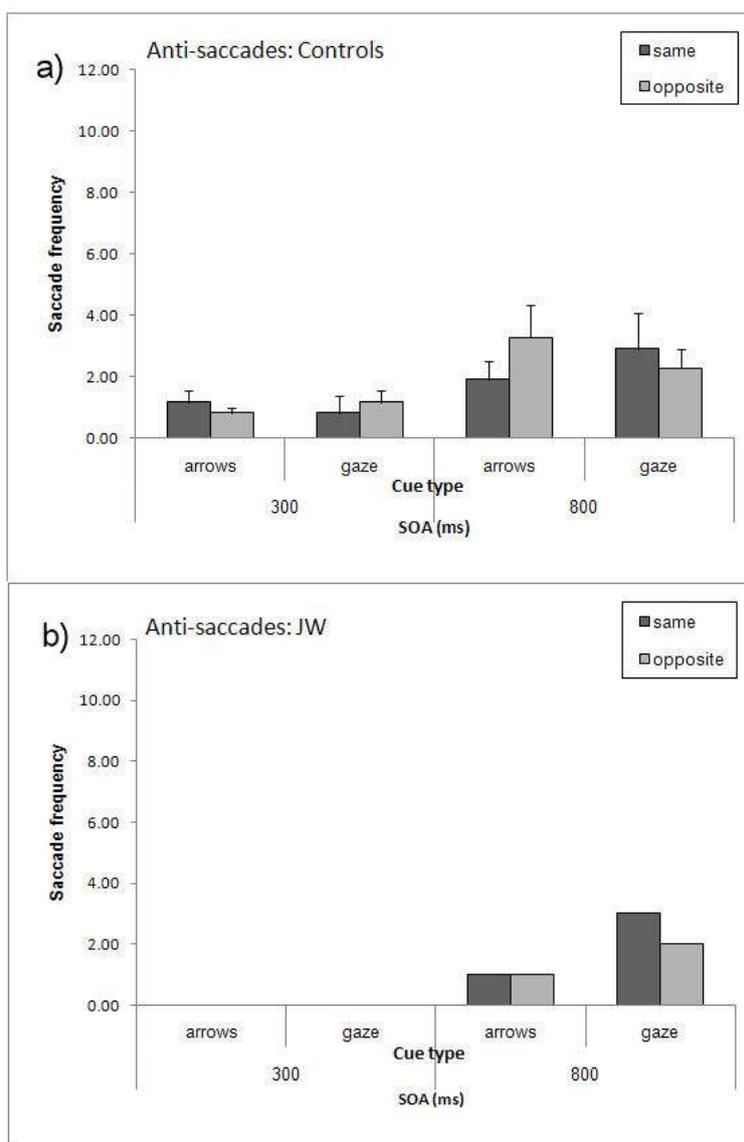


Figure 7.8: Mean frequency of anticipatory saccades in the anti-saccade task made in the same and opposite direction of gaze and arrow cues at both 300ms and 800ms SOA for a) controls and b) JW. Error bars in a) represent standard error of the mean. Patient LG made only one very small anticipatory saccade.

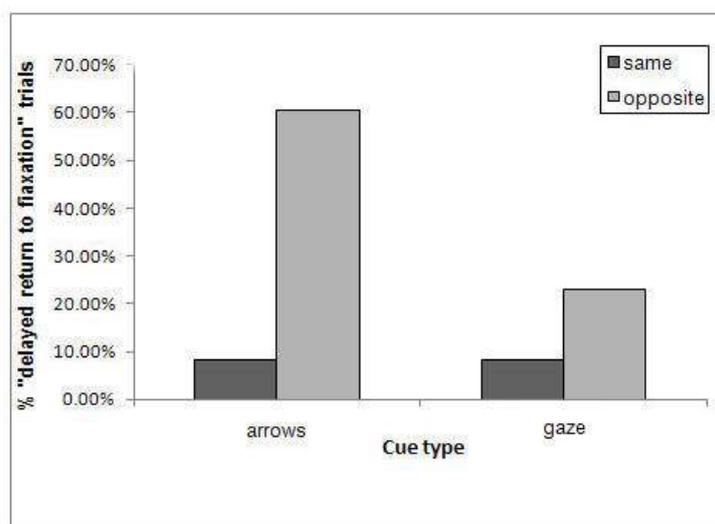


Figure 7.9: Trials in the anti-saccade task where patient BE's first saccade began on the left or right of the screen and the percentages of those trials that started on the same or opposite side to the target in the preceding trial.

7.7 General discussion

Experiment 9 sought to find evidence for the role of the orbitofrontal cortex (OFC) in automatic orienting to eye gaze cues. In Experiment 9a, patient LG, who has a bilateral lesion to the OFC and patients JW and BE who have lateral frontal cortical lesions, completed a pro-saccade task with gaze and arrow cues, along with a group of older control participants. In Experiment 9b, the patients and control group completed the anti-saccade version of the task. LG also completed two tasks of emotional and social processing.

The reaction time results from patient LG suggest that the OFC may have a role in the automatic processing of gaze cues. Despite being able to successfully discriminate between the left and right versions of both cue types, in the pro- and anti-saccade tasks LG showed reduced effects of the gaze cues whilst showing cueing effects in response to arrow cues. Orienting of attention at an SOA of 300ms may be considered to be more automatic

than at the longer, 800ms SOA where responses are liable to be influenced by volitional factors. Whilst at the shorter SOA in both tasks, the gaze cues had no effect on LG, at the longer SOA again in both tasks, she showed some influence of the gaze cues albeit in the opposite direction to controls (she was faster to saccade in the opposite direction to the cues in the pro-saccade task and in the same direction as the cues in the anti-saccade task, the reverse of the pattern seen in controls). The lack of automatic processing at the short SOA in the pro-saccade task was restricted to gaze cues only: LG's saccadic latency was influenced by arrow cues at 300ms SOA in the pro-saccade task, albeit again in the opposite direction to controls (LG was faster to respond on incongruent trials). Her responses to arrow cues in the anti-saccade task were comparable to controls, with no cueing effects apparent at either SOA.

In contrast to patient LG, JW was generally influenced by the cues to a greater extent than the controls. Unfortunately, as BE found both tasks difficult (the reason for this will be discussed in detail in a subsequent section), insufficient data was collected from this patient. However JW had had no difficulty in performing either pro- or anti-saccade tasks, despite the apparent presence of attentional neglect in his contralesional (left) hemisphere, a disorder frequently associated particularly with damage to the right frontoparietal cortex (Butter et al., 1988; Damasio et al., 1980). This resulted in JW's saccadic responses being slower than both controls and LG. In the pro-saccade task, this was because JW's responses were slower to the contralesional left hemisphere as he was less able to detect targets appearing there. In the anti-saccade task, his responses were slower to the ipsilesional right, which is consistent with difficulty in detecting the anti-saccade "target" on the left of the screen which would slow the programming of the correct anti-saccade response. Despite this, at the short SOA in the pro-saccade task, JW's congruency effects were comparable to

controls for both cue types. However at 800ms, JW was much faster to saccade in the opposite direction to both gaze and arrow cues (i.e. he was faster on incongruent trials). This incongruency advantage was also present in LG with gaze cues at 800ms SOA, albeit to a lesser degree (Figure 7.3; Table 7.4).

An apparent dissociation between the effects of gaze and arrow cues emerged in the frontal lateral patient JW in the anti-saccade task. At 300ms SOA, whilst being quicker to respond in the opposite direction to gaze cues like controls, he was faster to respond in the same direction as arrow cues, unlike controls (Figure 7.6; Table 7.8). This finding suggests that not only are gaze and arrow cues being processed automatically by JW, but that the processing of the two types of cue may be occurring via different mechanisms. Also unlike controls, JW was faster to saccade in the same direction as the cues at 800ms SOA. Although the gaze imitation hypothesis suggests that people automatically generate saccades in the direction of averted eye gaze, this thesis has challenged this view by demonstrating that the direction of the automatic response can be modulated, and indeed reversed, by altering the task instruction: Whilst in the anti-saccade task, arrow cues have less effect on saccadic responses, eye gaze cues cause a facilitation of SRTs in the *opposite* direction to the cue, and opposite to the direction of facilitation seen in the pro-saccade task. In respect of gaze cues, JW was relatively normal in the direction of his responses at 300ms SOA: He was faster to respond in the opposite direction to the gaze cues. However, his responses to arrow cues were not normal. Not only did they show large discrepancies between the SRTs on congruent and incongruent trials where controls show only small effects, he was a great deal faster to respond in the *same* direction as the arrow cues (Figure 7.6; Table 7.8). It appears, therefore, that patients with damage to the lateral frontal cortex may be less able to assert the same degree of “task level” control over

their responses as controls, and as the effect occurs only for arrow cues at the short SOA, suggests a stronger influence of this cue type on patients than on neurologically healthy controls.

The facilitation of response times in the same direction as both cue types seen with JW at the longer SOA in the anti-saccade task may reflect the involvement of different temporally dependent mechanisms than those responsible for the 300ms SOA effects. Indeed, LG who appeared unaffected by the gaze cues at 300ms SOA also produced an incongruency advantage at 800ms SOA like JW. With almost one second to programme the anti-saccade response, any influences of the cues cannot be regarded as automatic, as it is likely that more conscious or strategic influences (e.g. trying to predict the location of the target based on the cue direction) may be affecting performance on the task, causing more spatially direct cue-response facilitation.

The above section describes the individual influence of the cues on LG and JW's SRTs. But there is a more general dissociation in the magnitude of LG's oculomotor responses and those JW described above which extends further than just SRT. JW's error rate in the anti-saccade task approached 50% , whereas LG produced only one error in the course of the anti-saccade task (Figure 7.7). Although a clear picture of the influence of the cues on error rates did not emerge for the patients or the control group, the elevated error seen with JW is consistent with the literature on the role of lateral frontal cortex in inhibitory control of oculomotor behaviour. Guitton et al. (1985) first described elevated error rates in the anti-saccade task in patients with unilateral lesions to the frontal cortex. Work by Walker et al., (1998) demonstrated 100% error rates on anti-saccade tasks in a patient with a lesion to the right ventral and dorsal lateral frontal cortex (a similar locus to the lesions of JW current study), although error rates more comparable to those observed

here have been reported by Hodgson et al. (2007) in patients with lesions limited to ventrolateral frontal cortex.

One further measure, the frequency of saccades spontaneously generated after the onset of the cue but before the onset of the target, provided further evidence for differential levels of oculomotor control between LG and the lateral frontal patients. During this interest period, saccades generated despite the explicit instruction to maintain fixation throughout, can be considered to be spontaneously or automatically generated. Any discrepancy between the frequency of left and right saccades in this period can be attributed to the possible influence of the directionality of the cues. In LG's case, neither gaze nor arrow cues caused spontaneous saccadic execution during the period that only the cue was visible, in either pro- or anti-saccade tasks. Her complete lack of saccadic activity could be considered "supra-normal" in that every control participant produced at least several saccades during this period, with the mean rate per participant between 14 and 24 depending upon the task. JW showed a level of saccadic activity during this period which was comparable to controls in both tasks.

The performance of BE in the pro- and anti-saccade tasks highlighted a common but as yet not well documented feature of patients with damage to the frontal cortex (anecdotal observation of supervisor). BE, although appearing to understand the task instructions was unable to shift his point of gaze back to the central fixation cross for the beginning of every trial. Instead his starting position was influenced by the location of the target on the previous trial. In the pro-saccade task, BE tended to start more trials on the side of the screen where the target had been in the previous trial, whilst in the anti-saccade task he started more often on the side of the screen opposite to where the target had been on the previous trial. These findings suggest that BE continued to fixate the side of the correct

response on the previous trial in both tasks, which may be due to a failure of the oculomotor disengage mechanism. Alternatively, it may be characterised as a form of oculomotor apraxia, an inability to make purposeful eye movements. Interestingly, the locus of BE's lesion may encroach onto the frontal eye fields (FEF) according to one meta-analysis (Mort et al., 2003). Indeed damage to the left FEF (the same hemisphere as BE's lesion) has been shown to cause difficulty in disengaging from visual stimuli (Rivaud et al., 1994). In addition, BE's tendency to make considerably smaller amplitude saccades to the right hemifield is also consistent with left FEF damage (Rivaud et al., 1994). These two possible explanations for BE's behaviour – failure of oculomotor disengagement or oculomotor apraxia – may be quite distinct possibilities. Should his behaviour relate to a deficit in disengaging the saccadic system from visual stimuli, rather than from an inability to make purposeful, voluntary eye movements, it would be anticipated that it would only manifest in the presence of visual stimuli. This could be investigated by asking BE to follow moving points on a computer screen and observing whether he was able to shift his gaze from one point to the next. The alternative explanation, that he is unable to make voluntary eye movements, could be tested in the same manner, but instead of the presence of visual stimuli he could be verbally instructed to saccade to the same locations on the computer screen.

The evidence from the frontal lateral patient, JW, points towards a heightened sensitivity to arrow cues relative to both controls and patient LG which may result from a deficit in inhibitory oculomotor control observed more generally in JW. These findings implicate the lateral frontal cortex in mediating inhibitory oculomotor control in neurologically healthy individuals when successfully performing pro- and anti-saccade tasks in the presence of gaze and arrow cues.

Although evidence has been provided earlier in this thesis, which suggests that social cues have a greater quantitative influence on oculomotor responses than non-social cues, the findings from the current chapter have added weight to the claims in the literature that eye gaze and arrow cues are categorically distinct directional cues, their effects on attention and eye movements subserved by separable cognitive and neural processes. OFC patient, LG, was unaffected by the gaze cues in either task at the short SOA, but she also demonstrated some deficits in social and emotional processing as indicated by her results on the Reading the Mind in the Eyes test (Baron-Cohen et al., 2001) and the Faux Pas Recognition test (Baron-Cohen et al., 1999; Stone et al., 1998). These findings suggest the presence of a relationship between orbitofrontal cortex, orienting to gaze cues and social and emotional functioning and may provide a clue to why patients with OFC damage often encounter difficulties in social situations. If sensitivity to the normal social cues that most people take for granted is removed, then so too is one method of determining intentions and emotional states in others which can only hinder effective social interaction. The idea that the perception of eye gaze direction assists in the attribution of mental states in others is not new (e.g. Baron-Cohen, 1995; Baron-Cohen, Campbell, Karmiloff-Smith, Grant, & J. Walker, 1995; Calder et al., 2002; Emery, 2000; Lee, Eskritt, Symons, & Muir, 1998), but the view that desensitisation to other peoples' eye gaze might contribute to inappropriate social conduct in people with brain injuries is a novel one.

This conclusion that may be drawn from LG's results, that automatic orienting to eye gaze occurs because it is a specifically *social* stimulus, and not simply because of the development of a stimulus-response association, is not without challenge. In the only other report of responses to eye gaze cues in a patient with OFC damage (Vecera & Rizzo, 2004,

2006), the authors concluded that the reason patient EVR did not respond automatically to non-predictive gaze cues or predictive word cues, is that the OFC is responsible for the learning and implementing of rewarding stimulus-response associations of all kinds, social and non-social, and that damage to this area disrupts these associations. However, whilst a wealth of evidence exists in support of this role for OFC (e.g. Bechara, Tranel, & Damasio, 2000; Kringelbach & Rolls, 2004; Rolls, 2004), Vecera and Rizzo's suggestion does not account for LG's apparently automatic processing of arrow cues in the pro-saccade task. However, without further examination of patients like LG, strong conclusions cannot be drawn as to the precise function of OFC in processing of socially and non-socially relevant stimuli.

7.8 Conclusions

Although clearly preliminary and utilising individual rather than groups of patients, Chapter 7 has provided a second case of the absence of automatic orienting to eye gaze cues in a patient with OFC damage, who also showed some deficits in "social intelligence". In addition, it has demonstrated that a patient with a lesion to the lateral frontal cortex appears to have an intact automatic gaze processing system, but atypical responses to arrow cues, suggesting the possibility of dissociable neural substrates for gaze and arrow cues. Finally, Chapter 7 presents evidence in support of the use of pro- and anti-saccade tasks as potentially useful tools in the identification of social and emotional difficulties after damage to the frontal cortex.

Chapter 8: *Towards a neurocognitive model of saccadic orienting to socio-biological cues*

8.1 Aims of the thesis

This thesis set out to test the hypothesis that eye gaze cues cause automatic or imitative eye movements in observers and investigate whether such effects are also seen with other social, biologically relevant cues (finger pointing) and non-social cues (arrows and words). Pro- and anti-saccade tasks as well as gap versions were used to explore the effects of these cues on the saccadic system under varying cognitive and attentional demands. The importance of ecological validity of eye gaze and arrow cues was examined, as was the relationship between autistic traits and susceptibility to gaze and arrow cues. Finally, the oculomotor responses of three neurological patients to gaze and arrow cues were investigated in an attempt to assess the existence of differential neural substrates in the processing of social and non-social cues and more generally the feasibility of using cueing pro- and anti-saccade paradigms with neurological patients

8.2 Overview of the chapter

In this final chapter, the empirical findings of this thesis will be interpreted in terms of the original objectives. It will begin by detailing the evidence in support of automatic programming of eye movements by social and non-social cues. It will then go on to propose the mechanism by which some cues can come to achieve “special” status whilst others do not. Task dependent effects of the cues will then be discussed. The

neuropsychological evidence from patients LG and JW will then be interpreted in terms of a neural model that explains eye movement orienting in response to social and non-social cues. The role of eye gaze specifically in social behaviour will be discussed, followed by some conclusions relating to the part that ecological validity may play in the study of social attention. An adaptation to an existing model of saccade generation will be presented which accounts for the orienting effects of both social and non-social directional cues before the limitations of the research, potential directions for future research and the wider implications of the current work are explored.

8.3 The influence of social and non-social cues on saccadic eye movements

8.3.1 Automatic, but not “imitative” programming of eye movements by gaze, pointing and arrow cues

The central aim of this thesis was to find evidence of a direct or “automatic” activation of the oculomotor system by eye gaze cues, thereby supporting the gaze imitation hypothesis. Whilst this thesis presented evidence that *both* gaze and arrow cues can cause automatic saccadic responses, these effects are more robust and pronounced in response to gaze cues, with arrow cues appearing to be more susceptible to top-down cognitive control than gaze cues, as demonstrated by greatly reduced influence of arrow cues in the more cognitively demanding anti-saccade task (Experiments 3 and 5). Evidence from two neurological patients with different loci of frontal lobe damage further supports this view, and suggests that the reason for this may be because orienting to gaze and arrow cues, at least to some extent, rely on different neural substrates.

Chapters 2 and 3 demonstrated that in a pro-saccade task, real-world, ecologically valid gaze and arrow cues cause equivalent reductions in saccadic latencies towards targets located in the cued direction. Furthermore, in Experiment 3, overt oculomotor responses by way of spontaneous saccades were produced in the direction of the cues even when participants had been explicitly instructed to ignore them. It was further demonstrated that these SRT congruency advantages were not caused by people making small saccades in the cued direction before the target appeared. This finding therefore strongly argues against “spatial-correspondence” explanations of symbolic cueing, which suggest that asymmetric cues cause a bias in attention towards the side with greatest perceptual information (Downing et al., 2004; Lambert & Duddy, 2002; Muller & Rabbitt, 1989). There was some evidence that the naturalistic gaze cues may have caused more pre-response oculomotor activation than arrow cues, but this may have been due to participants looking back and forward between the two eyes of gaze cue stimuli. Aside from this latter observations, in the pro-saccade task, gaze and arrow cues were indistinguishable in their effects on saccadic responses.

In the anti-saccade tasks presented in Chapters 2 and 3 (Experiments 2 and 4), a different pattern of results emerged which is strongly suggestive that eye gaze has a more pervasive influence on the oculomotor system than arrows, being more resistant to top-down control. In Experiment 4, arrow cues were much less influential on SRTs than gaze cues and in Experiment 2 they had no effect at all. The anti-saccade task requires participants to avoid making the prepotent pro-saccade towards a sudden onset target, in favour of making an anti-saccade to the mirror opposite location. The process of inhibiting the reflexive response requires what participants themselves describe as

“more concentration” than the pro-saccade task, which in neuropsychological terms is achieved by increased activity in ocular fixation or attentional engagement mechanisms. It would appear that this voluntary cognitive engagement may over-ride most of the automatic effects of the arrow cues on saccadic response times, but that the automaticity of the gaze cue response is relatively unaffected under these conditions. In addition to the effects of cue direction on SRT, response times were generally quicker with eye gaze cues. Here then, this thesis presents evidence that the orienting caused by gaze cues is more automatic than that caused by arrow cues and therefore that eye gaze cues may be “special”.

The distinction between the two types of cue in the anti-saccade task is largely restricted to SRT. The cues had comparable effects on both overt spontaneous saccades made before the onset of the target and on pro-saccade errors during the reaction time period, although as observed and described with Experiment 3, people made more small saccades before the target onset with gaze cues.

However, it would appear that gaze cues are not alone in producing robust and automatic effects of eye movements in both pro- and anti-saccade tasks. Experiment 6 demonstrated that photographic finger pointing cues were able to cause the same effects on SRT and anticipatory saccades as gaze and arrow cues in the pro-saccade task, but in the anti-saccade task they appeared to be even more effective than gaze cues in producing automatic facilitation of SRTs. This finding suggests that social biological cues may have privileged access to the saccadic system, rather than there being some inherent special property of eye gaze specifically, an issue which will be discussed in detail in a later section. However, caution should be exercised when interpreting the magnitude of effect sizes across separate experiments performed by

different groups of participants. Although the pointing cues appeared to have even greater influence on saccadic responses than gaze cues, this is not statistically justifiable. The only firm direct comparisons regarding the magnitude of congruency advantages can be made between cues examined within the same experiment (i.e. between gaze and arrow cues). Nevertheless, it is clear that pointing and gaze cues both caused reliable congruency advantages in both the pro- and anti-saccade task. However, it might also be argued that as the four different cue types were not balanced in any regard, except in the attempt to equate their likeness to familiar everyday stimuli, the differences between the effects of the cue could be attributed to differences in perceptual processing of the cues. Although this may seem a reasonable critique, by perceptually matching the stimuli used in the current research, one of the central aims of the thesis would be negated: To investigate responses to real-world stimuli. In order to do this, an acceptance of the stimuli's inherent dissimilarities is essential.

In contrast to arrow cues, directional word cues caused no facilitation of saccadic responses in either pro or anti-saccade tasks, suggesting that not all familiar directional stimuli are capable of automatically recruiting the saccadic system. Although it could be argued that the semantic meaning of the word cues take longer to extract than it does from any of the other cues examined, SOAs of almost one second did still not allow a congruency advantage to emerge. It is therefore probable that directional word cues are not processed via the same cognitive mechanisms as gaze, arrow and pointing cues, and instead are reliant on more voluntary attentional processes.

8.3.2 The acquisition of cue-response associations

The findings of this thesis indicate that social and non-social directional cues can cause automatic facilitation of eye movements in their direction. Not only this, but with certain cues under certain circumstances the relationship between the cue direction and the response can be effortlessly reversed as will be discussed in the next section. But before a relationship can be reversed, it must first be established.

The social cues of eye gaze and finger pointing investigated in this thesis had robust and pervasive effects of eye movements, regardless of the task. Arrow cues caused reliable congruency effects in a simple pro-saccade task, but their influence in the anti-saccade task was much reduced in comparison to gaze cues. Directional word cues had no effect on saccadic responses in either pro- or anti-saccade task. How can this range of cue influence be explained? An explanation can be found when considering the development of stimulus-response associations through associative learning mechanisms.

As discussed in the introduction to this thesis, although some researchers have regarded the perception of gaze direction as an innate ability present from birth (Baron-Cohen, 1995; Farroni et al., 2002, 2004), a more common view is that gaze following is an acquired response, where infants learn that objects and events of interest happen where other people are looking (Corkum & Moore, 1998), with the outcome that eventually, just the perception of the averted gaze of another causes spontaneous gaze following in the infant (Butterworth & Jarrett, 1991; Corkum & Moore, 1998; Morales et al., 1998). At the neural level, connections between neurons for action and perception become strengthened through repeated activation (Hebb, 1949) so that responses can be activated by the presentation of the stimulus alone. Different brain regions are thought to be responsible for rewarding associations related to primary reinforcers such as pain and pleasure, including

social reward, thought to rely on the OFC (Rolls, 1999) whereas more arbitrary stimulus-response associations are thought to be mediated by more lateral frontal cortical areas (Petrides, 1997).

If such stimulus-response associations mediate the responses to all cues which appear to have an automatic effect on the saccadic system, it is logical that those cues to which individuals have had the most exposure and therefore the greatest strengthening of those associations, should have the greatest and most pervasive influence on eye movements. Of the four cues investigated in this thesis, the social cues of finger pointing and eye gaze were clearly the most effective in their influence as well as being likely to be the most frequently encountered of the four in the wider world, being involved in the development of joint attention from the first year of life. In addition, they are arguably the most rewarding stimuli of the four cues examined. A lack of appreciation of the rewarding nature of eye gaze has been posited as one reason that individuals with autism fail to spontaneously follow the gaze of others (Mundy & Sigman, 2006). Therefore, this combination of rewarding value and extensive exposure may be the answer to why social cues have a more automatic influence on oculomotor responses than other cues.

A further issue relates to the role of mirror neurons, which are active not only when an action is performed but also when the same action is observed in someone else (Fogassi et al., 2005; Gallese et al., 1996; Rizzolatti et al., 1997). Perhaps these neurons constitute a third possible mechanism in the formation of particularly strong stimulus-response associations for social cues. Perhaps we learn to imitate others' gestures because of the existence of such neurons. Such an explanation would suggest that imitation may be an innate ability, as the eye gaze following from birth literature might also suggest. A recent article by Heyes (2010) argues against this view. Mirror neurons, it is argued, are also the

product of associative learning. Their development occurs through the simultaneous execution of action by others, for example when a parent imitates an infant's facial expression. Furthermore, despite early reports, the evidence of imitation from birth is sparse, limited to some accounts of tongue protrusion, which has been alternatively attributed to a general arousal mechanism rather than imitation (Anisfeld, 1996; Jones, 2009). Therefore, an innate mirror neuron system seems an unlikely candidate for the development of automatic orienting to social cues such as gaze and arrows. Moreover, it would be difficult to explain the automatic effect of arrow cues on eye movements observed under some conditions, by a mirror neuron account. Rather, the effects of gaze and pointing cues described in the current research are likely to be the product of early to develop and constantly reinforced stimulus-response associations, which perhaps do result in the emergence of mirror neurons, but are unlikely to be caused by them.

The following section will explore how, once such stimulus-response associations are acquired, they might be reversed as demonstrated in this thesis.

8.3.3 Task dependent re-mapping of responses to social and non-social cues

Although in the anti-saccade tasks, gaze (and pointing) cues had what might be described as an *automatic* effect, in that it could not be completely suppressed, it was not imitative as it was predicted to be by the gaze imitation hypothesis. Whereas in the pro-saccade tasks, gaze, arrow and pointing cues caused facilitation of responses in the same direction as the cue (a direct stimulus-response association), in the anti-saccade tasks, the gaze and pointing cues in particular facilitated oculomotor programming in the *opposite* direction (a reversed mapping between stimulus and response). In terms of the gaze imitation hypothesis specifically, this reversal of direction of responses from

pro- to anti-saccade tasks demonstrates that imitative eye movements in response to observing averted eye gaze in others, is not an obligatory outcome: Top-down factors such as in this case, the task instruction to make an anti-saccade can disrupt the direct spatial association between cue and motor response. For the same reason, responses to eye gaze cannot be described as reflexive, as the predominant view in the literature asserts.

An initial explanation for the finding that responses were facilitated in the opposite direction to the cues in the anti-saccade task was that on congruent trials, where the cue pointed towards the target, and therefore in the *wrong* direction for a correct anti-saccade, the cue caused a shift of covert attention in the direction of the target. This meant the onset of the target may have been detected more quickly than had the cue been pointing away from it. This early facilitation of target detection would speed the programming of the saccadic response in the correct (opposite) direction. It was further proposed that the observation that in Experiments 4, 7 and 8, participants produced more pro-saccade errors, again in the opposite direction to the gaze and arrow cues (i.e. where cue and target were incongruent), occurred due to the same mechanism: The cue had caused a shift of attention to the empty side of the screen and the sudden onset of the target on the opposite side had a capturing effect on attention and saccades, activating the visual grasp reflex and resulting in an error saccade to the target.

However, several issues argue against this interpretation of the effects seen in the anti-saccade task. Firstly, the pre-motor theory of attention (Rizzolatti et al., 1994, 1987; Sheliga et al., 1997, 1994) states that apparent shifts of covert attention are actually by-products of the oculomotor system preparing a saccade to the same

location. In the current explanation, if covert attention was facilitated in the same direction as the cue, so should the motor response, leading to faster response times and more overt errors in the cued direction. This is not what was observed. Secondly, In Experiment 7 people also made more anticipatory saccades in the opposite direction to the cues even before a target stimulus was present. Similar trends were seen in other experiments which contrast with the rates of anticipatory saccades in pro-saccade tasks, which were always significantly greater in the cued direction. These effects cannot relate to early target detection via covert attention, as there was no target present when these saccades occurred. Instead, these findings argue that the learned association between cue and response can be reversed via task level control.

The effect of peripheral *pro*-cues in an anti-saccade task has been reported by Weber et al. (1998). A pro-cue occurs always in the correct location for the anti-saccade response prior to the onset of the target and therefore at the opposite location to the cue (i.e. the target and cue are incongruent). The 100% validity of the cue relative to the correct saccade location was anticipated by the authors to improve anti-saccade performance relative to when no cue was present, as participants would be able to commence the programming of a saccade to the cued location before the target appeared which at short SOAs, should happen reflexively as the cues would “capture” attention automatically. However, the opposite was found to be the case. Correct SRTs were slower when the pro-cue was present and error rates higher, than when no cue indicated the correct response location. There are clear parallels between Weber et al.’s findings and those from the anti-saccade tasks in this thesis. In their task the cue was a sudden onset peripheral stimulus as opposed to a centrally presented symbolic cue, but

it was always incongruent (it always appeared in the opposite location to the target). The effects on SRT and error rates are the same in Weber et al.'s task as with the incongruent social cues in this thesis. The explanation put forward by these authors also accounts for the effects on anticipatory saccades observed in some experiments in this thesis. They suggested that participants adopt a task-set or "anti-response mode" when they perform the anti-saccade task. They are prepared to initiate a saccade in the opposite direction to a sudden onset stimulus and when they encounter the pro-cue in Weber et al.'s task, the "go opposite" instruction is transposed onto it, and a saccade is generated away from it: "anti-orienting", as Weber et al. describe it. A similar result was reported by Reuter, Herzog, & Kathmann (2006). These authors showed peripheral cues on correct and incorrect sides for a subsequent anti-saccade, and also found that participants were slower and made more errors when the cue appeared at the opposite side from the target (i.e. when cue and target were incongruent, equivalent to Weber et al.'s pro-cue task) than when the cue appeared on the same side.

That this effect, where saccades are facilitated in the opposite direction to cues, also happens with socially relevant symbolic cues in particular is important as it implies that symbolic, social cues are processed in the same way as the sudden onset peripheral cues in Weber et al. and Reuter et al.'s experiments (orienting to which is usually described as "reflexive"; however, even the accuracy of this term for such exogenous cues must be questioned if task set can over-ride their influence on saccadic behaviour).

What cognitive mechanisms underlie the anti-responding seen in this thesis and previous studies? One possible explanation relates to the "remote distractor effect" (Walker, Deubel, Schneider, & Findlay, 1997). If a visual saccade target appears in close

temporal proximity, but at the mirror opposite location to an irrelevant distractor stimulus, saccadic latencies are increased relative to when the two stimuli appear in the same hemifield. In terms of Findlay and Walker's (1998) model of saccade generation, the two remote stimuli increase competition in the WHEN pathway, thereby increasing response time. It is possible that the same process underlies the anti-responding seen in this thesis. On congruent trials, the cue and the target activate the same location on the salience map, whereas on incongruent trials, the cue and target activate opposite spatial locations on the map (refer to Figure 3.5 for 2D representation of activity on the salience map in congruent and incongruent conditions). Therefore, on incongruent trials, the target stimulus may act as a remote distractor. The competition between the two activated points on the salience map influences the WHEN pathway and has the effect of increasing the latency of correct anti-saccade responses, relative to congruent trials, where no competition needs to be resolved.

A further possible suggestion comes from the work on saccade trajectories in response to irrelevant distractor stimuli, including gaze cues. For example, Nummenmaa and Hietanen (2006) showed that when participants were required to make a vertical saccade to a target at the same time as an irrelevant gaze cue looking towards the left or right of the screen, the trajectories of the saccades curved away from the cued location. Furthermore, in a recent study by Hermens and Walker (2010) using a similar paradigm, the trajectory of saccades again deviated away from the direction cued by gaze cues. However, these authors demonstrated qualitatively similar effects with arrow cues, which emerged at an even earlier SOA than with gaze cues. The mechanism for this effect on saccade trajectories is thought to occur through oculomotor inhibition of the cued location. As in the anti-saccade task, participants

must try to ignore the cues and instead initiate saccades towards another area of the computer screen. When the saccade target and cue are presented in temporal proximity, competition ensues between the two activated locations on the saccade motor map, described in an earlier section. The resulting curvature away from the cued location reflects the inhibition of that location on the motor map as the participant attempts to ignore the cue as they make their correct saccade to the target (Hermens & Walker, 2010).

Could such a mechanism of inhibition of the cued location be responsible for the task-dependent effects of the gaze, pointing and to a lesser extent, arrow cues in this thesis? Although compelling, there are reasons why this account does not fully explain the present results. Firstly, as Hermens and Walker point out, inhibition of the cued location appears to take some time to build up (maximal at 300ms SOA in their experiment), whereas the facilitation of SRTs in the opposite direction to the cues in this thesis was already present at 100ms SOA. Furthermore, even basic arrow cues (< and >) caused the same trajectory deviation as gaze cues in Hermens and Walker's study, whereas they had less robust effects in the work presented here.

Despite these unresolved issues, there is clear merit in an account which involves inhibition of prepotent responses in producing the facilitation of saccades in the opposite direction to the cues in the anti-saccade task. The anti-saccade task is usually described as consisting of two components: The inhibition of the prepotent saccade to the target and the programming of a voluntary saccade away from it. This "don't look/go opposite" task set appears to have neuronal correlates: Even the instruction to make an anti-saccade is associated with increased activity in fixation neurons in the SC (Everling & Munoz, 2000) as well as increased activity in frontal and

parietal cortex (Ford et al., 2005) before the target even appears. However, it seems that if a cue which is of sufficient salience, such as a pair of eyes or a pointing hand is presented before the imperative stimulus, it is processed within the “don’t look/go opposite” task set where inhibition of prepotent responses is integral.

8.3.4 Neuropsychological evidence

The evidence presented in Chapter 7 from the neurological patient JW, suggests that the implementation of this anti-response task set may rely upon lateral areas of the frontal cortex. Patients with lesions to this area of the brain have repeatedly been shown to be impaired on the anti-saccade task in that they produce elevated rates of error saccades towards the targets (Guitton et al., 1985; Hodgson et al., 2007; Walker et al., 1998).

However, not only did JW have these same high error rates, he also appeared to lack the task dependent effects of arrow cues. Whereas controls show reduced influence of the arrow cues on responses in the anti-saccade task relative to the pro-saccade task, which if present at all, are also reversed as they are with gaze cues in the anti-saccade task, JW was not only greatly influenced by the arrow cues, but the direction of the effect did not reflect the typical “anti-response”, as they were faster to respond in the same direction as the cues. Importantly, however, this lack of task-set implementation did not influence JW’s responses to gaze cues, where his automatic responses were in the opposite direction to the cues, like controls. This latter finding therefore suggests dissociable neural substrates for the processing of gaze and arrow cues. Furthermore, that the influence of gaze cues was not disrupted by JW’s frontal lateral lesions suggests that gaze cues may be processed more automatically than arrow cues, without the need for the same level of involvement from frontal cortex.

In contrast to patient JW, OFC patient LG performed the anti-saccade task almost flawlessly. In addition, she showed the typical reduced effect of arrow cues in the anti-saccade task relative to the pro-saccade task, suggesting that she was exerting task level control that JW could not. However, LG did not show a congruency advantage for gaze cues at the shorter SOA in either task. The data from the patients therefore suggests a possible double dissociation between normal processing of gaze and arrow cues: Typical automatic responding to arrow cues, but not gaze cues requires lateral frontal involvement, whereas normal processing of gaze cues requires OFC whereas arrow cues do not.

The fact that JW still responded in the opposite direction to gaze cues in the anti-saccade task, as well as generally appearing to understand the anti-saccade instruction, suggests that he was able to reverse the direct mappings between stimulus and response. His deficit appears to be more related to the implementation and control of that mapping. This suggests that the anti-response task set is not a unitary process but rather encompasses different components underpinned by different regions of the cortex. A likely candidate for the inversion or re-mapping of the cue-response association is the posterior parietal cortex, areas of which have been shown to be specifically active during the anti-saccade task (Ford et al., 2005; Medendorp, Goltz, & Vilis, 2005; Zhang & Barash, 2000). In particular, some studies have demonstrated an inter-hemisphere shift of activation in the intraparietal sulcus (IPS) during the anti-saccade task, thought to reflect the shift from stimulus location encoding to saccade location encoding during the vector inversion process (Medendorp et al., 2005; Moon et al., 2007). Therefore, the IPS may also be responsible for the reversal of the cue-response mapping, if it is being processed by the same task-set as the anti-saccade target.

A model for the processing of social and non-social cues in the anti-saccade task is therefore proposed from the findings of this thesis and those from the neuroimaging and neurophysiological literature on the anti-saccade task and is presented in Figure 8.1. In this model, the instruction to make an anti-saccade is received via the lateral frontal cortex. Within this area, arbitrary stimulus-response associations are formed, such as those between the direction implied by an arrow and the motor response associated with that. Importantly, in this model, this area of the lateral frontal cortex is preserved in patient JW. This element of the model accounts for the presence of an arrow stimulus-response association in this patient, despite his lesion involving this general area of the cortex. The processing of non-social stimuli such as arrows is performed by the lateral frontal cortex whilst social stimuli are processed via the orbitofrontal cortex, which is known to be involved in the formation of reward contingent stimulus response associations. The processing of these social cues does not require involvement of the lateral frontal cortex in this model. This accounts for JW's normal processing of gaze cues. The direction of both social and non-social cues are remapped within the "anti-response" task set via connections from the intraparietal sulcus, which effects the motor response, to orbitofrontal and lateral frontal cortex respectively. However, this only occurs for non-social cues if the original stimulus response association is strong enough. This will vary across individuals, and could be dependent on individual differences such as gender and level of autistic traits. If it is not initially strong, the association will be overridden altogether and the mapping will not be reversed. That the processing of social cues occurs without the involvement of lateral frontal cortex renders social cues less susceptible to top-down control than non-social cues, as has been demonstrated in the anti-saccade experiments presented in this thesis.

The model accounts for the finding that lateral frontal patient JW, as well as performing poorly on the anti-saccade task, also failed to reverse the mapping between arrow cue and response but was able to do so for gaze cues. Furthermore, it allows for the fact that in controls, non-social cues have little effect but if present at all their effects are reversed relative to the pro-saccade task. Furthermore, it accounts for the almost flawless anti-saccade performance of LG, who showed a normal absence of arrow anti-responding but atypically showed no effects of gaze cues. Finally, the model also explains the reduced frontal cortex activation in response to gaze cueing compared with arrow cueing noted in the fMRI study by Hietanen et al. (2006).

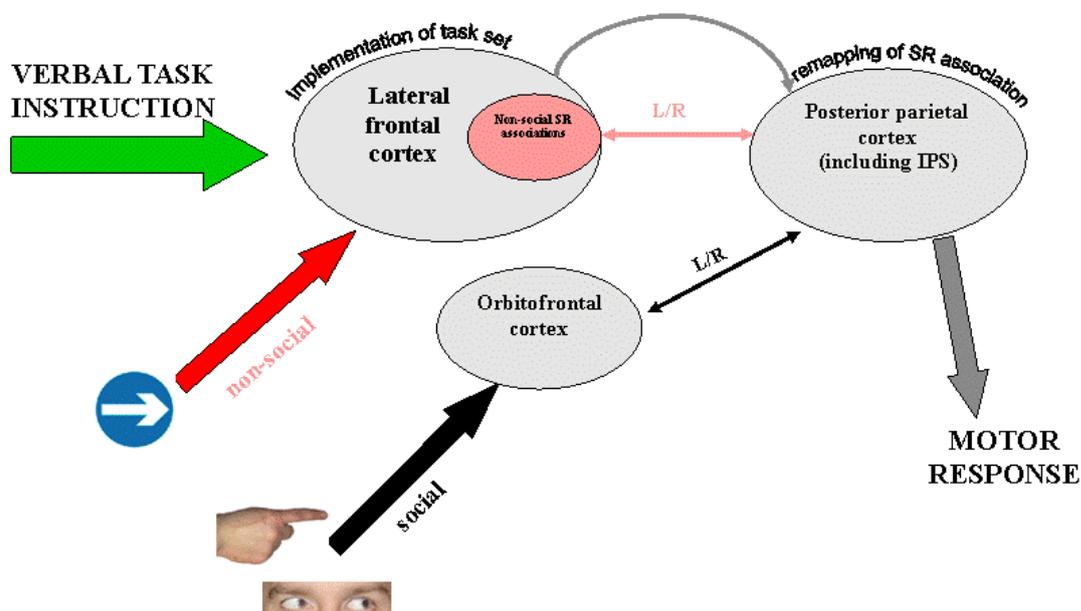


Figure 8.1: A model of “anti-responding” to social and non-social cues in the anti-saccade task. The anti-saccade instruction is initially processed by lateral frontal cortex. Already present over-learned stimulus-response associations are formed for non-social cues via a lateral frontal cortical route (preserved in patient JW), whereas social associations are mediated by the reward-sensitive orbitofrontal cortex. The remapping of the direct non-social cue-response associations depends on the strength of the association. If strong enough it will be remapped (otherwise it is over-ridden altogether), together with the social cue-response associations from orbitofrontal cortex and the anti-saccade response itself, in the posterior parietal cortex. The implementation of the “anti-response” task set on general task performance and the strong non-social cue-response associations, occurs via the lateral frontal cortex. The generation of the reversed social cue-response mapping bypasses the lateral frontal cortex, and is therefore more automatic, being resistant to top-down influences.

8.3.5 Eye gaze processing and social behaviour

One of the main aims of this thesis was to find evidence for the involvement of gaze processing in social behaviour or social “intelligence”. In this respect, the findings of Chapter 6 were inconclusive. In a large group of men there was no correlation between the magnitude of the cueing effects of gaze and arrows in an anti-saccade task and their scores on the AQ, which in part measures social abilities. The finding that in this experiment the male participants were just as influenced by the arrow cues as they were by the gaze cues was unreplicated in other experiments which were largely comprised of female participants. It is an interesting possibility that men may have stronger arrow stimulus-response associations than women, but without an equivalent study with a female-only cohort, this remains speculative. However, as the Extreme Male Brain theory of autism (Baron-Cohen, 2002) proposes, men are better *systemisers* than women, being more interested in mechanics and workings of systems than women, and perhaps this is why arrows may have more effect on men’s oculomotor performance. A further explanation for the lack of correlation between gaze or arrow cueing and scores on the AQ was discussed in Chapter 6 and relates to the sensitivity of the AQ to social behaviour per se. The fact that the AQ measures ability in areas other than the social behaviour and this may be why no relationship emerged. A more appropriate scale for measuring specifically social ability may be the Empathy Quotient (EQ) (Baron-Cohen & Wheelwright, 2004), developed by the same authors as the AQ and future work could examine whether scores on the EQ have any relationship with gaze and arrow cueing.

The findings from OFC patient LG do provide evidence pointing towards a role for eye gaze perception in social functioning and that the OFC may be involved in both. Although LG showed some automatic processing of arrow cues, she did not demonstrate

the same automaticity of responses to gaze cues. Furthermore, her score on the Reading the Mind in the Eyes test (Baron-Cohen et al., 2001) was atypically low and she made several errors on the Faux Pas Recognition test (Baron-Cohen et al., 1999; Stone et al., 1998) suggesting that she does have some impairments in “social intelligence”. As has already been described, the OFC is thought to mediate the acquisition of reward related stimulus-response associations (Rolls, 1999; Rolls et al., 1994) as well as having a apparently critical role in social and emotional decision making (Bechara et al., 1994, 1999, 2000; Rolls, 1999; Rolls et al., 1994). If the OFC is the common neural substrate that connects eye gaze processing to social behaviour as work with patient EVR (Vecera & Rizzo, 2004, 2006) and now LG may suggest, then other clinical groups aside from OFC patients who exhibit socially undesirable or ineffective behaviour, such as individuals with antisocial personality disorder (APD) may also show reduced levels of orienting to eye gaze cues in the tasks presented here. Indeed, evidence suggests that individuals with APD have reduced volume in the OFC (Raine, Lencz, Bihrlé, LaCasse, & Colletti, 2000; Raine, Yang, Narr, & Toga, 2011) and criminals with psychopathic tendencies exhibit Theory of Mind impairments resembling those of OFC patients (Shamay-Tsoory, Harari, Aharon-Peretz, & Levkovitz, 2010). It is an intriguing possibility that a reduced sensitivity to eye gaze may actually cause difficulties in social functioning. Future work might consider social problem solving paradigms where the availability and perhaps also the validity of eye gaze cues can be manipulated. These are unexplored avenues of research which would further our understanding of the role of eye gaze perception in social behaviour.

8.3.6 A glance at ecological validity

At the outset, this thesis adopted the use of real-world gaze and arrow cues. The rationale for this was that the study of a real-world phenomenon such as spontaneously following another person's direction of gaze in the laboratory was artificial enough without using cartoons of faces as eye gaze cues. Therefore, it was proposed that cues which were more naturalistic would be more likely to elicit genuinely social effects than their black circle and line counterparts. Furthermore, no studies in the literature had used arrow cues which had definite and specific meaning that even approached that associated with human eye gaze. For this reason photographic gaze cues and road sign arrow cues were used throughout, until Chapter 5, where the same schematic gaze and arrow cues as used by Kuhn and colleagues (Kuhn & Benson, 2007; Kuhn & Kingstone, 2009; Kuhn et al., 2010) were substituted for the ecologically valid versions in an anti-saccade task. The outcome of this substitution was interesting if not definitive. Schematic gaze cues had little effect on participants' responses, unlike in the experiments that used the photographic cues, but the effects of the schematic arrow cues were actually greater than in previous experiments. Importantly however, the direction of the effects of both schematic cue types was comparable to that seen with the ecologically valid cues. This finding led to the conclusion that the ecological validity of the gaze stimuli in particular, influenced the magnitude of the effect but not its quality: They were basically doing the same thing, but to different degrees. However, again there are potential problems with comparing the magnitude of effects across experiments with different procedures and carried out by different groups of participants. Nevertheless, the results from the individual experiments of ecologically

valid and schematic cues demonstrated that real-world gaze cues influenced saccadic responses in the anti-saccade task, but the schematic gaze cues, statistically, did not.

The argument that it is only the magnitude of saccadic responses which might be influenced by the relative ecological validity of gaze cues, although plausible and one which would no doubt find agreement amongst most researchers of eye gaze and attention, is not the only possible interpretation of the findings. It is clear that many non-social cues, as has been outlined in this thesis, can also cause automatic effects on eye movements and attention. What also seems to be apparent is that both schematic and realistic gaze cues can influence saccades and attention in a qualitatively same way. However, what is not clear is whether the removal of the real-life characteristics from that gaze cue, its gender, its attractiveness, its age, its ethnicity, also removes its special social status, as far as the brain is concerned. Without evidence from neuroimaging or neuropsychological studies (of which there appear to be none), the possibility that schematic gaze cues are processed in the same way as arrow cues for example, rather than as genuinely social cues, remains a possibility.

There is some evidence that suggests that at least for social cues, stimulus-response associations may be very specific. The study by Ariga and Watanabe (2009) cited in earlier chapters, suggested that when it comes to eliciting automatic orienting of covert attention by pointing cues, the index finger has a particularly pronounced effect. Although these authors found evidence for some automatic orienting with unlikely looking pointing cues, where digits other than the index finger were making the pointing gesture, even the 5th (little) finger extended to match the length of the index finger, did not produce the same magnitude effect as the index finger cue. This finding demonstrates that even biologically implausible social cues can result in some

degree of automatic orienting of attention, but that the precise configuration and appearance is important in generating the maximal influence on attention. Furthermore, it provides an indication that you can't fool the brain into believing something is real when it isn't.

This thesis has presented evidence that non-social arrow cues can influence saccadic responses of neurologically healthy individuals in a qualitatively similar manner to the socio-biological cues, although the effects are less robust and smaller in magnitude. Although generally considered to be devoid of social meaning (an assumption which has also been made throughout this thesis), the origins of the arrow stimuli used to direct attention and action in the real world suggest that this may be an inaccurate interpretation of the nature of this directional stimulus. The traditional road signs which are commonplace in rural and suburban areas in the UK are known as *fingerposts*. Originally they depicted a hand indicating the direction of a nearby village or town by pointing in its direction (Figure 8.2a shows a replica of the oldest finger post in England dating to the 17th Century). They are now more commonly designed as arrow heads rather than pointing hands (Figure 8.2b). The evolution of this British transport signage suggests that arrows may be appropriately considered as representing schematicised pointing hands and that perhaps this is why arrows are used to indicate the direction in which we should travel or attend outside of the laboratory. In the same way that the schematic gaze cues had less effect than the naturalistic gaze cues, the arrow cues may have exerted their attenuated influence relative to the pointing cues because they too were schematicised versions of real-world, socio-biological cues. Such an interpretation may pose some problems for work which has compared gaze

and arrow cues as social and non-social exemplars respectively. However, it may explain why some studies which have used simple paradigms and schematic versions of gaze and arrow cues have found little to distinguish their effects on attention and eye movements, if they both represent rather impoverished versions of biological cues.

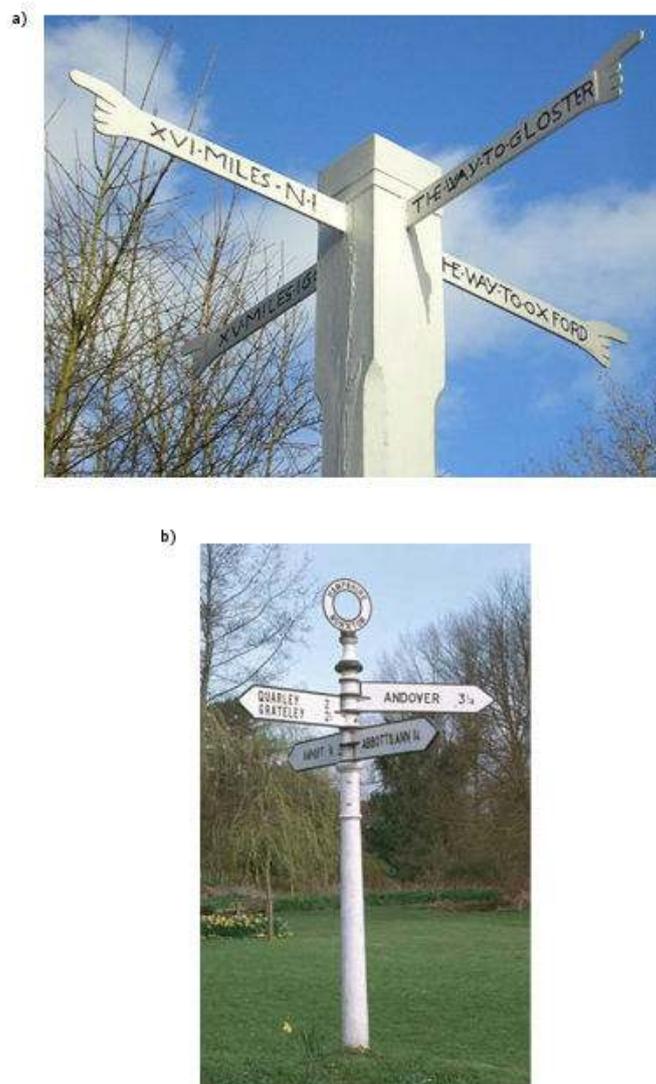


Figure 8.2: a) Replica of fingerpost designed by Joseph Izod, 1669, Chipping Campden, Gloucestershire, UK. (Copyright John V. Nicholls and licensed for reuse under this Creative Commons Licence). b) Contemporary fingerpost, Monxton, Hampshire, UK (Copyright Department of Transport, 2005).

A final consideration of the role of ecological validity relates more generally to the paradigms used to study gaze cueing. Even with the use of ecologically valid (i.e. photographic) gaze cues, some authors have argued that the sort of tasks commonly used may not be measuring social attention at all, but rather a more general form of attentional orienting (Kingstone, 2009; Kuhn et al., 2010). For example, the finding that individuals with ASD appear to automatically orient attention in the direction of even photographic eye gaze cues in the laboratory but fail to do so in real life would support this view (Kylliäinen & Hietanen, 2004; Swettenham et al., 2003). A potential solution is to use paradigms where behaviour can be investigated in a real-world context rather than continually attempting to constrain behaviour in the laboratory, what Kingstone (2009) refers to as the *cognitive ethology approach*. For example, Kuhn and colleagues (Kuhn & Land, 2006; Kuhn et al., 2008) have performed magic tricks where the magician's direction of gaze is critical in misdirecting the attention of observers into believing a ball which has been dropped has actually vanished into thin air. Similar experimental manipulation of gaze in face to face social interactions may provide a richer and complex environment within which genuine social attention may be more certain to be operating.

8.3.7 A distinct level of visual orienting?

This thesis has presented evidence that social cues cause automatic effects on the oculomotor system which are more resistant to top down control and appear to rely less on the involvement of the lateral frontal cortex, than non-social cues such as arrows.

Furthermore, the use of the anti-saccade task has shown that social cues are processed within the same anti-response task set as the target, which are traditionally considered to be

exogenous stimuli, in addition to having the same effects within the anti-saccade task as reported with peripheral cues (Reuter et al., 2006; Weber et al., 1998). In contrast the congruency effects of arrow cues in the pro-saccade tasks were greatly reduced in the anti-saccade task, and directional word cues had no effects on saccades in either task. Previous work has described the orienting caused by eye gaze cues as “reflexive”, likening it to the innate orienting produced by sudden onset stimuli via the visual grasp reflex. However, Experiment 3 demonstrated that averted gaze cues did not disengage attention as the visual grasp reflex would, as a gap effect on SRTs was observed. Therefore, responses to gaze cues cannot be truly reflexive, but rather appear to be a particularly strong and rewarding examples of stimulus-response associations, resulting in what is referred to here as *automatic* effects. Therefore, with these origins and these effects, is there a role for a distinct level of visual orienting to socio-biological cues?

Models of saccade generation have generally failed to distinguish between more than two modes of visual orienting: Exogenous and endogenous. Findlay and Walker’s (1999) model of saccade generation however, with some amendment, can accommodate the type of automatic orienting caused by particularly strong stimulus-response associations such as gaze and finger pointing. In their model, Level 3 is where typically exogenous cues affect the saccade execution decision, with Level 4 reserved for “automated” responses which may be based on learned responses but operate outside of conscious awareness, and Level 5 accounting for typically endogenous or voluntary orienting. Whereas Level 5 accommodates directional word cues, Level 4 appears to be where gaze, pointing but also arrow cues are most likely to be causing the congruency effects seen here, However, as discussed, the social and non-social cues appear to act via distinct routes. Therefore, in order account for the findings of this thesis, Findlay and Walker’s Level 4 would need to be

expanded to account for social/rewarding learned responses as well as more arbitrary over-learned stimulus-response associations: Levels 4a and 4b respectively, perhaps. A further adjustment would allow for flexibility of the positioning of influences at Level 4b and Level 4a. This is clearly necessary if associations vary in their strength between individuals, be that related to gender, pathology or even political temperament (as has been suggested by Dodd, Hibbing and Smith, 2010).

A tentative adaptation of Findlay and Walker's (1999) model is therefore presented which accounts for the implementation of semantic or rule-based associations (i.e. voluntary), over-learned arbitrary stimulus-response associations such as arrows, and socio-biological cues which have a privileged role in directing attention via a more automated route, and which may be mediated by reward value of the stimuli. Note that the boundary between Levels 4a and 4b is permeable to allow for some change over time and across individuals. The shading between Levels 4a and 4b indicates the presence of a continuum of stimulus-response associations with darker shading at Level 4a indicating more robust associations. The model has been simplified from the original to aid clarity. Adaptations to the original model are shown in green.

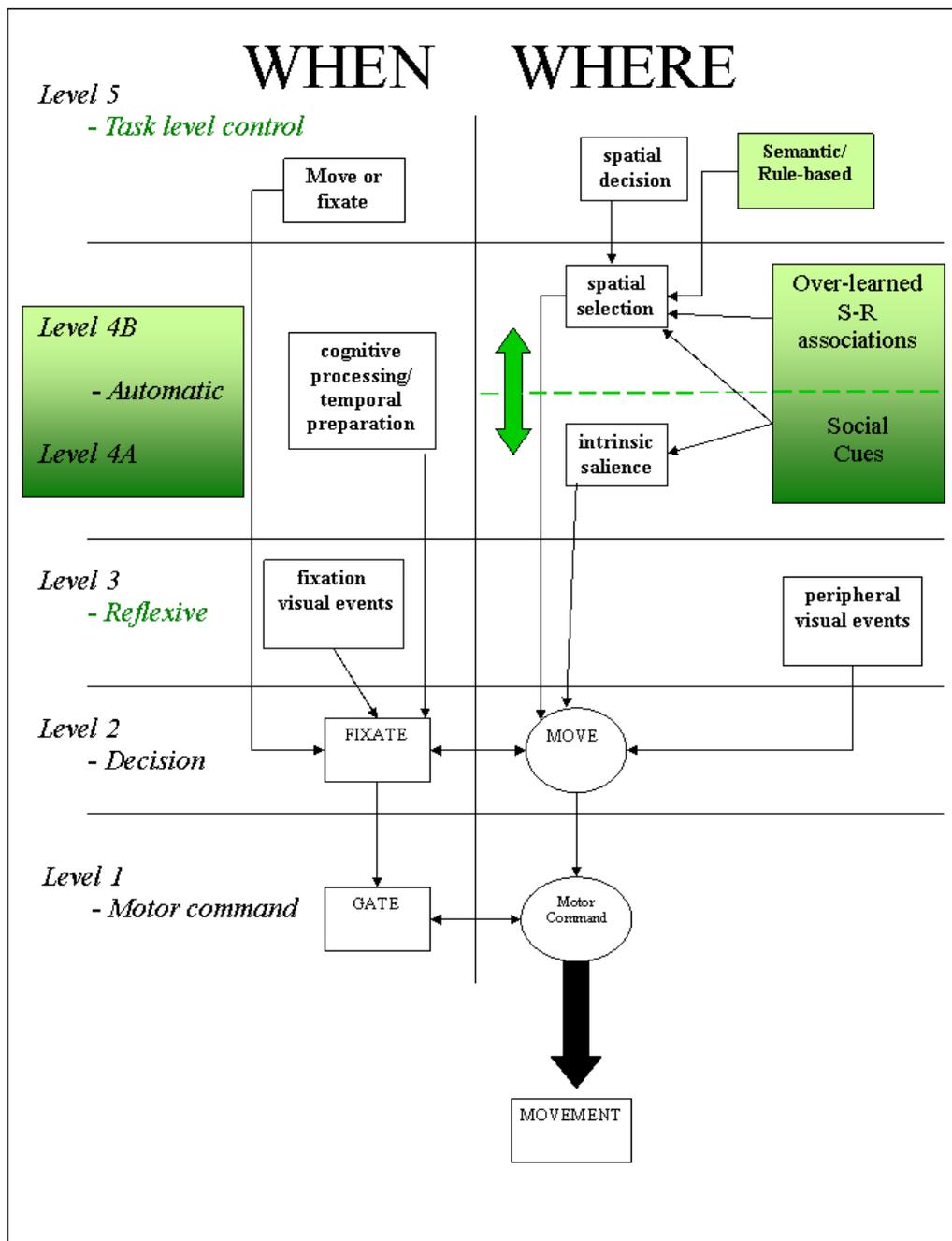


Figure 8.3: Adaptation of Findlay and Walker's model of saccade generation (1999). Amendments to the original are shown in green, with darker shading at Level 4 indicating more automated processes but acknowledging the presence of a continuum of magnitude of stimulus response associations. Note that the original model has been simplified for the purposes of clarity.

8.4 Limitations of research, past and present

For over a decade, there has been a concerted effort in the literature on attention, to find some clear distinction between the effects of cartoon-like faces and stick arrows within experimental paradigms which appear to have little in common with natural behaviour, in order to say something important about the nature of the social brain. The argument for this drastic schematicisation of cues is to control for low-level visual features of the stimuli, such as colour and contrast, thereby allowing only the social aspect of the cues to be investigated. It could be argued that such research may miss the point of what social behaviour is about. It is rich and complex; it has far reaching consequences, and is influenced by a multitude of factors, both conscious and unconscious. The subtleties of it are taken for granted by neurologically healthy, typically developed people. It is only in the case of dysfunction that the true meaning of “social intelligence” is fully appreciated.

Reducing the visual complexity of eye gaze cues in cueing paradigms to match them perceptually to simple arrows for example, removes most of the components that makes the eyes social: The colouring, contours, gender, attractiveness, emotional state. These are all components of real people and social interaction happens with real people. It is therefore not surprising that gaze and arrow cues have the same effects on attention when their visual appearance is controlled to such an extent that they look virtually identical. This is not to say that using photographic, “real-world” stimuli in cueing paradigms solves the problem entirely, for the context in which they are presented remains the same, although it is a move in the right direction. In this sense, experimental psychology may not be the most appropriate method for the study of

social attention. Furthermore, it risks overlooking the very real problems that result in people for whom social intelligence is not an implicit ability.

The *cognitive ethology* approach (Kingstone, 2009), mentioned earlier, may provide a more insightful and faithful framework within which to study social attention. Furthermore, social attention research must more convincingly apply itself to real-life social dysfunction, outside of just the Autistic Spectrum Disorders where it has proved such an attractive avenue of research. Damage to the orbitofrontal cortex has been extensively discussed in this thesis in terms of social behaviour difficulties, including reduced social attention, but bar the work of Vecera and Rizzo (2004; 2006) social attention and OFC damage has remained an unexplored area. Furthermore, other conditions where social dysfunction is common may also lack automatic orienting to social cues, but this possibility has been little explored by researchers of social attention.

The future directions for further research will be discussed in detail in the following section, starting with the potential for extending the use of the current paradigms used in this thesis and their possible clinical application, before moving on to describe a more naturalistic paradigm for studying social attention.

8.5 Further work

The applicability of the current research to clinical populations provides one clear potential avenue for further study. Having presented preliminary evidence of a possible double dissociation between the neurocognitive mechanisms responsible for gaze and arrow cueing, future work would benefit from recruiting additional participants with lesions to the OFC and others with more lateral frontal lesions

sparing more medial ventral areas. Further evidence of social dysfunction in OFC patients would be required in order to provide support for the hypothesis that gaze cueing is a genuinely social ability, rather than a more general attentional process. The Empathy Quotient (EQ) (Baron-Cohen & Wheelwright, 2004) may prove to be more suitable than the AQ (Baron-Cohen, Wheelwright, Skinner, et al., 2001) in assessing social functioning and together with the Mind in the Eyes test (Baron-Cohen et al., 2001) and the Faux Pas Recognition test (Baron-Cohen et al., 1999; Stone et al., 1998) could provide a useful index of social intelligence in OFC and other neurological patients. The performance of the neurological patients in pro- and anti- saccade tasks examined in this thesis suggests that they are feasible paradigms for use with clinical groups. In addition to gaze and arrow cues, the influence of finger pointing cues could also be examined with these tasks to ascertain whether other socio-biological cues are also processed via an orbitofrontal cortical route.

To find further evidence for differential roles of lateral frontal and orbitofrontal cortices in the processing of socio-biological and non-social cues proposed in section 8.3.4, functional neuroimaging of healthy controls whilst performing oculomotor tasks, could be a potential future research area. Whilst previous fMRI research examining neural activation in response to gaze and arrow cues used heavily schematised cues in covert detection tasks (Greene et al., 2009; Hietanen et al., 2006), and others which have employed more naturalistic cues have studied directional versus non-directional cues only under passive viewing conditions (Sato et al., 2009), none have examined neural activation in response to ecologically valid socio-biological cues and non-social cues during oculomotor tasks. Therefore, future work might consider utilising fMRI to test

the model proposed in Figure 8.1, that behavioural responses to socio-biological and non-social stimuli are mediated by separate neural mechanisms.

As suggested in Chapter 7 and earlier in this chapter, it is possible that social dysfunction in other clinical groups such as those with anti-social personality disorder and traumatic brain injury, may relate to the automatic processing of social cues. The oculomotor paradigms used in this thesis are brief to administer and may therefore be suitable as preliminary measures of social processing in these groups. The anti-saccade task would be particularly suitable as it is already used to assess voluntary control mechanisms in clinical populations (for a review see Hutton & Ettinger, 2006) so would allow investigation of two cognitive processes with one task, therefore providing indicators of both social processing as well as inhibitory control mechanisms.

If further evidence can be accumulated which indicates a common deficit in eye gaze processing in clinical groups who exhibit difficulties in social interactions, it would have potential implications for the rehabilitation or management of such conditions. From the perspective of care givers, friends and family, the knowledge that a great deal of our communication relies on non-verbal communication and that patients may not respond to the subtle social cues that are otherwise taken for granted, may enable them to modify their behaviour to take this into account when interacting with patients. From the perspective of the patient, otherwise confusing social exchanges may be made more comprehensible and transparent if such behavioural modification is adopted by others.

As has been suggested earlier in this chapter, the study of social attention may benefit from the development of more “real-world” paradigms which more closely resemble every day scenarios in which the ability to interpret indicators of other peoples’ locus of attention is important. The magic tricks performed by Kuhn and colleagues (Kuhn & Land, 2006; Kuhn et al., 2008) offer a starting point for the development of such naturalistic paradigms. For example, video vignettes of social interactions could be recorded, where the gaze direction of the protagonists either validly or invalidly indicates the onset of events in the scene. Participants could then be asked to provide a manual response as soon as they detect the events have occurred. In addition, eye tracking could be utilised to provide a measure of spontaneous following of the gaze of the protagonists whilst viewing the same vignettes. Evidence for attentional orienting, reduced reaction times or spontaneous execution of saccades in the direction of eye gaze in such a paradigm may be more likely to be tapping into genuinely social attention than more controlled experimental paradigms such as those employed previous and indeed those in this thesis.

8.6 Wider impact of research

The evidence provided in this thesis indicates that socio-biological stimuli such as eye gaze and finger pointing have a privileged ability to produce attentional orienting which outweighs the effects produced by non-social cues such as arrows. The implications of these findings may be of benefit in applied settings.

For example, if pointing hands are processed more readily than pointing arrows, public information and traffic signage designers might reconsider the use of finger pointing as a means of directing action in populated areas, in public buildings and on

the roads, including reinstating “fingerposts” which more closely resemble their predecessors. Furthermore, eyes looking left or right painted on the road surface should be more influential than the words LOOK LEFT or LOOK RIGHT, which are currently used, in causing pedestrians to look in the direction of oncoming traffic before they cross a busy road. Where conditions allow, less schematised images of eyes gazing could be substituted for linguistic signage in public places which ought to result in more automatic conveyance of the directional instruction. The use of socio-biological cues may also be of use in advertising, perhaps providing more subtle means of directing observers’ attention towards and even preference for (King, Rowe, & Leonards, in press) the parts of a scene that have been designed to be most influential in selling the product.

8.7 Conclusions

The current work has provided evidence that social, biologically relevant direction stimuli have special a status within the brain and therefore argues against a body of literature which has failed to uncover any substantial differences in the way that eye gaze and arrow cues in particular influence attention and eye movements. It has further demonstrated that eye gaze is not the only directional cue with particular social relevance that can influence eye movements in an obligatory manner, and suggests that the social reward value of the stimuli, their biological nature, as well as the degree of exposure to them, may be the reasons cues such as finger pointing and eye gaze are processed in a more automatic manner. The use of the anti-saccade paradigm in particular has been instrumental in uncovering the differences in automaticity between social and non-social cues which have otherwise eluded experimental psychologists. In

addition, the use of this paradigm with individuals with lesions to the frontal lobes of the brain has provided some preliminary neuropsychological evidence for a possible double dissociation between the roles of lateral frontal and orbitofrontal cortex in automatic saccadic orienting to gaze and arrow cues as well as further indicating that gaze cueing and “social intelligence” may share common cognitive and neural bases.

References

- Adams, R., Gordon, H., Baird, A., Ambady, N., & Kleck, R. (2003). Effects of gaze on amygdala sensitivity to anger and fear faces. *Science*, *300*(5625), 1536-1536.
- Aggleton, J., & Passingham, R. (1981). Syndrome produced by lesions of the amygdala in monkeys (*Macaca mulatta*). *Journal of Comparative and Physiological Psychology*, *95*(6), 961-977.
- Akiyama, T., Kato, M., Muramatsu, T., & Kashima, H. (2008). Deficits in gaze-triggered orienting in cases with superior temporal sulcus lesion and amygdala lesions. *Neuroscience Research*, *61*, S200-S200.
- Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Nakachi, R., & Kashima, H. (2006). A deficit in discriminating gaze direction in a case with right superior temporal gyrus lesion (vol 44, pg 161, 2006). *Neuropsychologia*, *44*(14), 3016-3016.
doi:10.1016/j.neuropsychologia.2006.08.001
- Akiyama, T., Kato, M., Muramatsu, T., Saito, F., Umeda, S., & Kashima, H. (2006). Gaze but not arrows: A dissociative impairment after right superior temporal gyrus damage. *Neuropsychologia*, *44*(10), 1804-1810.
doi:10.1016/j.neuropsychologia.2006.03.007
- Allison, T., Puce, A., & McCarthy, G. (2000). Social perception from visual cues: role of the STS region. *Trends in Cognitive Sciences*, *4*(7), 267-278.
- Altman, G. (2011). Language can mediate eye movement control within 100 milliseconds, regardless of whether there is anything to move the eyes to. *Acta Psychologica*, *137*(2), 190-200. doi:10.1016/j.actpsy.2010.09.009

- Anisfeld, M. (1996). Only tongue protrusion modeling is matched by neonates. *Developmental Review, 16*(2), 149-161.
- Ariga, A., & Watanabe, K. (2009). What is special about the index finger?: The index finger advantage in manipulating reflexive attentional shift. *Japanese Psychological Research, 51*(4), 258-265. doi:10.1111/j.1468-5884.2009.00408.x
- Baron-Cohen, S. (1995). *Mindblindness: An Essay on Autism and Theory of Mind*. MIT Press.
- Baron-Cohen, S. (2002). The extreme male brain theory of autism. *Trends in Cognitive Sciences, 6*(6), 248-254. doi:10.1016/S1364-6613(02)01904-6
- Baron-Cohen, S., & Wheelwright, S. (2004). The empathy quotient: An investigation of adults with Asperger syndrome or high functioning autism, and normal sex differences. *Journal of Autism and Developmental Disorders, 34*(2), 163-175.
- Baron-Cohen, S., Campbell, R., Karmiloff-Smith, A., Grant, J., & Walker, J. (1995). Are children with autism blind to the mentalistic significance of the eyes. *British Journal of Developmental Psychology, 13*, 379-398.
- Baron-Cohen, S., Cox, A., Baird, G., Swettenham, J., Nightingale, N., Morgan, K., Drew, A., et al. (1996). Psychological markers in the detection of autism in infancy in a large population. *The British Journal of Psychiatry, 168*(2), 158-163.
doi:10.1192/bjp.168.2.158
- Baron-Cohen, S., Jolliffe, T., Mortimore, C., & Robertson, M. (1997). Another advanced test of theory of mind: evidence from very high functioning adults with Autism or Asperger Syndrome. *Journal of Child Psychology and Psychiatry, 38*(7), 813-822.
doi:10.1111/j.1469-7610.1997.tb01599.x

- Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a “theory of mind”? *Cognition*, *21*(1), 37-46.
- Baron-Cohen, S., O’Riordan, M., Stone, V., Jones, R., & Plaisted, K. (1999). Recognition of faux pas by normally developing children and children with Asperger Syndrome or high-functioning Autism. *Journal of Autism and Developmental Disorders*, *29*(5), 407-18.
- Baron-Cohen, S., Ring, H. A., Bullmore, E. T., Wheelwright, S., Ashwin, C., & Williams, S. C. R. (2000). The amygdala theory of autism. *Neuroscience and Biobehavioral Reviews*, *24*(3), 355-364.
- Baron-Cohen, S., Wheelwright, S., Hill, J., Raste, Y., & Plumb, I. (2001). The “Reading the Mind in the Eyes” test revised version: A study with normal adults, and adults with Asperger syndrome or high-functioning autism. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *42*(2), 241-251.
- Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The Autism-Spectrum Quotient (AQ): Evidence from Asperger syndrome/high-functioning autism, males and females, scientists and mathematicians. *Journal of Autism and Developmental Disorders*, *31*(1), 5-17.
- Baron-Cohen, S., Wheelwright, S., Spong, A., Scahill, V., & Lawson, J. (2001). Are intuitive physics and intuitive psychology independent? A test with children with Asperger Syndrome. *Journal of Developmental and Learning Disorders*, *5*(1), 47–78.
- Batki, A., Baron-Cohen, S., Wheelwright, S., Connellan, J., & Ahluwalia, J. (2000). Is there an innate gaze module? Evidence from human neonates. *Infant Behavior and Development*, *23*(2), 223-229.

- Bayliss, A. P., Pellegrino, G. di, & Tipper, S. P. (2005). Sex differences in eye gaze and symbolic cueing of attention. *The Quarterly Journal of Experimental Psychology Section A*, *58*(4), 631 - 650.
- Bechara, A., Damasio, A., Damasio, H., & Anderson, S. (1994). Insensitivity to future consequences following damage to human prefrontal cortex. *Cognition*, *50*(1-3), 7-15.
- Bechara, A., Damasio, H., Damasio, A., & Lee, G. (1999). Different contributions of the human amygdala and ventromedial prefrontal cortex to decision-making. *Journal of Neuroscience*, *19*(13), 5473-5481.
- Bechara, A., Tranel, D., & Damasio, H. (2000). Characterization of the decision-making deficit of patients with ventromedial prefrontal cortex lesions. *Brain*, *123*, 2189-2202.
- Bechara, A., Tranel, D., Damasio, H., & Damasio, A. (1996). Failure to respond autonomically to anticipated future outcomes following damage to prefrontal cortex. *Cerebral Cortex*, *6*(2), 215-225.
- Bonato, M., Priftis, K., Marenzi, R., & Zorzi, M. (2009). Normal and impaired reflexive orienting of attention after central nonpredictive cues. *Journal of Cognitive Neuroscience*, *21*(4), 745-759.
- Braun, D., Weber, H., Mergner, T., & Schulte-Monting, J. (1992). Saccadic reaction-times in patients with frontal and parietal lesions. *Brain*, *115*, 1359-1386.
- Brett, M., Leff, A. P., Rorden, C., & Ashburner, J. (2001). Spatial normalization of brain images with focal lesions using cost function masking. *NeuroImage*, *14*(2), 486-500. doi:10.1006/nimg.2001.0845

- Brignani, D., Guzzon, D., Marzi, C., & Miniussi, C. (2008). Attentional orienting induced by arrows and eye-gaze compared with an endogenous cue. *Neuropsychologia*.
- Bristow, D., Rees, G., & Frith, C. D. (2007). Social interaction modifies neural response to gaze shifts. *Social Cognitive and Affective Neuroscience*, 2(1), 52-61.
doi:10.1093/scan/nsl036
- Bushnell, I. (2001). Mother's face recognition in newborn infants: Learning and memory. *Infant and Child Development*, 10(1-2), 67-74.
- Butter, C. M., Rapcsak, S., Watson, R. T., & Heilman, K. M. (1988). Changes in sensory inattention, directional motor neglect and release of the fixation reflex following a unilateral frontal lesion: A case report. *Neuropsychologia*, 26(4), 533-545.
doi:10.1016/0028-3932(88)90110-8
- Butterworth, G., & Jarrett, N. (1991). What minds have in common is space - spatial mechanisms serving joint visual-attention in infancy. *British Journal of Developmental Psychology*, 9, 55-72.
- Cador, M., Robbins, T. W., & Everitt, B. J. (1989). Involvement of the amygdala in stimulus-reward associations: interaction with the ventral striatum. *Neuroscience*, 30(1), 77-86.
- Calder, A., Lawrence, A., Keane, J., Scott, S., Owen, A., Christoffels, I., & Young, A. (2002). Reading the mind from eye gaze. *Neuropsychologia*, 40(8), 1129-1138.
- Cavegn, D. (1996). Bilateral interactions in saccade programming - A saccade-latency study. *Experimental Brain Research*, 109(2), 312-332.
- Chawarska, K., Klin, A., & Volkmar, F. (2003). Automatic attention cueing through eye movement in 2-year-old children with autism. *Child Development*, 74(4), 1108-1122.

- Cicerone, K., & Tanenbaum, L. (1997). Disturbance of social cognition after traumatic orbitofrontal brain injury. *Archives of Clinical Neuropsychology*, *12*(2), 173-188.
- Connolly, J., Goodale, M., Goltz, H., & Munoz, D. P. (2005). fMRI activation in the human frontal eye field is correlated with saccadic reaction time. *Journal of Neurophysiology*, *94*(1), 605-611. doi:10.1152/jn.00830.2004
- Connolly, J., Goodale, M., Menon, R., & Munoz, D. (2002). Human fMRI evidence for the neural correlates of preparatory set. *Nature Neuroscience*, *5*(12), 1345-1352. doi:10.1038/mn969
- Corbetta, M. (1998). Frontoparietal cortical networks for directing attention and the eye to visual locations: Identical, independent, or overlapping neural systems? *Proceedings of the National Academy of Sciences of the United States of America*, *95*(3), 831-838.
- Corbetta, M., & Shulman, G. (2002). Control of goal-directed and stimulus-driven attention in the brain. *Nature Reviews Neuroscience*, *3*(3), 201-215. doi:10.1038/nrn755
- Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., Linenweber, M. R., et al. (1998). A common network of functional areas for attention and eye movements. *Neuron (Science Direct)*, *21*(4), 761-773.
- Corkum, V., & Moore, C. (1998). The origins of joint visual attention in infants. *Developmental Psychology*, *34*(1), 28-38.
- Corsi, J. (1972). *Human memory and the human temporal region of the brain*. McGill University, Montreal, Canada.
- Crawford, T. J., & Muller, H. J. (1992). Spatial and temporal effects of spatial attention on human saccadic eye-movements. *Vision Research*, *32*(2), 293-304.

- Damasio, A. R., Damasio, H., & Chui, H. C. (1980). Neglect following damage to frontal lobe or basal ganglia. *Neuropsychologia*, *18*(2), 123-132. doi:10.1016/0028-3932(80)90058-5
- Damasio, A., Tranel, D., & Damasio, H. (1990). Individuals with sociopathic behavior caused by frontal damage fail to respond autonomically to social-stimuli. *Behavioural Brain Research*, *41*(2), 81-94.
- Deaner, R., Khera, A., & Platt, M. (2005). Monkeys pay per view: Adaptive valuation of social images by rhesus macaques. *Current Biology*, *15*(6), 543-548. doi:10.1016/j.cub.2005.01.044
- Dodd, M. D., Hibbing, J. R., & Smith, K. B. (2010). The politics of attention: gaze-cuing effects are moderated by political temperament. *Attention, Perception, & Psychophysics*, *73*(1), 24-29. doi:10.3758/s13414-010-0001-x
- Dorris, M. C., & Munoz, D. P. (1995). A neural correlate for the gap effect on saccadic reaction times in monkey. *Journal of Neurophysiology*, *73*(6), 2558-2562.
- Dorris, M. C., Pare, M., & Munoz, D. P. (1997). Neuronal activity in monkey superior colliculus related to the initiation of saccadic eye movements. *Journal of Neuroscience*, *17*(21), 8566-8579.
- Downing, P., Dodds, C., & Bray, D. (2004). Why does the gaze of others direct visual attention? *Visual Cognition*, *11*, 71.
- Doyle, M., & Walker, R. (2001). Curved saccade trajectories: Voluntary and reflexive saccades curve away from irrelevant distractors. *Experimental Brain Research*, *139*(3), 333-344.

- Driver, J., Davis, G., Ricciardelli, P., Kidd, P., Maxwell, E., & Baron-Cohen, S. (1999). Gaze perception triggers reflexive visuospatial orienting. *Visual Cognition*, 6(5), 509-540.
- Eco, U. (1979). *A theory of semiotics*. Indiana University Press.
- Emery, N. (2000). The eyes have it: the neuroethology, function and evolution of social gaze. *Neuroscience and Biobehavioral Reviews*, 24(6), 581-604.
- Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research*, 43(9), 1035-1045. doi:10.1016/S0042-6989(03)00084-1
- Engell, A., Nummenmaa, L., Oosterhof, N., Henson, R., Haxby, J., & Calder, A. (2010). Differential activation of frontoparietal attention networks by social and symbolic spatial cues. *Social Cognitive and Affective Neuroscience*, 5(4), 432-440. doi:10.1093/scan/nsq008
- Evdokimidis, I., Smyrnis, N., Constantinidis, T., Stefanis, N., Avramopoulos, D., Paximadis, C., Theleritis, C., et al. (2002). The antisaccade task in a sample of 2,006 young men - I. Normal population characteristics. *Experimental Brain Research*, 147(1), 45-52. doi:10.1007/s00221-002-1208-4
- Everling, S., & Fischer, B. (1998). The antisaccade: a review of basic research and clinical studies. *Neuropsychologia*, 36(9), 885-899.
- Everling, S., & Munoz, D. P. (2000). Neuronal correlates for preparatory set associated with pro-saccades and anti-saccades in the primate frontal eye field. *Journal of Neuroscience*, 20(1), 387-400.
- Everling, S., Dorris, M. ., & Munoz, D. P. (1998). Reflex suppression in the anti-saccade task is dependent on prestimulus neural processes. *Journal of Neurophysiology*, 80(3), 1584-1589.

- Everling, S., Dorris, M. C., Klein, R. M., & Munoz, D. P. (1999). Role of primate superior colliculus in preparation and execution of anti-saccades and pro-saccades. *Journal Of Neuroscience, 19*(7), 2740-2754.
- Farroni, T., Csibra, G., Simion, G., & Johnson, M. H. (2002). Eye contact detection in humans from birth. *Proceedings of the National Academy of Sciences of the United States Of, 99*(14), 9602-9605.
- Farroni, T., Massaccesi, S., Pividori, D., & Johnson, M. H. (2004). Gaze following in newborns. *Infancy, 5*(1), 39-60.
- Fecteau, J., & Munoz, D. (2006). Saliency, relevance, and firing: a priority map for target selection. *Trends in Cognitive Sciences, 10*, 382-390. doi:10.1016/j.tics.2006.06.011
- Findlay, J. M., & Gilchrist, I. D. (2003). *Active vision the psychology of looking and seeing*. Oxford; New York: Oxford University Press.
- Findlay, J. M., & Walker, R. (1999). A model of saccade generation based on parallel processing and competitive inhibition. *Behavioral and Brain Sciences, 22*(4), 661-+.
- Fischer, B., & Weber, H. (1992). Characteristics of antisaccades in man. *Experimental Brain Research, 89*(2), 415-424.
- Fischer, B., & Weber, H. (1997). Effects of stimulus conditions on the performance of antisaccades in man. *Experimental Brain Research, 116*(2), 191-200.
- Fischer, B., Gezeck, S., & Hartnegg, K. (1997). The analysis of saccadic eye movements from gap and overlap paradigms. *Brain Research Protocols, 2*(1), 47-52.
- Fischer, B., Gezeck, S., & Hartnegg, K. (2000). On the production and correction of involuntary prosaccades in a gap antisaccade task. *Vision Research, 40*(16), 2211-2217.

- Fogassi, L., Ferrari, P., Gesierich, B., Rozzi, S., Chersi, F., & Rizzolatti, G. (2005). Parietal lobe: From action organization to intention understanding. *Science*, *308*(5722), 662-667. doi:10.1126/science.1106138
- Folstein, M. F., Folstein, S. E., & McHugh, P. R. (1975). "Mini-mental state". A practical method for grading the cognitive state of patients for the clinician. *Journal of Psychiatric Research*, *12*(3), 189-198.
- Forbes, K., & Klein, R. M. (1996). The magnitude of the fixation offset effect with endogenously and exogenously controlled saccades. *Journal of Cognitive Neuroscience*, *8*(4), 344-352.
- Ford, K., Goltz, H., Brown, M., & Everling, S. (2005). Neural processes associated with antisaccade task performance investigated with event-related fMRI. *Journal of Neurophysiology*, *94*(1), 429-440. doi:10.1152/jn.00471.2004
- Freedman, E. G., Stanford, T. R., & Sparks, D. L. (1996). Combined eye-head gaze shifts produced by electrical stimulation of the superior colliculus in rhesus monkeys. *Journal of Neurophysiology*, *76*(2), 927-952.
- Friesen, C. K., & Kingstone, A. (1998). The eyes have it! Reflexive orienting is triggered by nonpredictive gaze. *Psychonomic Bulletin & Review*, *5*(3), 490-495.
- Friesen, C. K., & Kingstone, A. (2003). Covert and overt orienting to gaze direction cues and the effects of fixation offset. *Neuroreport*, *14*(3), 489-493.
- Friesen, C. K., Ristic, J., & Kingstone, A. (2004). Attentional effects of counterpredictive gaze and arrow cues. *Journal Of Experimental Psychology-Human Perception And Performance*, *30*(2), 319-329.

- Frischen, A., Bayliss, S. P., & Tipper, S. P. (2007). Gaze cueing of attention: Visual attention, social cognition, and individual differences. *Psychological Bulletin*, *133*(4), 694-724.
- Gallese, V., & Goldman, A. (1998). Mirror neurons and the simulation theory of mind-reading. *Trends in Cognitive Sciences*, *2*(12), 493-501.
- Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*(2), 593.
- Gaymard, B., Ploner, C. J., Rivaud-Péchoix, S., & Pierrot-Deseilligny, C. (1999). The frontal eye field is involved in spatial short-term memory but not in reflexive saccade inhibition. *Experimental Brain Research*, *129*(2), 288-301.
- Geary, D. C. (1998). *Male, female: the evolution of human sex differences*. American Psychological Association.
- Gibson, B., & Bryant, T. (2005). Variation in cue duration reveals top-down modulation of involuntary orienting to uninformative symbolic cues. *Perception and Psychophysics*, *67*(5), 749-758.
- Gilchrist, I. D., Brown, V., Findlay, J. M., & Clarke, M. P. (1998). Using the eye-movement system to control the head. *Proceedings of the Royal Society B: Biological Sciences*, *265*(1408), 1831-1836.
- Gliga, T., & Csibra, G. (2009). One year old infants appreciate the referential nature of deictic gestures and words. *Psychological Science*, *20*(3), 347-353.
doi:10.1111/j.1467-9280.2009.02295.x
- Godijn, R., & Theeuwes, J. (2002). Programming of endogenous and exogenous saccades: Evidence for a competitive integration model. *Journal of Experimental Psychology-Human Perception and Performance*, *28*(5), 1039-1054.

- Goldberg, M. E., & Wurtz, R. H. (1972a). Activity of superior colliculus in behaving monkey. I. Visual receptive fields of single neurons. *Journal of Neurophysiology*, 35(4), 542-559.
- Goldberg, M. E., & Wurtz, R. H. (1972b). Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. *Journal of Neurophysiology*, 35(4), 560-574.
- Greene, D., Mooshagian, E., Kaplan, J., Zaidel, E., & Iacoboni, M. (2009). The neural correlates of social attention: automatic orienting to social and nonsocial cues. *Psychological Research-Psychologische Forschung*, 73(4), 499-511.
doi:10.1007/s00426-009-0233-3
- Grosbras, M. N., Laird, A. R., & Paus, T. (2005). Cortical regions involved in eye movements, shifts of attention, and gaze perception. *Human Brain Mapping*, 25(1), 140-154.
- Guietton, D., Buchtel, H. A., & Douglas, R. M. (1985). Frontal lobe lesions in man cause difficulties in suppressing reflexive glances and in generating goal-directed saccades. *Experimental Brain Research*, 58(3), 455-472.
- Guzzon, D., Brignani, D., Miniussi, C., & Marzi, C. (2010). Orienting of attention with eye and arrow cues and the effect of overtraining. *Acta Psychologica*, 134(3), 353-362.
doi:10.1016/j.actpsy.2010.03.008
- Hafed, Z., Goffart, L., & Krauzlis, R. (2009). A neural mechanism for microsaccade generation in the primate superior colliculus. *Science*, 323(5916), 940-943.
doi:10.1126/science.1166112
- Hallett, P. (1978). Primary and secondary saccades to goals defined by instructions. *Vision Research*, 18(10), 1279-1296.

- Hallett, P., & Adams, B. D. (1980). The predictability of saccadic latency in a novel voluntary oculomotor task. *Vision Research*, 20(4), 329-39.
- Happé, F. G. E. (1995). The role of age and verbal ability in the theory of mind task performance of subjects with autism. *Child Development*, 66(3), 843-855.
doi:10.2307/1131954
- Hebb, D. O. (1949). *The organization of behavior: a neuropsychological theory*. Wiley.
- Henderson, J. M. (1992). Visual attention and eye movement control during reading and picture viewing. In K. Rayner (Ed.), *Eye movements and visual cognition: scene perception and reading* (pp. 260-83). Springer-Verlag.
- Henik, A., Rafal, R. D., & Rhodes, D. (1994). Endogenously generated and visually guided saccades after lesions of the human frontal eye fields. *Journal of Cognitive Neuroscience*, 6(4), 400-411.
- Hermens, F., & Walker, R. (2010). Gaze and arrow distractors influence saccade trajectories similarly. *Quarterly Journal of Experimental Psychology*, 63(11), 2120-2140. doi:10.1080/17470211003718721
- Hermens, F., Sumner, P., & Walker, R. (2010). Inhibition of masked primes as revealed by saccade curvature. *Vision Research*, 50(1), 46-56. doi:10.1016/j.visres.2009.10.008
- Hess, W. R., Brugi, S., & Bucher, V. (1946). Motor function of tectal and tegmental area. *Monatsschrift Fur Psychiatrie Und Neurologie*, 112, 1-52.
- Heyes, C. (2001). Causes and consequences of imitation. *Trends in Cognitive Sciences*, 5(6), 253-261.
- Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience and Biobehavioral Reviews*, 34(4), 575-583. doi:10.1016/j.neubiorev.2009.11.007

- Hietanen, J. ., & Leppänen, J. M. (2003). Does facial expression affect attention orienting by gaze direction cues? *Journal of Experimental Psychology: Human Perception and Performance*, 29(6), 1228-1243. doi:10.1037/0096-1523.29.6.1228
- Hietanen, J. K., Nummenmaa, L., Nyman, M., Parkkola, R., & Hamalainen, H. (2006). Automatic attention orienting by social and symbolic cues activates different neural networks: An fMRI study. *NeuroImage*, 33(1), 413.
- Ho, C., & Spence, C. (2006). Verbal interface design: Do verbal directional cues automatically orient visual spatial attention? *Computers in Human Behavior*, 22(4), 733-748. doi:10.1016/j.chb.2005.12.008
- Hodgson, T. L., Chamberlain, M., Parris, B., James, M., Gutowski, N., Husain, M., & Kennard, C. (2007). The role of the ventrolateral frontal cortex in inhibitory oculomotor control. *Brain*, 130, 1525-1537.
- Hodgson, T. L., Parris, B. A., Gregory, N. J., & Jarvis, T. (2009). The saccadic Stroop effect: Evidence for involuntary programming of eye movements by linguistic cues. *Vision Research*, 49(5), 569-574. doi:10.1016/j.visres.2009.01.001
- Hommel, B., Pratt, J., Colzato, L., & Godijn, R. (2001). Symbolic control of visual attention. *Psychological Science*, 12(5), 360-365.
- Hood, B. M., Willen, J. D., & Driver, J. (1998). Adults eyes trigger shifts of visual attention in human infants. *Psychological Science*, 9, 131.
- Hooker, C., Paller, K., Gitelman, D., Parrish, T., Mesulam, M., & Reber, P. (2003). Brain networks for analyzing eye gaze. *Cognitive Brain Research*, 17(2), 406-418.
- Hornak, J., Bramham, J., Rolls, E., Morris, R., O'Doherty, J., Bullock, P., & Polkey, C. (2003). Changes in emotion after circumscribed surgical lesions of the orbitofrontal and cingulate cortices. *Brain*, 126, 1691-1712. doi:10.1093/brain/awg168

- Hornak, J., Rolls, E., & Wade, D. (1996). Face and voice expression identification in patients with emotional and behavioural changes following ventral frontal lobe damage. *Neuropsychologia*, *34*(4), 247-261.
- Howard, M., Cowell, P., Boucher, J., Broks, P., Mayes, A., Farrant, A., & Roberts, N. (2000). Convergent neuroanatomical and behavioural evidence of an amygdala hypothesis of autism. *Neuroreport*, *11*(13), 2931-2935.
- Hutton, S. B. (2008). Cognitive control of saccadic eye movements. *Brain and Cognition*, *68*(3), 327-340. doi:10.1016/j.bandc.2008.08.021
- Hutton, S. B., & Ettinger, U. (2006). The antisaccade task as a research tool in psychopathology: A critical review. *Psychophysiology*, *43*(3), 302-313.
- Ignashchenkova, A., Dicke, P. W., Haarmeier, T., & Thier, P. (2004). Neuron-specific contribution of the superior colliculus to overt and covert shifts of attention. *Nature Neuroscience*, *7*(1), 56-64.
- Johnson, M. H., Griffin, R., Csibra, G., Halit, H., Farroni, T., De Haan, M., Tucker, L., et al. (2005). The emergence of the social brain network: Evidence from typical and atypical development. *Development and Psychopathology*, *17*(3), 599-619. doi:10.1017/S0954579405050297
- Johnston, K., & Everling, S. (2008). Neurophysiology and neuroanatomy of reflexive and voluntary saccades in non-human primates. *Brain and Cognition*, *68*(3), 271-283. doi:10.1016/j.bandc.2008.08.017
- Jones, B., DeBruine, L., Little, A., Conway, C., & Feinberg, D. (2006). Integrating gaze direction and expression in preferences for attractive faces. *Psychological Science*, *17*(7), 588-591.

- Jones, S. (2009). The development of imitation in infancy. *Philosophical Transactions of the Royal Society B-Biological Sciences*, 364(1528), 2325-2335.
doi:10.1098/rstb.2009.0045
- Jonides, J. (1981). *Voluntary versus automatic control over the mind's eye's movement*. (S. Long & A. Baddeley, Eds.) (Vol. IX). Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Jonides, J., & Mack, R. (1984). On the cost and benefit of cost and benefit. *Psychological Bulletin*, 96(1), 29-44.
- Kamide, Y., Altmann, G. T. ., & Haywood, S. L. (2003). The time-course of prediction in incremental sentence processing: Evidence from anticipatory eye movements. *Journal of Memory and Language*, 49(1), 133-156. doi:10.1016/S0749-596X(03)00023-8
- Kertesz, A. (1982). *The Western Aphasia Battery*. Grune & Stratton.
- King, D., Rowe, A., & Leonards, U. (in press). I trust you – hence I like the things you look at: Gaze cueing and sender trustworthiness influence object evaluation. *Social Cognition*.
- Kingstone, A. (2009). Taking a real look at social attention. *Current Opinion in Neurobiology*, 19(1), 52-56. doi:10.1016/j.conb.2009.05.004
- Kingstone, A., & Klein, R. M. (1993a). What are human express saccades. *Perception and Psychophysics*, 54(2), 260-273.
- Kingstone, A., & Klein, R. M. (1993b). Visual offsets facilitate saccadic latency - does predisengagement of visuospatial attention mediate this gap effect. *Journal of Experimental Psychology-Human Perception and Performance*, 19(6), 1251-1265.

- Kingstone, A., Tipper, C., Ristic, J., & Ngan, E. (2004). The eyes have it!: An fMRI investigation. *Brain and Cognition*, *55*(2), 269-271.
- Klein, J., Deaner, R., & Platt, M. (2008). Neural correlates of social target value in macaque parietal cortex. *Current Biology*, *18*(6), 419-424.
doi:10.1016/j.cub.2008.02.047
- Klein, J., Shepherd, S., & Platt, M. (2009). Social attention and the brain. *Current Biology*, *19*(20), R958-R962. doi:10.1016/j.cub.2009.08.010
- Klein, R. (2000). Inhibition of return. *Trends in Cognitive Sciences*, *4*(4), 138-147.
- Klein, R. M. (1980). Does oculomotor readiness mediate cognitive control of visual attention? In R. M. Nickerson (Ed.), *Attention and performance VIII* (pp. 259-276). Hillsdale, N.J.: L. Erlbaum Associates.
- Klein, R. M., & Pontefract, A. (1994). Does oculomotor readiness mediate cognitive control of visual-attention - revisited. *Attention and Performance Xv - Conscious and Nonconscious Information*, *15*, 333-350.
- Klier, E. M., Wang, H., & Crawford, J. D. (2001). The superior colliculus encodes gaze commands in retinal coordinates. *Nature Neuroscience*, *4*(6), 627-632.
doi:10.1038/88450
- Van Koningsbruggen, M., & Rafal, R. D. (2009). Control of oculomotor reflexes: independent effects of strategic and automatic preparation. *Experimental Brain Research*, *192*(4), 761-768. doi:10.1007/s00221-008-1655-7
- Koval, M., Thomas, B., & Everling, S. (2005). Task-dependent effects of social attention on saccadic reaction times. *Experimental Brain Research*, *167*(3), 475-480.

- Kringelbach, M., & Rolls, E. (2004). The functional neuroanatomy of the human orbitofrontal cortex: evidence from neuroimaging and neuropsychology. *Progress in Neurobiology*, *72*(5), 341-372.
- Kuhn, G., & Benson, V. (2007). The influence of eye-gaze and arrow pointing distractor cues on voluntary eye movements. *Perception and Psychophysics*, *69*(6), 966-971.
- Kuhn, G., & Kingstone, A. (2009). Look away! Eyes and arrows engage oculomotor responses automatically. *Attention Perception and Psychophysics*, *71*(2), 314-327.
doi:10.3758/APP.71.2.314
- Kuhn, G., & Land, M. (2006). There's more to magic than meets the eye. *Current Biology*, *16*(22), R950-R951.
- Kuhn, G., Benson, V., Fletcher-Watson, S., Kovshoff, H., McCormick, C., Kirkby, J., & Leekam, S. (2010). Eye movements affirm: automatic overt gaze and arrow cueing for typical adults and adults with autism spectrum disorder. *Experimental Brain Research*, *201*(2), 155-165. doi:10.1007/s00221-009-2019-7
- Kuhn, G., Tatler, B., & Cole, G. (2009). You look where I look! Effect of gaze cues on overt and covert attention in misdirection. *Visual Cognition*, *17*(6-7), 925-944.
doi:10.1080/13506280902826775
- Kuhn, G., Tatler, B., Findlay, J., & Cole, G. (2008). Misdirection in magic: Implications for the relationship between eye gaze and attention. *Visual Cognition*, *16*(2-3), 391-405.
- Kustov, A. A., & Robinson, D. L. (1996). Shared neural control of attentional shifts and eye movements. *Nature*, *384*(6604), 74-77.
- Kylliäinen, A., & Hietanen, J. K. (2004). Attention orienting by another's gaze direction in children with autism. *Journal of Child Psychology and Psychiatry*, *45*(3), 435-444.

- Lambert, A., & Duddy, M. (2002). Visual orienting with central and peripheral precues: Deconfounding the contributions of cue eccentricity, cue discrimination and spatial correspondence. *Visual Cognition*, 9(3), 303-336.
- Lambert, A., Roser, M., Wells, I., & Heffer, C. (2006). The spatial correspondence hypothesis and orienting in response to central and peripheral spatial cues. *Visual Cognition*, 13(1), 65-88.
- Land, M., Furneaux, S., & Gilchrist, I. (2002). The organization of visually mediated actions in a subject without eye movements. *Neurocase*, 8(1), 80-87.
- Langdon, R., & Smith, P. (2005). Spatial cueing by social versus nonsocial directional signals. *Visual Cognition*, 12(8), 1497-1527.
- Langton, S., & Bruce, V. (2000). You must see the point: Automatic processing of cues to the direction of social attention. *Journal of Experimental Psychology: Human Perception and Performance*, 26(2), 747-757. doi:10.1037/0096-1523.26.2.747
- Langton, S., O'Malley, C., & Bruce, V. (1996). Actions speak no louder than words: Symmetrical cross-modal interference effects in the processing of verbal and gestural information. *Journal of Experimental Psychology-Human Perception and Performance*, 22(6), 1357-1375.
- Lee, K., Eskritt, M., Symons, L., & Muir, D. (1998). Children's use of triadic eye gaze information for "mind reading." *Developmental Psychology*, 34(3), 525-539.
- Leekam, S., Baron-Cohen, S., Perrett, D. I., Milders, M., & Brown, S. (1997). Eye-direction detection: A dissociation between geometric and joint attention skills in autism. *British Journal of Developmental Psychology*, 15, 77-95.

- Leekam, S., Hunnisett, E., & Moore, C. (1998). Targets and cues: Gaze-following in children with autism. *Journal of Child Psychology and Psychiatry and Allied Disciplines*, *39*(7), 951-962.
- Lutchmaya, S., Baron-Cohen, S., & Raggatt, P. (2002). Foetal testosterone and eye contact in 12-month-old human infants. *Infant Behavior and Development*, *25*(3), 327-335. doi:10.1016/S0163-6383(02)00094-2
- Machado, L., & Rafal, R. D. (2000a). Control of eye movement reflexes. *Experimental Brain Research*, *135*(1), 73-80.
- Machado, L., & Rafal, R. D. (2000b). Strategic control over saccadic eye movements: Studies of the fixation offset effect. *Perception and Psychophysics*, *62*(6), 1236-1242.
- Machado, L., & Rafal, R. D. (2004). Control of fixation and saccades during an anti-saccade task: an investigation in humans with chronic lesions of oculomotor cortex. *Experimental Brain Research*, *156*(1), 55-63. doi:10.1007/s00221-003-1765-1
- Mah, L., Arnold, M., & Grafman, J. (2004). Impairment of social perception associated with lesions of the prefrontal cortex. *American Journal of Psychiatry*, *161*(7), 1247-1255.
- Mansfield, E. M., Farroni, T., & Johnson, M. H. (2003). Does gaze perception facilitate overt orienting? *Visual Cognition*, *10*(1), 7-14.
- Martinez-Conde, S., Macknik, S. L., & Hubel, D. H. (2004). The role of fixational eye movements in visual perception. *Nature Reviews Neuroscience*, *5*(3), 229-240.
- Materna, S., Dicke, P. W., & Thier, P. (2008). The posterior superior temporal sulcus is involved in social communication not specific for the eyes. *Neuropsychologia*, *46*(11), 2759-2765. doi:10.1016/j.neuropsychologia.2008.05.016

- McDowell, J. E., Dyckman, K. A., Austin, B. P., & Clementz, B. A. (2008). Neurophysiology and neuroanatomy of reflexive and volitional saccades: Evidence from studies of humans. *Brain and Cognition*, *68*(3), 255-270. doi:10.1016/j.bandc.2008.08.016
- McDowell, J., Kissler, J., Berg, P., Dyckman, K., Gao, Y., Rockstroh, B., & Clementz, B. (2005). Electroencephalography/magnetoencephalography study of cortical activities preceding prosaccades and antisaccades. *Neuroreport*, *16*(7), 663-668.
- McNeill, D. (2000). *Language and gesture*. Cambridge University Press.
- McPeck, R., & Keller, E. (2002a). Superior colliculus activity related to concurrent processing of saccade goals in a visual search task. *Journal of Neurophysiology*, *87*(4), 1805-1815. doi:10.1152/jn.00501.2001
- McPeck, R., & Keller, E. (2002b). Saccade target selection in the superior colliculus during a visual search task. *Journal of Neurophysiology*, *88*(4), 2019-2034. doi:10.1152/jn.00181.2002
- McPeck, R., Han, J., & Keller, E. (2003). Competition between saccade goals in the superior colliculus produces saccade curvature. *Journal of Neurophysiology*, *89*(5), 2577-2590. doi:10.1152/jn.00657.2002
- McSorley, E., Haggard, P., & Walker, R. (2004). Distractor modulation of saccade trajectories: spatial separation and symmetry effects. *Experimental Brain Research*, *155*(3), 320-333. doi:10.1007/s00221-003-1729-5
- Medendorp, W. P., Goltz, H. C., & Vilis, T. (2005). Remapping the remembered target location for anti-saccades in human posterior parietal cortex. *Journal of Neurophysiology*, *94*(1), 734-740. doi:10.1152/jn.01331.2004

- Meeter, M., Van der Stigchel, S., & Theeuwes, J. (2010). A competitive integration model of exogenous and endogenous eye movements. *Biological Cybernetics*, *102*(4), 271-291. doi:10.1007/s00422-010-0365-y
- Mesulam, M.-M. (2000). *Principles of behavioral and cognitive neurology* (2nd ed.). Oxford University Press, USA.
- Moon, S. Y., Barton, J. J. S., Mikulski, S., Polli, F. E., Cain, M. S., Vangel, M., Hämäläinen, M. S., et al. (2007). Where left becomes right: A magnetoencephalographic study of sensorimotor transformation for antisaccades. *NeuroImage*, *36*(4), 1313-1323. doi:16/j.neuroimage.2007.04.040
- Moore, C., & Corkum, V. (1994). Social understanding at the end of the 1st year of life. *Developmental Review*, *14*(4), 349-372.
- Morales, M., Mundy, P., & Rojas, J. (1998). Following the direction of gaze and language development in 6-month-olds. *Infant Behavior and Development*, *21*(2), 373-377.
- Mort, D. J., Perry, R. J., Mannan, S. K., Hodgson, T. L., Anderson, E., Quest, R., McRobbie, D., et al. (2003). Differential cortical activation during voluntary and reflexive saccades in man. *NeuroImage*, *18*(2), 231-246.
- Muller, H. J., & Rabbitt, P. M. A. (1989). Spatial cueing and the relation between the accuracy of where and what decisions in visual-search. *Quarterly Journal Of Experimental Psychology Section A-Human Experimental Psychology*, *41*(4), 747-773.
- Mundy, P., & Gomes, A. (1998). Individual differences in joint attention skill development in the second year. *Infant Behavior and Development*, *21*(3), 469-482.

- Mundy, P., & Sigman, M. (2006). Joint attention, social competence, and developmental psychopathology. *Developmental Psychopathology* (pp. 293-332). John Wiley and Sons.
- Munoz, D. P., & Everling, S. (2004). Look away: The anti-saccade task and the voluntary control of eye movement. *Nature Reviews Neuroscience*, 5(3), 218-228.
- Munoz, D. P., & Wurtz, R. H. (1992). Role of the rostral superior colliculus in active visual fixation and execution of express saccades. *Journal of Neurophysiology*, 67(4), 1000-1002.
- Neggers, S., Raemaekers, M., Lampmann, E., Postma, A., & Ramsey, N. (2005). Cortical and subcortical contributions to saccade latency in the human brain. *European Journal of Neuroscience*, 21(10), 2853-2863. doi:10.1111/j.1460-9568.2005.04129.x
- Nelson, H. E. (1982). *The National Adult Reading Test (NART): test manual*. NFER-Nelson.
- Nies, K. J. (1999). Cognitive and social-emotional changes associated with mesial orbitofrontal damage: Assessment and implications for treatment. *Neurocase*, 5(4), 313-324.
- Nummenmaa, L., & Hietanen, J. K. (2006). Gaze distractors influence saccadic curvature: Evidence for the role of the oculomotor system in gaze-cued orienting. *Vision Research*, 46(21), 3674-3680.
- Oberman, L., Hubbard, E., McCleery, J., Altschuler, E., Ramachandran, V., & Pineda, J. (2005). EEG evidence for mirror neuron dysfunction in autism spectrum disorders. *Cognitive Brain Research*, 24(2), 190-198. doi:10.1016/j.cogbrainres.2005.01.014

- Olk, B., & Kingstone, A. (2003). Why are antisaccades slower than prosaccades? A novel finding using a new paradigm. *Neuroreport*, *14*(1), 151-155.
doi:10.1097/01.wnr.0000053062.88427.d7
- Osterling, J., Dawson, G., & Munson, J. (2002). Early recognition of 1-year-old infants with autism spectrum disorder versus mental retardation. *Development and Psychopathology*, *14*(2), 239-251.
- Pageler, N., Menon, V., Merin, N., Eliez, S., Brown, W., & Reiss, A. (2003). Effect of head orientation on gaze processing in fusiform gyrus and superior temporal sulcus. *Neuroimage*, *20*(1), 318-329. doi:10.1016/S1053-8119(03)00229-5
- Pelphrey, K. A., Singerman, J. D., Allison, T., & McCarthy, G. (2003). Brain activation evoked by perception of gaze shifts: the influence of context. *Neuropsychologia*, *41*, 156.
- Pelphrey, K. A., Viola, R., & McCarthy, G. (2004). When strangers pass - Processing of mutual and averted social gaze in the superior temporal sulcus. *Psychological Science*, *15*(9), 598-603.
- Perra, O., & Gattis, M. (2010). The control of social attention from 1 to 4 months. *British Journal of Developmental Psychology*, *28*(4), 891-908.
doi:10.1348/026151010X487014
- Perrett, D. I., & Emery, N. J. (1994). Understanding the intentions of others from visual signals: Neurophysiological evidence. *Cahiers de Psychologie Cognitive/Current Psychology of Cognition*, *13*(5), 683-694.
- Perrett, D. I., Hietanen, J. K., Oram, M., & Benson, P. (1992). Organization and functions of cells responsive to faces in the temporal cortex. *Philosophical Transactions of the Royal Society of London Series*, *335*(1273), 23-30.

- Perrett, D. I., Smith, P., Potter, D., Mistlin, A., Head, A., Milner, A., & Jeeves, M. (1985). Visual cells in the temporal cortex sensitive to face view and gaze direction. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 223(1232), 293-317.
- Petrides, M. (1997). Visuo-motor conditional associative learning after frontal and temporal lesions in the human brain. *Neuropsychologia*, 35(7), 989-997.
- Pierrot-Deseilligny, C., Muri, R., Ploner, C., Gaymard, B., Demeret, S., & Rivaud-Pechoux, S. (2003). Decisional role of the dorsolateral prefrontal cortex in ocular motor behaviour. *Brain*, 126, 1460-1473.
- Pierrot-Deseilligny, C., Ploner, C., Muri, R., Gaymard, B., & Rivaud-Pechoux, S. (2002). Effects of cortical lesions on saccadic eye movements in humans. *Neurobiology of Eye Movements: From Molecules to Behavior*, 956, 216-229.
- Pierrot-Deseilligny, C., Rivaud, S., Gaymard, B., & Agid, Y. (1991). Cortical control of reflexive visually-guided saccades. *Brain*, 114, 1473-1485.
- Port, N. L., & Wurtz, R. H. (2003). Sequential activity of simultaneously recorded neurons in the superior colliculus during curved saccades. *Journal of Neurophysiology*, 90(3), 1887 -1903. doi:10.1152/jn.01151.2002
- Posner, M. I. (1978). *Chronometric explorations of mind*. Erlbaum Hillsdale, N. J.
- Posner, M. I. (1980). Orienting of attention. *Quarterly Journal Of Experimental Psychology*, 32(FEB), 3-25.
- Posner, M., Walker, J., Friedrich, F., & Rafal, R. D. (1984). Effects of parietal injury on covert orienting of attention. *Journal Of Neuroscience*, 4(7), 1863-1874.

- Puce, A., & Perrett, D. I. (2003). Electrophysiology and brain imaging of biological motion. *Philosophical Transactions of the Royal Society of London Series*, 358(1431), 435-445. doi:10.1098/rstb.2002.1221
- Pulvermüller, F. (2005). Brain mechanisms linking language and action. *Nature Reviews Neuroscience*, 6, 576-582. doi:10.1038/nrn1706
- Quadflieg, S., Mason, M. F., & Macrae, C. N. (2004). The owl and the pussycat: Gaze cues and visuospatial orienting. *Psychonomic Bulletin and Review*, 11(5), 826-831.
- Quaia, C., Aizawa, H., Optican, L. M., & Wurtz, R. H. (1998). Reversible inactivation of monkey superior colliculus. ii. maps of saccadic deficits. *Journal of Neurophysiology*, 79(4), 2097-2110.
- Raine, A., Lencz, T., Bihrlé, S., LaCasse, L., & Colletti, P. (2000). Reduced prefrontal gray matter volume and reduced autonomic activity in antisocial personality disorder. *Archives of General Psychiatry*, 57(2), 119-127.
- Raine, A., Yang, Y., Narr, K., & Toga, A. (2011). Sex differences in orbitofrontal gray as a partial explanation for sex differences in antisocial personality. *Molecular Psychiatry*, 16(2), 227-236. doi:10.1038/mp.2009.136
- Reitan, R. M., & Wolfson, D. (1985). *The Halstead-Reitan Neuropsychological Test Battery: Therapy and clinical interpretation*. Tucson, AZ: Neuropsychological Press.
- Remington, R. W. (1980). Attention and saccadic eye-movements. *Journal of Experimental Psychology-Human Perception and Performance*, 6(4), 726-744.
- Reuter, B., Herzog, E., & Kathmann, N. (2006). Antisaccade performance of schizophrenia patients: Evidence of reduced task-set activation and impaired error detection. *Journal of Psychiatric Research*, 40(2), 122-130. doi:10.1016/j.jpsychires.2005.02.007

- Reuter-Lorenz, P. A., Hughes, H. C., & Fendrich, R. (1991). The reduction of saccadic latency by prior offset of the fixation point: an analysis of the gap effect. *Perception and Psychophysics*, *49*(2), 167-75.
- Reuter-Lorenz, P., & Fendrich, R. (1992). Oculomotor readiness and covert orienting - differences between central and peripheral precues. *Perception and Psychophysics*, *52*(3), 336-344.
- Reuter-Lorenz, P., Oonk, H., Barnes, L., & Hughes, H. (1995). Effects of warning signals and fixation point offsets on the latencies of prosaccades versus antisaccades - implications for an interpretation of the gap effect. *Experimental Brain Research*, *103*(2), 287-293.
- Ricciardelli, P., Bricolo, E., Aglioti, S. M., & Chelazzi, L. (2002). My eyes want to look where your eyes are looking: Exploring the tendency to imitate another individual's gaze. *Neuroreport*, *13*(17), 2259-2264.
- Ristic, J., Friesen, C. K., & Kingstone, A. (2002). Are eyes special? It depends on how you look at it. *Psychonomic Bulletin and Review*, *9*(3), 507-513.
- Ristic, J., Mottron, L., Friesen, C., Iarocci, G., Burack, J., & Kingstone, A. (2005). Eyes are special but not for everyone: The case of autism. *Cognitive Brain Research*, *24*(3), 715-718.
- Rivaud, S., Muri, R., Gaymard, B., Vermesch, A., & Pierrot-Deseilligny, C. (1994). Eye-movement disorders after frontal eye field lesions in humans. *Experimental Brain Research*, *102*(1), 110-120.
- Rizzolatti, G., Fadiga, L., Fogassi, L., & Gallese, V. (1997). The space around us. *Science*, *277*(5323), 190-191.

- Rizzolatti, G., Riggio, L., & Sheliga, B. M. (1994). Space and selective attention. *Attention and Performance Xv*, Attention and Performance (Vol. 15, pp. 231-265). Retrieved from <Go to ISI>://A1994BB48F00009
- Rizzolatti, G., Riggio, L., Dascola, I., & Umiltà, C. (1987). Reorienting attention across the horizontal and vertical meridians - evidence in favor of a premotor theory of attention. *Neuropsychologia*, 25(1A), 31-40.
- Rolls, E. (2004). The functions of the orbitofrontal cortex. *Brain and Cognition*, 55(1), 11-29. doi:10.1016/s0278-2626(03)00277-x
- Rolls, E. T. (1999). The functions of the orbitofrontal cortex. *Neurocase: The Neural Basis of Cognition*, 5(4), 301. doi:10.1080/13554799908411984
- Rolls, E., Hornak, J., Wade, D., & McGrath, J. (1994). Emotion-related learning in patients with social and emotional changes associated with frontal-lobe damage. *Journal of Neurology Neurosurgery and Psychiatry*, 57(12), 1518-1524.
- Ross, L., & Ross, S. (1980). Saccade latency and warning signals - stimulus onset, offset, and change as warning events. *Perception and Psychophysics*, 27(3), 251-257.
- Ross, S. M., & Ross, L. E. (1981). Saccade latency and warning signals: effects of auditory and visual stimulus onset and offset. *Perception and Psychophysics*, 29(5), 429-437.
- Saslow, M. (1967). Effects of components of displacement-step stimuli upon latency for saccadic eye movement. *Journal of the Optical Society of America*, 57(8), 1024-&.
- Sato, W., Kochiyama, T., Uono, S., & Yoshikawa, S. (2009). Commonalities in the neural mechanisms underlying automatic attentional shifts by gaze, gestures, and symbols. *Neuroimage*, 45(3), 984-992. doi:10.1016/j.neuroimage.2008.12.052
- Sato, W., Kochiyama, T., Uono, S., & Yoshikawa, S. (2010). Automatic attentional shifts by gaze, gestures, and symbols. *Psychologia*, 53(1), 27-35.

- Sato, W., Yoshikawa, S., Kochiyama, T., & Matsumura, M. (2004). The amygdala processes the emotional significance of facial expressions: an fMRI investigation using the interaction between expression and face direction. *Neuroimage*, *22*(2), 1006-1013. doi:10.1016/j.neuroimage.2004.02.030
- Scaife, M., & Bruner, J. (1975). Capacity for joint visual attention in infant. *Nature*, *253*(5489), 265-266.
- Schneider, K. A., & Kastner, S. (2005). Visual responses of the human superior colliculus: A high-resolution functional magnetic resonance imaging study. *Journal of Neurophysiology*, *94*(4), 2491-2503.
- Schulte-Ruther, M., Markowitsch, H., Fink, G., & Piefke, M. (2007). Mirror neuron and theory of mind mechanisms involved in face-to-face interactions: A functional magnetic resonance imaging approach to empathy. *Journal of Cognitive Neuroscience*, *19*(8), 1354-1372.
- Senju, A., & Hasegawa, T. (2005). Direct gaze captures visuospatial attention. *Visual Cognition*, *12*(1), 127-144.
- Senju, A., Tojo, Y., Dairoku, H., & Hasegawa, T. (2004). Reflexive orienting in response to eye gaze and an arrow in children with and without autism. *Journal of Child Psychology and Psychiatry*, *45*(3), 445-458.
- Shamay-Tsoory, S., Harari, H., Aharon-Peretz, J., & Levkovitz, Y. (2010). The role of the orbitofrontal cortex in affective theory of mind deficits in criminal offenders with psychopathic tendencies. *Cortex*, *46*(5), 668-677. doi:10.1016/j.cortex.2009.04.008
- Sheliga, B. M., Craighero, L., Riggio, L., & Rizzolatti, G. (1997). Effects of spatial attention on directional manual and ocular responses. *Experimental Brain Research*, *114*(2), 339-351.

- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1994). Orienting of attention and eye-movements. *Experimental Brain Research*, 98(3), 507-522.
- Sheliga, B. M., Riggio, L., & Rizzolatti, G. (1995). Spatial attention and eye-movements. *Experimental Brain Research*, 105(2), 261-275.
- Shepherd, M., Findlay, J. M., & Hockey, R. J. (1986). The relationship between eye-movements and spatial attention. *Quarterly Journal of Experimental Psychology Section a-Human Experimental Psychology*, 38(3), 475-491.
- Shepherd, S. V., Klein, J., Deaner, R., & Platt, M. (2009). Mirroring of attention by neurons in macaque parietal cortex. *Proceedings of the National Academy of Sciences of the United States Of*, 106(23), 9489-9494.
doi:10.1073/pnas.0900419106
- Slater, A., Von der Schulenburg, C., Brown, E., Badenoch, M., Butterworth, G., Parsons, S., & Samuels, C. (1998). Newborn infants prefer attractive faces. *Infant Behavior and Development*, 21(2), 345-354.
- Slessor, G., Phillips, L. H., & Bull, R. (2008). Age-related declines in basic social perception: Evidence from tasks assessing eye-gaze processing. *Psychology and Aging*, 23(4), 812-822. doi:10.1037/a0014348
- Smith, D. T., Rorden, C., & Jackson, S. R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. *Current Biology*, 14(9), 792-795.
- Sparks, D. L. (1986). Translation of sensory signals into commands for control of saccadic eye movements: role of primate superior colliculus. *Physiological Reviews*, 66(1), 118-171.

- Sparks, D. L. (1999). Conceptual issues related to the role of the superior colliculus in the control of gaze. *Current Opinion in Neurobiology*, 9(6), 698–707.
- Spence, C., & Driver, J. (1997). Audiovisual links in exogenous covert spatial orienting. *Perception & psychophysics*, 59(1), 1-22.
- Spreen, O., & Strauss, E. (1998). *A compendium of neuropsychological tests: administration, norms, and commentary* (2nd ed.). Oxford University Press, USA.
- Van der Stigchel, S., & Theeuwes, J. (2005). The influence of attending to multiple locations on eye movements. *Vision Research*, 45(15), 1921-1927.
doi:10.1016/j.visres.2005.02.002
- Van der Stigchel, S., Meeter, M., & Theeuwes, J. (2006). Eye movement trajectories and what they tell us. *Neuroscience and Biobehavioral Reviews*, 30(5), 666-679.
- Stone, V., Baron-Cohen, S., & Knight, R. T. (1998). Frontal lobe contributions to theory of mind. *Journal of Cognitive Neuroscience*, 10(5), 640-656.
- Stroop, J. (1935). Studies of interference in serial verbal reactions. *Journal of Experimental Psychology*, 18, 643-662.
- Swettenham, J., Baron-Cohen, S., Charman, T., Cox, A., Baird, G., Drew, A., Rees, L., et al. (1998). The frequency and distribution of spontaneous attention shifts between social and nonsocial stimuli in autistic, typically developing, and nonautistic developmentally delayed infants. *Journal of Child Psychology and Psychiatry*, 39(5), 747-753. doi:10.1111/1469-7610.00373
- Swettenham, J., Condie, S., Campbell, R., Milne, E., & Coleman, M. (2003). Does the perception of moving eyes trigger reflexive visual orienting in autism? *Philosophical Transactions of the Royal Society B-Biological Sciences*, 358(1430), 325-334. doi:10.1098/rstb.2002.1203

- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain: 3-dimensional proportional system: an approach to cerebral imaging*. Thieme.
- Tannen, D. (2001). *You just don't understand: women and men in conversation*. Harper.
- Theeuwes, J., Kramer, A., Hahn, S., & Irwin, D. (1998). Our eyes do not always go where we want them to go: Capture of the eyes by new objects. *Psychological Science*, *9*(5), 379-385.
- Theeuwes, J., Kramer, A., Hahn, S., Irwin, D., & Zelinsky, G. (1999). Influence of attentional capture on oculomotor control. *Journal of Experimental Psychology-Human Perception and Performance*, *25*(6), 1595-1608.
- Tipper, C., Handy, T., Giesbrecht, B., & Kingstone, A. (2008). Brain responses to biological relevance. *Journal of Cognitive Neuroscience*, *20*(5), 879-891.
- Tipples, J. (2002). Eye gaze is not unique: Automatic orienting in response to uninformative arrows. *Psychonomic Bulletin & Review*, *9*(2), 314-318.
- Tipples, J. (2005). Orienting to eye gaze and face processing. *Journal of Experimental Psychology: Human Perception and Performance*, *31*(5), 843-856.
doi:10.1037/0096-1523.31.5.843
- Tipples, J. (2008). Orienting to counterpredictive gaze and arrow cues. *Perception & Psychophysics*, *70*(1), 77-87. doi:10.3758/PP.70.1.77
- Tomasello, M., Savage-Rumbaugh, S., & Kruger, A. (1993). Imitative learning of actions on objects by children, chimpanzees, and enculturated chimpanzees. *Child Development*, *64*(6), 1688-1705.
- Tomonaga, M., & Imura, T. (2009). Human gestures trigger different attentional shifts in chimpanzees (*Pan troglodytes*) and humans (*Homo sapiens*). *Animal Cognition*, *12*, S11-S18. doi:10.1007/s10071-009-0268-2

- Trappenberg, T., Dorris, M. C., Munoz, D. P., & Klein, R. M. (2001). A model of saccade initiation based on the competitive integration of exogenous and endogenous signals in the superior colliculus. *Journal of Cognitive Neuroscience, 13*(2), 256-271. doi:10.1162/089892901564306
- Vecera, S. P., & Rizzo, M. (2004). What are you looking at? Impaired “social attention” following frontal-lobe damage. *Neuropsychologia, 42*(12), 1657-1665.
- Vecera, S. P., & Rizzo, M. (2006). Eye gaze does not produce reflexive shifts of attention: Evidence from frontal-lobe damage. *Neuropsychologia, 44*(1), 150.
- Vuilleumier, P. (2002). Perceived gaze direction in faces and spatial attention: a study in patients with parietal damage and unilateral neglect. *Neuropsychologia, 40*(7), 1013-1026. doi:10.1016/S0028-3932(01)00153-1
- Walker, R., Deubel, H., Schneider, W., & Findlay, J. M. (1997). Effect of remote distractors on saccade programming: Evidence for an extended fixation zone. *Journal of Neurophysiology, 78*(2), 1108-1119.
- Walker, R., Husain, M., Hodgson, T. L., Harrison, J., & Kennard, C. (1998). Saccadic eye movement and working memory deficits following damage to human prefrontal cortex. *Neuropsychologia, 36*(11), 1141-1159.
- Weber, H., Durr, N., & Fischer, B. (1998). Effects of pre-cues on voluntary and reflexive saccade generation II. Pro-cues for anti-saccades. *Experimental Brain Research, 120*(4), 417-431. doi:10.1007/s002210050415
- Werner, E., Dawson, G., Osterling, J., & Dinno, N. (2000). Brief report: Recognition of autism spectrum disorder before one year of age: A retrospective study based on home videotapes. *Journal of Autism and Developmental Disorders, 30*(2), 157-162.

- Wicker, B., Michel, F., Henaff, M. A., & Decety, J. (1998). Brain regions involved in the perception of gaze: a PET study. *NeuroImage*, *8*, 221.
- Williams, J. H. G., Waiter, G. D., Perra, O., Perrett, D. I., & Whiten, A. (2005). An fMRI study of joint attention experience. *Neuroimage*, *25*(1), 133-140.
- Williams, J. H. G., Whiten, A., Suddendorf, T., & Perrett, D. I. (2001). Imitation, mirror neurons and autism. *Neuroscience and Biobehavioral Reviews*, *25*(4), 287-295.
- Woodward, A., & Guajardo, J. (2002). Infants' understanding of the point gesture as an object-directed action. *Cognitive Development*, *17*(1), 1061-1084.
- Zhang, M., & Barash, S. (2000). Neuronal switching of sensorimotor transformations for antisaccades. *Nature*, *408*(6815), 971-975.
- Zhang, M., & Barash, S. (2004). Persistent LIP activity in memory antisaccades: Working memory for a sensorimotor transformation. *Journal of Neurophysiology*, *91*(3), 1424-1441. doi:10.1152/jn.00504.2003

Appendix A

The Autism Spectrum Quotient (Baron-Cohen, Wheelwright, Skinner, et al., 2001)

Participants answer “definitively agree”, “slightly agree”, “slightly disagree” or “definitively disagree” to each of the following 50 questions.

Scoring is as follows: 1 point is given for “definitively agree” or “slightly agree” on questions 2, 4, 5, 6, 7, 9, 12, 13, 16, 18, 19, 20, 21, 22, 23, 26, 33, 35, 39, 41, 42, 43, 45, 46 and 1 point for “slightly disagree” or “definitively disagree” on questions 1, 3, 8, 10, 11, 14, 15, 17, 24, 25, 27, 28, 29, 30, 31, 32, 34, 36,37, 38, 40, 44, 47, 48, 49, 50. Maximum score is 50 points.

1. I prefer to do things with others rather than on my own.
2. I prefer to do things the same way over and over again.
3. If I try to imagine something, I find it very easy to create a picture in my mind.
4. I frequently get so strongly absorbed in one thing that I lose sight of other things.
5. I often notice small sounds when others do not.
6. I usually notice car number plates or similar strings of information.
7. Other people frequently tell me that what I've said is impolite, even though I think it is polite.
8. When I'm reading a story, I can easily imagine what the characters might look like.
9. I am fascinated by dates.
10. In a social group, I can easily keep track of several different people's conversations.
11. I find social situations easy.
12. I tend to notice details that others do not.
13. I would rather go to a library than a party.
14. I find making up stories easy
15. I find myself drawn more strongly to people than to things.
16. I tend to have very strong interests, which I get upset about if I can't pursue.
17. I enjoy social chitchat.
18. When I talk, it isn't always easy for others to get a word in edgeways.
19. I am fascinated by numbers.
20. When I'm reading a story, I find it difficult to work out the characters' intentions
21. I don't particularly enjoy reading fiction.
22. I find it hard to make new friends.
23. I notice patterns in things all the time.

24. I would rather go to the theatre than a museum.
25. It does not upset me if my daily routine is disturbed.
26. I frequently find that I don't know how to keep a conversation going.
27. I find it easy to "read between the lines" when someone is talking to me.
28. I usually concentrate more on the whole picture rather than the small details.
29. I am not very good at remembering phone numbers.
30. I don't usually notice small changes in a situation, or a person's appearance.
31. I know how to tell if someone listening to me is getting bored.
32. I find it easy to do more than one thing at once.
33. When I talk on the phone, I'm not sure when it's my turn to speak.
34. I enjoy doing things spontaneously.
35. I am often the last to understand the point of a joke.
36. I find it easy to work out what someone is thinking or feeling just by looking at their face.
37. If there is an interruption, I can switch back to what I was doing very quickly.
38. I am good at social chitchat.
39. People often tell me that I keep going on and on about the same thing.
40. When I was young, I used to enjoy playing games involving pretending with other children.
41. I like to collect information about categories of things (types of cars, types of birds, types of trains, types of plants, etc.).
42. I find it difficult to imagine what it would be like to be someone else.
43. I like to plan any activities I participate in carefully.
44. I enjoy social occasions.
45. I find it difficult to work out people's intentions.
46. New situations make me anxious.
47. I enjoy meeting new people.
48. I am a good diplomat.
49. I am not very good at remembering other people's date of birth.
50. I find it very easy to play games with children that involve pretending.