Sensorimotor Differences in Autism Spectrum Disorder: An evaluation of potential mechanisms.

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I certify that all material in this thesis which is not my own work has been identified and that any material that has previously been submitted and approved for the award of a degree by this or any other University has been acknowledged.

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Abstract

This thesis examined the aetiology of sensorimotor impairments in Autism Spectrum Disorder: a neurodevelopmental condition that affects an individual's socio-behavioural preferences, personal independence, and quality of life. Issues relating to clumsiness and movement coordination are common features of autism that contribute to wide-ranging daily living difficulties. However, these characteristics are relatively understudied and there is an absence of evidence-based practical interventions. To pave the way for new, scientifically-focused programmes, a series of studies investigated the mechanistic underpinnings of sensorimotor differences in autism. Following a targeted review of previous research, study one explored links between autistic-like traits and numerous conceptually-significant movement control functions. Eye-tracking analyses were integrated with force transducers and motion capture technology to examine how participants interacted with uncertain lifting objects. Upon identifying a link between autistic-like traits and context-sensitive predictive action control, study two replicated these procedures with a sample of clinically-diagnosed participants. Results illustrated that autistic people are able to use predictions to guide object interactions, but that uncertainty-related adjustments in sensorimotor integration are atypical. Such findings were advanced within a novel virtual-reality paradigm in study three, which systematically manipulated environmental uncertainty during naturalistic interception actions. Here, data supported proposals that precision weighting functions are aberrant in autistic people, and suggested that these individuals have difficulties with processing volatile sensory information. These difficulties were not alleviated by the experimental provision of explicit contextual cues in study four. Together, these studies implicate the role of implicit neuromodulatory mechanisms that regulate dynamic sensorimotor behaviours. Results support the development of evidence-based programmes that 'make the world more predictable' for autistic people, with various theoretical and practical implications presented. Possible applications of these findings are discussed in relation to recent multi-disciplinary research and conceptual advances in the field, which could help improve daily living skills and functional quality of life.

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List of Abbreviations

ACC	Anterior Cingulate Cortex
ADHD	Attention Deficit Hyperactivity Disorder
ASD	Autism Spectrum Disorder
AQ	The adult Autism Spectrum Quotient
AQ-26	The 26-item Autism Spectrum Quotient
DCD	Developmental Coordination Disorder
DSM	Diagnostic and Statistical Manual of Mental Disorders
EMG	Electromyography
ICD	International Classification of Diseases
IUS-S	Intolerance of Uncertainty Scale – Shortened version
pGFR	Peak Grip Force Rate
pGFRdiff	Index score illustrating differences in Peak Grip Force Rate between initial lifts of large and small objects
pLFR	Peak Load Force Rate
pLFRdiff	Index score illustrating differences in Peak Load Force Rate between initial lifts of large and small objects
MLV	Maximum Lift Velocity
MRV	Maximum Reach Velocity
NT	Neurotypical
ROM	Range of Motion
SCQ	Social Communication Questionnaire
SD	Standard Deviation
SRS-S	Social Responsiveness Scale – Shortened version
SWI	Size-Weight Illusion
VR	Virtual-Reality

Introduction

Autism Spectrum Disorder (ASD; hereafter autism[1]) is diagnosed in 1-2% of people according to patterns of restricted behaviour and differences in social interaction and communication (American Psychiatric Association, 2013; World Health Organisation, 2018; Baio et al., 2018). These core features are relatively well-established, having formed the basis of longstanding empirical and theoretical enquiry (Kanner, 1943; Asperger, 1944; Wing & Gould, 1979; Cashin & Barker, 2009). However, autistic people typically face a number of additional difficulties that can adversely impact on independence, health, and quality of life (Jasmin et al., 2009; Ikeda et al., 2014; Croen et al., 2015; Van Heijst & Geurts, 2015; Lord et al., 2018). Such outcomes represent a key priority for research, as highlighted by the National Institute for Health and Care Excellence (NICE, 2013) and the UK autism community (Pellicano et al., 2014). Academic studies are often perceived to overlook these aspects of day-to-day life, by focusing on medically-driven hypotheses in neurology, genetics and cognitive sciences (Pellicano et al., 2014). In particular, there is a lack of research into many 'secondary' characteristics that are fundamental to the lives of autistic people (e.g., gastrointestinal issues, co-occurring conditions, clumsiness, and sensory disturbances; Chaidez et al., 2014; Lai et al., 2014; Robertson & Baron-Cohen, 2017). Research into these secondary features could help elucidate diverse clinical manifestations and neurological mechanisms of autism, whilst improving our ability to effectively diagnose and manage the condition (Haker et al., 2016; Robertson & Baron-Cohen, 2017).

A prevalent aspect of daily living difficulty in autism relates to impairments in *sensorimotor control*, defined as: "the sensory, motor, and central integration and processing components involved in maintaining joint homeostasis during bodily movements" (Lephart et al., 2000). Indeed, some of the earliest accounts of autism recorded movement-based disturbances, with descriptions of "clumsiness" appearing in both Kanner's (1943) and Asperger's (1944; in Hippler & Klicpera, 2003) seminal work. Numerous first-hand reports have since supported these accounts, with challenges relating to movement control and skill execution often conveyed by autistic people (for overview, see Robledo et al., 2012). Though not yet considered essential for diagnosis, such features are unmistakably common in autism, with prevalence rates

[1] To acknowledge the preferences held by many individuals within the UK autism community, the present work uses identity-first language and refers to ASD as "autism" (see Kenny et al., 2016).

estimated at 79% (Green et al., 2009). In fact, some researchers argue that sensorimotor differences should be treated as 'primary' or 'cardinal' features of the condition (Leary & Hill, 1996; Ben-Sasson et al., 2009; Fournier et al., 2010; Whyatt & Craig, 2013b; Mosconi & Sweeney, 2015; Coll et al., 2020). This growing consensus has prompted calls for substantive empirical investigations in the field.

Research suggests that sensorimotor issues are associated with key autistic-like traits and clinical outcomes. Autistic-like traits represent behavioural characteristics such as social imperviousness, directness in conversation, lack of imagination, affinity for solitude, and difficulty displaying emotions (Gernsbacher et al., 2017). While present in all individuals, these stable characteristics are generally high in autistic populations and form the basis of most clinical assessment procedures (e.g., Lord et al., 2000; Baron-Cohen et al., 2001). They also appear related to a person's sensorimotor abilities, with levels of impairment on fundamental movement skill tests predicting various social communicative traits and clinically-related patterns of behaviour (Sutera et al., 2007; MacDonald et al., 2013; Hannant et al., 2016). Some of these features may vary over the course of development (Coll et al., 2020), though it is clear that there remains a strong and persistent continuation into adulthood (Fournier et al., 2010; Mosconi & Sweeney, 2015; Hannant et al., 2016; Coll et al., 2020).

From a wider perspective, autism-related sensorimotor difficulties can restrict key day-to-day abilities that enable independent living, such as handwriting, getting dressed, or learning to drive (Fuentes et al., 2009; Jasmin et al., 2009; Robledo et al., 2012; Cox et al., 2017). They may also contribute to increased obesity rates and reduced physical activity levels in autistic populations (Must et al., 2015; McCoy et al., 2016; Scharoun et al., 2017). Nevertheless, little is known about how to effectively manage these movement-related issues (Colombo-Dougovito & Block, 2019). Investigation into the mechanisms that cause sensorimotor differences in autism is crucial for effective practical interventions to be developed (Fournier et al., 2010; Coll et al., 2020). However, such research is currently limited in scope and quality, and significant gaps in our knowledge remain (Mosconi & Sweeney, 2015; Colombo-Dougovito & Block, 2019). Given the close relationships between sensorimotor abilities and wide-ranging daily living functions, there is a compelling rationale for well-controlled, multidisciplinary studies in the field. This research could provide a foundation for future interventions aiming to improve health, independence, and quality of life in autistic people.

Accordingly, the present thesis investigated the aetiology of sensorimotor differences in autism. To do this effectively, while addressing shortfalls in current research, a holistic investigative approach has been adopted. Firstly, a range of multi-disciplinary evidence is reviewed and evaluated (Chapter 1), using a well-established model of human sensorimotor control (Land, 2009). Here, a number of potential mechanisms and empirically-derived hypotheses have been identified, which were subsequently examined in a series of novel experiments (Chapters 2-4). Initially, these experiments aimed to refine our understanding of *why* autistic people experience sensorimotor difficulties, through integrating methodologies from cognitive psychology, kinesiology, virtual-reality and applied autism research (Chapters 2-3). Thereafter, the focus of the work shifts onto elucidating potentially fruitful avenues for prospective research and practical interventions that could be pursued to help autistic people manage and/or overcome sensorimotor issues in their day-to-day lives (Chapters 4-5).

Chapter 1

Sensorimotor difficulties are extremely common in autism and are potentially cardinal features of the condition (Ben-Sasson et al., 2009; Fournier et al., 2010; Donnellan et al., 2013; Whyatt & Craig, 2013b; Mosconi & Sweeney, 2015; Coll et al., 2020). However, the mechanisms that underpin these functional impairments remain unclear (Fournier et al., 2010; Coll et al., 2020). This literature review examines what is currently understood about sensorimotor control in autism. Specifically, the nature of movement-related impairments is first summarised (*Section 1.1*) and various potential mechanisms are considered (*Section 1.2*). Following a growing consensus that predictive processing may be atypical in autism, *Section 1.3* elucidates the computational processes that underpin neurotypical sensorimotor control. From here, a set of empirically-falsifiable hypotheses for autistic sensorimotor behaviours are formulated, using an established conceptual framework (Land, 2009). These novel hypotheses are then examined from previous research studies (*Section 1.4*), where a number of consistent themes and observations emerge. Together, this synthesis of the literature aimed to refine the potential sources of sensorimotor impairment in autism, so that precise empirical scrutiny could subsequently be applied in Chapters 2-4.

1.1. An Overview of Sensorimotor Differences in Autism

In recent years, differences in autistic sensorimotor control have been empirically examined. Here, diverse impairments in movement efficiency, sensorimotor integration, and action-related task performance have all been observed (Fournier et al., 2010; Gowen & Hamilton, 2013; Coll et al., 2020). However, these difficulties are highly variable, and a number of methodological limitations must be considered.

Numerous investigations have studied performances on standardised sensorimotor tests, such as the Movement Assessment Battery for Children (Henderson & Sugden, 1992) and the Physical and Neurological Examination for Subtle Motor Signs (Denckla, 1985). Fournier *et al.* (2010) identified over fifty studies utilising such assessment protocols, highlighting a large pooled effect size for autism-related impairments in both upper- and lower-limb sensorimotor functions. Lower standardised scores were consistently detected during these battery tests, with particular difficulties emerging for dynamic interception skills like throwing and catching (see Green et al., 2002;

Vanvuchelen et al., 2007; Whyatt & Craig, 2013a; Ament et al., 2015). These findings align with reports of atypical hand-eye coordination and postural control in autistic people (Kohen-Raz et al., 1992; Ghaziuddin & Butler, 1998; Gepner & Mestre, 2002; Molloy et al., 2003; Glazebrook et al., 2009; Robledo et al., 2012) and have been replicated in more recent empirical work (Coll et al., 2020). However, the nature and severity of these impairments markedly varies between studies, and such variability can be obscured by standardised scoring methods (Whyatt & Craig, 2013b). Indeed, the reported prevalence of sensorimotor deficits varies from 21% to 100% (Ghaziuddin et al., 1994; Manjiviona & Prior, 1995; Miyahara et al., 1997; Green et al., 2002; Pan et al., 2009), and many tests can overlook subtle, potentially-significant indices relating to the underlying *process* of movement (Berkeley et al., 2001; Gowen & Hamilton, 2013). Consequently, impairments in skill performance are a significant but potentially variable aspect of autism that require more thorough empirical scrutiny.

Studies that focus on action kinematics (rather than general performance outcomes) illustrate that autistic people show atypical movement profiles. These differences emerge during simple tasks like pointing, reaching and grasping (Glazebrook et al., 2006; Cook et al., 2013; Stoit et al., 2013; Sacrey et al., 2014; Crippa et al., 2015; Campione et al., 2016). For example, Cook *et al.* (2013) found that autistic people utilise more jerky arm movements than neurotypical controls when making horizontal sinusoidal reach actions. These clinically-related motor patterns deviated from established velocity profiles that are said to produce smooth and efficient actions (e.g., the two-thirds power law and minimum jerk principles of motion; Flash & Hogan, 1985; Todorov & Jordan, 1998). Atypicalities have also been detected in reflexive and involuntary motor responses (Teitelbaum et al., 1998; Karmel et al., 2010; Torres et al., 2013; Torres & Denisova, 2016), with autistic 'micro-movement' signals showing excess noise and randomness (Torres et al., 2013; Torres & Denisova, 2016). Therefore, kinematic studies consistently highlight compromised movement control in autistic people. These differences appear to be inherently linked to the phenotype of autism, and not a secondary consequence of co-occurring developmental delays or conditions (e.g., Attention Deficit Hyperactivity Disorder: ADHD; Developmental Coordination Disorder: DCD; see Piek & Dyck, 2004). Further scrutiny of these action profiles could present fruitful avenues for diagnostic and therapeutic developments (e.g., see Anzulewicz et al., 2016; Vabalas et al., 2020).

Atypicalities in sensorimotor integration are also broadly prevalent in autism. Sensory disturbances now form part of clinical diagnostic criteria (e.g., American Psychiatric Association, 2013), with hyper- and hypo-sensitivities common across touch, vision, smell, and sound (Robertson & Baron-Cohen, 2017). Though many of these features specifically relate to perceptual functions, disturbances also emerge in tasks that contain dynamic motor elements (Hannant et al., 2016). Indeed, reported differences in mechanoreception and movement sensitivity may represent key sources of difficulty in autism (Tomchek & Dunn, 2007; Fuentes et al., 2009; Blanche et al., 2012; Siaperas et al., 2012), with Gowen and Miall (2005) observing pronounced impairments in actions that involve a high degree of multi-sensory processing. However, there is a clear absence of low-level deficits in autistic sensory perception (Bertone et al., 2005; O'Riordan & Passetti, 2006). In fact, evidence suggests that some visual, tactile and proprioceptive inputs may even be enhanced in autistic people (Dakin & Frith, 2005; Blakemore et al., 2006; Mottron et al., 2006; Tommerdahl et al., 2007; Cascio et al., 2008). Such findings indicate that autism-related atypicalities must exist at the level of *interpretation* and/or *regulation* of sensorimotor information (Gowen & Hamilton, 2013). By deciphering which underlying mechanisms are driving these atypical processing functions, research could help autistic people reach their full potential in various practical tasks (see recommended research in Cusack & Sterry, 2016).

In spite of the significant and widespread differences discussed above, sensorimotor learning abilities are often unaffected in autism (Mostofsky et al., 2004; Gidley-Larson et al., 2008; Haswell et al., 2009; see Gowen & Hamilton, 2013). For example, a study by Mostofsky and colleagues (2004) found that adaptation rates during a ball catching task were not significantly different in autistic children when compared to neurotypical controls. These results are noteworthy, as they imply that sensorimotor differences are unlikely to result from any broad deficits in skill acquisition. However, findings are inconsistent in the field, with some studies observing autism-related learning difficulties during procedural action-based tasks (Mostofsky et al., 2000) and fundamental motor competencies (e.g., riding a tricycle; Larson & Mostofsky, 2008; see Bo et al., 2016). These inconsistencies further highlight the task-specific nature of clinical sensorimotor research and reinforce the need for greater, more detailed scrutiny into the mechanisms that underpin movement-related difficulties.

Crucially, many well recognised autistic-like traits and behaviours are preceded, and potentially caused, by sensorimotor differences (Dyck et al., 2006; Dziuk et al., 2007; Boyd et al., 2010; Turner-Brown et al., 2013; Estes et al., 2015; Casartelli et al., 2016; Hannant et al., 2016). This is perhaps unsurprising, as movement-based competencies are said to provide building blocks for adaptive social and cognitive development (Villalobos et al., 2005; Gernsbacher et al., 2008). The theoretical implications of these findings are significant as they suggest that sensorimotor atypicalities are a *not* simply a secondary consequence of inherent socio-behavioural traits. Instead, researchers claim that they may play a more central role than previously believed (Mosconi & Sweeney, 2015; Z. Wang et al., 2015). Indeed, at a neurocognitive level, disruptions in the sensorimotor system could represent a critical 'intermediate phenotype' of autism that lead to cascading secondary effects (e.g., language delays and socio-emotional issues; Trevarthen & Delafield-Butt, 2013; Casartelli et al., 2016). Furthermore, difficulties with coordinating movements and integrating contextual cues could limit interpersonal interactions and learning opportunities during childhood (Bhat et al., 2011; Hannant et al., 2016). Together, these findings emphasise the importance of sensorimotor differences in autism and reinforce the need for research into the aetiology and mechanistic underpinnings of these key features.

1.2. Theories of Autism and Possible Causes of Sensorimotor Differences

When exploring the causes of sensorimotor differences in autism, one must first consider the multi-disciplinary evidence that already exists in the field. Indeed, proven 'interdependencies' between autistic-like traits and functional sensorimotor abilities (Dyck et al., 2006) suggest that these wide-ranging features may share common mechanistic underpinnings (Leary & Hill, 1996; Nayate et al., 2005; Trevarthen & Delafield-Butt, 2013). This section examines various cognitive, neurological, and computational atypicalities that have been identified in autism and applied onto wider behavioural domains (e.g., perception, learning, and social functions). The possible influence of these factors on sensorimotor control are initially evaluated, to elucidate which specific mechanisms may be involved in limiting autistic movement skill abilities.

1.2.1. Existing Neurobiological and Psychological Research

A substantive proportion of previous empirical literature has focused on the biological underpinnings of autism, with numerous brain regions exhibiting structural and/or functional differences that could affect sensorimotor control (see Amaral et al., 2008; Ecker et al., 2015). These include, but are not limited to: the prefrontal cortex (Prior & Hoffmann, 1990), parietal lobes (Courchesne et al., 1993), cerebellum (Courchesne, 1997; Fatemi et al., 2012), anterior cingulate cortex (ACC; Thakkar et al., 2008) and basal ganglia (Sears et al., 1999; Qiu et al., 2010). Cerebellar and fronto-striatal circuits are thought to play particularly critical roles in the integrative control of movement (Mori et al., 2001; Miall et al., 2007; Franklin & Wolpert, 2011), and autistic individuals have been found to display functional differences in these regions during action-based tasks (Mostofsky et al., 2009; Verhoeven et al., 2010). However, separate atypicalities in the organisation and connectivity of key cortical structures have also been observed (Casanova et al., 2002; Herbert et al., 2004; Rane et al., 2015), including areas of the motor cortex (Nebel et al., 2014). Furthermore, sensorimotor integration could be affected by the aberrant neuromodulatory signalling and GABAergic transmission patterns shown in clinical populations (Lake et al., 1977; Gillberg & Coleman, 1992; Cook & Leventhal, 1996; Perry et al., 2001; Lam et al., 2006; Harrington et al., 2013; Hannant et al., 2016). Therefore, sensorimotor differences are likely underpinned by heterogeneous atypicalities in neural organisation, modulation and connectivity (see discussions in: Fournier et al., 2010 and Mosconi & Sweeney, 2015).

From a practical perspective, it may thus be prudent to focus on common processing mechanisms that account for diverse biological phenotypes (rather than single structures or functions). This approach is evident in many cognitive theories of autism (Rajendran & Mitchell, 2007), where deficits in executive functioning (Ciesielski et al., 1990; Ozonoff et al., 1991; 1994) and top-down attention (Happé & Frith, 2006) have been proposed. Such global processing atypicalities not only explain socio-behavioural traits of autism (Pennington & Ozonoff, 1996; Russell, 1997; Turner, 1999; Happé & Frith, 2006), they could also underlie key sensorimotor difficulties. Indeed, impairments in attention and working memory are associated with suboptimal sensorimotor integration (Mann et al., 2007; Talsma et al., 2010; Rigoli et al., 2012). Executive functions shape what goal-directed actions are generated or inhibited over time and are controlled by the same neural structures that regulate many sensorimotor

operations (e.g., the prefrontal cortex and cerebellum; Diamond, 2000; Barkley, 2012). Moreover, differences in top-down attention can affect how certain action-related cues are processed in a task, with autistic people proposed to have difficulties integrating component parts of sensory information into a coherent global percept (Happé & Frith, 2006). However, these psycho-cognitive features are neither *universal* nor *specific* to autism, and there is very little unity between the implicated mechanisms (Happé et al., 2006). So, while their contribution to certain action-related differences should not be overlooked, these reductionist cognitive perspectives fail to account for some of the more complex and variable features of autism that define sensorimotor interactions.

Overall, current research lacks a clear, well-defined explanation that can tie together the diverse neurobiological, cognitive, socio-behavioural, and *sensorimotor* profile of autism (Lai et al., 2014). Movement-related differences are particularly complex and heterogeneous characteristics, and the process of identifying a unifying mechanistic explanation is a significant challenge for autism research. Despite the growing number of investigations in this field, the underlying causes of sensorimotor impairments remain unclear (Coll et al., 2020) and wide-ranging peripheral, central, and/or behavioural mechanisms could be involved (see Cook et al., 2013). Given the notable inter-task and inter-individual variability that exists in clinical studies, it is conceivable that these underlying aetiologies may differ from person to person (see related discussion in Mosconi & Sweeney, 2015). Such a possibility is at odds with many traditional, biologically-focused theories of autism. However, recent frameworks have presented exciting avenues of investigation in this domain, by uniting the fragmented and diverse features of autism under computational models of the brain (e.g., Pellicano & Burr, 2012; Lawson et al., 2014; Van de Cruys et al., 2014). Here, shared phenotypes of autism are explained via empirically quantifiable differences in Bayesian inference and/or predictive processing (see below). Such an approach could offer promising implications for research and clinical practice (Haker et al., 2016), while potentially increasing our understanding of sensorimotor difficulties (Casartelli et al., 2016; Palmer et al., 2017). As such, the theoretical basis of these computational models must now be considered.

1.2.2. Bayesian and Predictive Processing Theories of Autism

According to Bayesian Inference theory (Bayes, 1763; Helmholtz, 1867), the brain computes generative models of the world (*belief systems*) from incoming sensory information (*likelihood* distributions) and top-down expectations (*prior* distributions), which are based on previous experience and contextual knowledge. These inputs combine to form *posterior* beliefs, or causal inferences about the world, with each source weighted according to precision estimates (i.e., the relative reliability and/or uncertainty of each informational source; Gregory, 1980). The resultant models, and their associated prediction error (i.e., differences between predicted and observed sensory inputs), are proposed to guide sensory perception and learning (Knill & Pouget, 2004; Friston, 2008; Kiebel et al., 2009), while shaping the dynamic connections among attention, action and behaviour (Lee et al., 2002; Feldman & Friston, 2010; Friston et al., 2010). These latter functions are referred to as *predictive processing* (Friston, 2005; Hohwy, 2013; Clark, 2015a), and variations in these canonical, probabilistically-driven mechanisms have become a key focus for clinical research (see Friston et al., 2014).

A group of theories propose that autism stems from impairments in the formation and/or application of these predictive models (for review, see Palmer et al., 2017). Supposedly, autistic people rely on prior information to a lesser extent than neurotypical individuals, leading to an over-dependence on 'noisy' incoming sensory cues (Pellicano & Burr, 2012). The exact source of these atypicalities is disputed, leading to contrasting mechanistic explanations (see Table 1.1). Initially, simple normative models posited that such effects may result from persistently attenuated Bayesian priors (Pellicano & Burr, 2012), overly-dominant likelihood distributions (Brock, 2012) or generic differences in detecting/learning conditional probabilities (Qian & Lipkin, 2011; Sinha et al., 2014). Many of these explanations have since been reframed using predictive processing terms and hierarchical models of the brain, with weaker top-down predictions (Van Boxtel & Lu, 2013), chronically elevated prediction errors (Van de Cruys et al., 2014), and aberrant precision modulation (Friston et al., 2013; Lawson et al., 2014; Quattrocki & Friston, 2014; Palmer, Seth, et al., 2015) all proposed.

Table 1.1. Summary of Bayesian and Predictive Processing Theories of Autism.

	Domain	Main Testable Hypothesis
Simple Models		
Pellicano & Burr (2012)	Perception	Chronically reduced influence of prior expectations in autism.
Brock (2012)	Perception	Incoming sensory information is overly-dominant in autism, relative to prior expectations.
Qian & Lipkin (2011)	Cognition/ Learning	Impaired ability to extract statistical regularities from the world and make predictions in autism.
Sinha *et al.* (2014)	Cognition/ Learning	Domain-general impairments in predictive learning in autism.
Hierarchical Models		
van Boxtel & Lu (2013)	Perception	Top-down predictions are less precise in autism, leading to constant sensory surprises.
Friston *et al*. (2013)	Perception	High-level prior precision is attenuated in autism, relative to sensory precision.
Van de Cruys *et al*. (2014)	Perception/ Action	Chronically high and inflexible weighting of prediction errors in autism.
Lawson *et al*. (2014)	Perception/ Neurobiology	Aberrant encoding of precision in autism and impaired context-sensitive sensory weightings.
Quattrocki & Friston (2014)	Social/ Neurobiology	Suboptimal weighting of interoceptive sensory signals and oxytocinergic modulation in autism
Palmer *et al.* (2015b)	Social/ Action	Maladaptive low-level precision weighting impairs higher-level predictive models in autism.

In spite of their specific conceptual discrepancies, the theories in Table 1 can encompass multi-factorial neural, cognitive, and developmental causes of autism. Here, the heterogeneous neurobiological pathologies discussed in *Section 1.2.1* may converge in common processing imbalances (Van de Cruys et al., 2021); and it is these computational differences that are seen to form the universal basis of autism. Indeed, such 'shared phenotypes' would account for the developmental, spectrum-like nature of the condition, as predictions are uniquely shaped by a person's individual experiences and knowledge about the world (Palmer et al., 2017). Therefore, academics and practitioners are increasingly utilising such perspectives to address problems of diagnosis and treatment in autistic populations (see Haker et al., 2016).

Bayesian and predictive processing theories of autism also provide compelling mechanistic explanations for a host of socio-behavioural traits and primary diagnostic features. For example, repetitive behaviours (e.g., 'stimming') and an insistence on sameness could signify coping strategies aimed at reducing prediction errors and/or uncertainty in inherently 'noisy' sensory environments (Pellicano & Burr, 2012; Froese & Ikegami, 2013; Palmer et al., 2017). Similarly, suboptimal inferential modelling would explain difficulties in 'Theory of Mind' and social interactions, where an individual is required to predict one's mental state or actions using ambiguous, higher-level implicit cues (Sinha et al., 2014; Palmer, Seth, et al., 2015). Although these normative rationales were initially seen to reflect convenient post-hoc fitting exercises (Maloney & Zhang, 2010), their notable explanatory capabilities in autism have since been able to unify numerous interrelated socio-behavioural traits and clinical characteristics.

By detailing how precision-modulated error signals are transmitted across the brain, predictive coding frameworks provide a biologically plausible means through which Bayesian inference could be enacted (Rao & Ballard, 1999; Friston, 2005; Friston & Kiebel, 2009). Here, prediction error signals are seen to communicate physical differences between incoming sensory data (i.e., bottom-up neural activity relayed from the peripheral sensory receptors) and top-down state expectations (i.e., neural activity that is predicted to occur on basis of the brain's current environmental representations; Mumford, 1992). Through applying these concepts into autism research, one can marry proposed computational differences with the established neuropathological factors discussed in *Section 1.2.1*. For instance, structural and/or functional abnormalities in the cerebellum could impact on crucial circuits that are involved in the hierarchical integration of probabilistic sensory information (e.g., see Mori et al., 2001; Friston, 2005). Furthermore, modulators of cortical gain (e.g., phasic noradrenaline, oxytocin, serotonin) have been implicated in recent neuro-computational explanations, which offer novel hypotheses regarding the biochemical and genetic basis of autism (e.g., Lawson et al., 2014; Quattrocki & Friston, 2014; Wiggins et al., 2014; Rosenberg et al., 2015). Therefore, Bayesian and predictive processing theories not only support previous neurobiological findings, they are also stimulating new directions for future investigations and clinical practice (Kok & de Lange, 2015; Haker et al., 2016).

However, these frameworks have also received notable criticism. Indeed, while the aforementioned proposals are entirely plausible (both from a behavioural and

neurological perspective), it is empirically challenging to isolate certain implicated mechanisms (Palmer et al., 2017). For instance, it can be difficult to distinguish attenuated prior beliefs from increased likelihood precisions (Brock, 2012), or aberrant prediction error signalling from impaired contingency learning (Cannon et al., 2021). Moreover, recent attempts at evaluating these models find inconsistent results (Karvelis et al., 2018), with many studies highlighting prediction-related functions that are *not* impaired in autism (e.g., Aitkin et al., 2013; Bedford et al., 2016; Ego et al., 2016; Pell et al., 2016; Manning et al., 2017; Tewolde et al., 2018; Lieder et al., 2019; Noel et al., 2020). For example, Tewolde *et al.* (2018) found preserved anticipation abilities in autistic children during dynamic visual extrapolation and false memory tasks. These null effects are consistent with wider research, where prediction-related differences are typically consigned to more complex and/or uncertain experimental conditions (Bertone et al., 2003; Cannon et al., 2021). However, such context-dependent patterns are at odds with simple Bayesian models of autism (e.g., Brock, 2012; Pellicano & Burr, 2012), as they show that the generic processing of prior information is *not* disrupted. Instead, findings imply that these 'one-level' accounts may be inadequate to capture the demands of real-world environments, where sensory information is produced by complex, dynamic external causes (Palmer et al., 2017).

Although prior beliefs may not be universally or chronically diminished in autism, differences could still lie in *hierarchical* predictive processing functions (Table 1.1). Inconsistent findings clearly undermine proposals that prediction errors are given *uniformly* high weighting in autism (Van de Cruys et al., 2014), but difficulties could still relate to suboptimal precision control systems (Friston et al., 2013; Lawson et al., 2014). Indeed, precision estimates are shaped by *context-sensitive* representations of uncertainty that span multi-level neural networks (Yu & Dayan, 2003; Mathys et al., 2011; 2014). A recent study by Lawson *et al.* (2017) showed that autism-related differences in sensory receptiveness were accompanied by atypical learning rates and phasic pupil responses; functions which are directly proportional to cortical gain and precision-related noradrenergic modulation (Behrens et al., 2007; Nassar et al., 2010; Costa & Rudebeck, 2016). On inspection of their behavioural and physiological data, the authors suggest that autistic people may overestimate the volatility of sensory environments. Such effects may limit confidence in prior beliefs and would disrupt how stable expectations are learnt about the world, with precision modulation determining

whether unexpected outcomes are disregarded or taken seriously (Behrens et al., 2007; Mathys et al., 2011; 2014). These more nuanced proposals correspond with recent clinical observations, where context-sensitive adjustments in cortical activity appear diminished over time (e.g., Kleinhans et al., 2009; Ewbank et al., 2017). They can also directly account for inconsistent research findings in the field, as precision control is partly-independent across sensory modalities and processing levels (e.g., see Yin et al., 2019). Therefore, it is possible that autistic sensorimotor control is underpinned by context-sensitive differences in neural gain signalling, as opposed to persistently 'weightier' prediction errors or bottom-up sensory inputs.

Nevertheless, future research is required to decipher specifically which prediction-related mechanisms are implicated in autism, and action-based tasks may "hold the greatest promise" for illuminating these mechanistic underpinnings (Palmer et al., 2017; p.522). Here, the differential roles of top-down and bottom-up signalling can be isolated using objective measurement techniques, which are neither dependent on motivation or communication (see Haker et al., 2016). Indeed, action can be conceived of as a series of hierarchical predictions, which operate as a vehicle for changing sensory and environmental inputs (Friston et al., 2010). As such, various context-sensitive mechanisms relating to predictions, precision, error, and uncertainty can be examined from an individual's motor responses and sensory sampling behaviour (Palmer et al., 2017). However, before exploring these processes in autism, one must first establish the role of these mechanisms in neurotypical sensorimotor control.

1.3. Underlying Mechanisms of Sensorimotor Control

The human sensorimotor system is extremely complex: almost infinite movement degrees of freedom are underpinned by unstable and non-linear neurobiological activity, which must be integrated with rapidly-changing environmental information. To solve such complexities, actions are guided and monitored using multi-sensory cues, with even automated routine activities demanding high levels of continuous feedback (Land, 2009). This influx of sensory data is used to tune movement parameters in a computationally optimal and energetically efficient manner, while minimising the effects of noise in the motor system (Franklin & Wolpert, 2011). However, there are notable sources of imprecision that exist in the retrieval and processing of sensory evidence,

which limit the reliability and/or accuracy of feedback-driven motor control (e.g., from signalling delays, poor peripheral resolution etc. Faisal et al., 2008; Tong et al., 2017).

To combat these proposed shortfalls, the nervous system is hypothesised to use predictive generative models, which explain and stabilise inherently noisy and ambiguous sensory information (Franklin & Wolpert, 2011; Clark, 2015a). In line with Bayesian Inference, these top-down models are said to embody probabilistic distributions about the world, making them critical in the planning and execution of goal-directed actions (see Fiehler et al., 2019). For example, when attempting to intercept a ball in sport, individuals will adapt their movements based on multi-level predictions about its likely position, speed, and trajectory. These *a-priori* estimations are shaped by recent sensory observations (e.g., information extracted from an opponent's movements or from previous trial attempts; Diaz et al., 2013; Loffing & Cañal-Bruland, 2017) as well as long-term 'structural' expectations and constraints (e.g., implicitly-embedded representations about gravity and its influence on moving objects; Zago et al., 2009; Hayhoe et al., 2012; Diaz et al., 2013). Predictions are then iteratively refined over time, in a manner that facilitates rapid modelling adjustments and learning (Körding et al., 2007; Burge et al., 2008; see Figure 1.1 for illustration).

As with perceptual inference, the brain is biased towards reliable sensorimotor cues, meaning that highly precise expectations will readily dominate over uncertain and noisy feedback information (Knill & Pouget, 2004; Vilares & Kording, 2011; Figure 1.1). Indeed, 'Bayes-optimal' strategies emerge in numerous action-related functions, including: multi-sensory cue combination (Jacobs, 1999; Adams et al., 2004; Körding et al., 2007), motion perception (Weiss et al., 2002; Stocker & Simoncelli, 2006), interceptive timing (Miyazaki et al., 2005; Jazayeri & Shadlen, 2010), gaze tracking (Deravet et al., 2018), movement planning (Hudson et al., 2007; Kwon & Knill, 2013), and visuomotor integration (Körding & Wolpert, 2004; Tassinari et al., 2006; Stevenson et al., 2009; Vilares et al., 2012; O'Reilly et al., 2013; Sato & Kording, 2014). For example, Stevenson *et al.* (2009) found that increases in visual feedback uncertainty during a snowboarding simulation task led to more temporally-stable motor patterns that were less influenced by current proprioceptive information. By resolving sensory uncertainty in this manner, neurotypical individuals are theoretically able to maintain adaptive sensorimotor control and learning functions (Vilares & Kording, 2011).

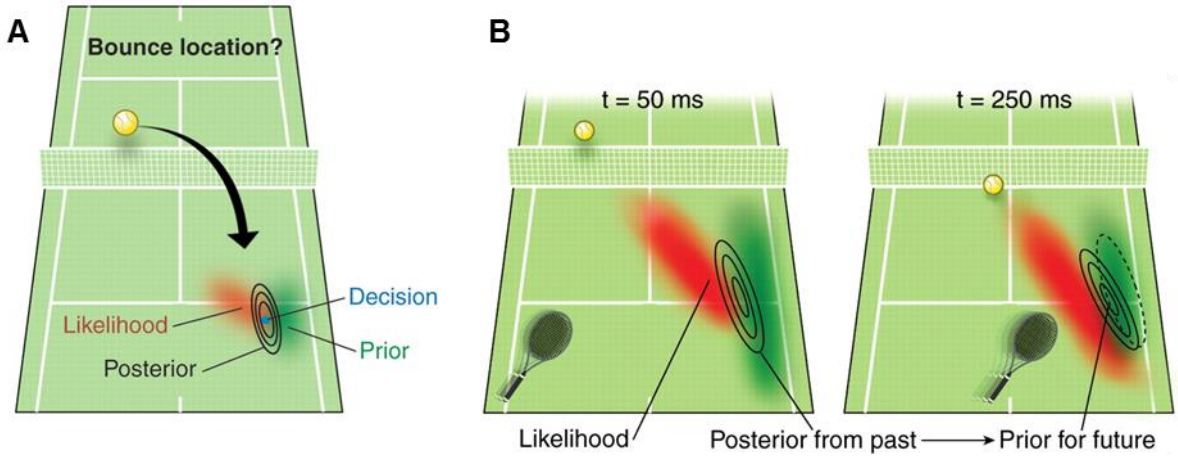

Figure 1.1. Example of Bayesian Inference in tennis, copied from Körding (2007) with permission from American Association for the Advancement of Science (copyright 2007). Illustrates how prior and likelihood information combine when predicting the bounce location of a ball (**A**) and how this information is dynamically adjusted (**B**). Note how prior expectations (green circles) and incoming visual feedback (red circles) are integrated according to their uncertainty, such that posterior beliefs (black outline) are biased by more precise estimations. In panel **B**, expectations about bounce location become more refined over time, meaning that their relative influence also increases.

The computational mechanisms of sensorimotor control have been further developed by active inference theories (e.g., Adams et al., 2013; Shipp et al., 2013; Friston et al., 2017). According to these frameworks, an agent will constantly seek to minimise prediction error through physical bodily movements. To do this, they will preferentially select actions that have low *expected free energy* (i.e., movements that are estimated to generate the least prediction error; Parr & Friston, 2019). In essence, this means that dynamic sensorimotor adjustments will aim to fulfil an individual's predictions about the world. From a practical perspective, this implies a fundamental role of prior expectations in the control of goal-directed movements and daily living behaviours. Indeed, these subjective beliefs are not only seen to influence the generic planning of an action, they are also proposed to shape the iterative updating and online regulation of an ensuing sensorimotor response (Friston et al., 2010). For example, when attempting to make timely and accurate interceptions in tennis, anticipated changes in

proprioceptive inputs and upcoming ball trajectory will determine moment-by-moment adjustments in motor activity and swing kinematics.

Furthermore, prior expectations will influence how an agent actively *samples* sensory information (Friston, Adams, et al., 2012). During interceptive visuomotor tasks like tennis, agents will frequently employ anticipatory eye movements that shift gaze towards predicted future ball locations (Land & McLeod, 2000; Hayhoe et al., 2002; 2012; Diaz et al., 2013; Mann et al., 2013). Analogous 'proactive' gaze strategies are additionally shown in conventional daily living functions, such as driving (Land & Lee, 1994; Land & Furneaux, 1997; Land & Tatler, 2001; Chattington et al., 2007), walking (Patla, 1998; Patla & Vickers, 2003; Moraes et al., 2004; Matthis et al., 2018), reading (Buswell, 1920; Land & Furneaux, 1997; Furneaux & Land, 1999), and making a cup of tea (Land et al., 1999; see Land, 2009). This further highlights the crucial role of prior expectations when controlling movements and integrating sensorimotor cues.

Notably, superior predictive abilities are a defining characteristic of various high-skilled performances (e.g., medicine: Currie & MacLeod, 2017; sport: Williams et al., 2011). Sporting professionals, in particular, will implement strategies that increase the accuracy and/or precision of prior expectations while ensuring the sampling of 'optimal' sensory cues (e.g., through studying opponents, repetitive practice, or executing pre-performance routines; Körding & Wolpert, 2004; Cappuccio et al., 2020). An example of this enhanced anticipatory ability was demonstrated by Runswick *et al.* (2020), who showed that professional rugby players are more accurate than novices in predicting the 'seemingly-random' future bounce of a rugby ball. Such effective anticipation would require extremely complex and dynamic computations of physical statistics (Cross, 2010), which seem to be implicitly acquired in professional participants through their extended practice and engagement in the sport. These, expert-like predictions will often then coincide with more efficient gaze patterns (Williams & Davids, 1998; Mann et al., 2013; Murphy et al., 2016), while suboptimal visual sampling responses have been shown in individuals with clinically-related sensorimotor difficulties (Wilson et al., 2013; Licari et al., 2018). Consequently, accurate prior expectations appear to be an integral aspect of proficient movement control and adaptive skill performances.

However, natural environments are rarely stable or certain, meaning that predictions can vary in accuracy and reliability over time. In spite of these rapidly changing

environmental ambiguities, most sensorimotor functions remain optimal due to context-sensitive adjustments in predictive processing. Here, the brain dynamically weighs prior inputs according to expected uncertainty and inferred volatility estimates, with unreliable sources of information less readily attended to and retained over time (Burge et al., 2008; O'Reilly et al., 2013; Deravet et al., 2018). Computationally, this is achieved through precision modulation, with top-down signals suppressed (relative to new bottom-up sensory evidence) under more uncertain or volatile conditions (Yu & Dayan, 2003; Behrens et al., 2007; Mathys et al., 2011; 2014; Yon, 2021).

These context-sensitive mechanisms are crucial determinants of dynamic movement control (Adams et al., 2013; Shipp et al., 2013) and sensory sampling behaviours (Friston, Adams, et al., 2012), with eye movement responses proving particularly sensitive to environmental statistics (Vossel et al., 2014; Deravet et al., 2018; Domínguez-Zamora et al., 2018; Pasturel et al., 2020). According to predictive coding perspectives (e.g., Rao & Ballard, 1999; Friston, 2005; 2008), precision estimates are encoded via activity-dependent changes in synaptic gain (i.e., in cell populations that signal prediction error), with neuromodulators such as noradrenaline and/or acetylcholine likely involved (Yu & Dayan, 2003; Friston, 2008; Bland & Schaefer, 2012; Lawson et al., 2021). These regulatory processes represent fundamental mechanisms in dynamic sensorimotor performance and learning operations.

Additionally, various task-specific estimates also underpin adaptive sensorimotor behaviours. Probabilistic distributions of the world are combined with goal-relevant contextual information, such as expected rewards (Wu et al., 2009), time constraints (Zhang et al., 2010), energetic demands (O'Sullivan et al., 2009; Li et al., 2018), and attributions of error (Yin et al., 2019). Though there is much debate as to how these factors are neurally represented (e.g., see Friston, 2011), such dynamic modelling further magnifies the complex, context-sensitive nature of sensorimotor control. Indeed, probabilistically ‘optimal’ inferences are sometimes overridden by non-linear, compensatory action preferences. Elite batsmen in baseball, for instance, will often plan their motor responses for faster-than-expected ball pitches (Cañal-Bruland et al., 2015), as the performance costs associated with prediction error are greater when speed is under- as opposed to over-estimated (Gray & Cañal-Bruland, 2018).

Furthermore, by viewing behaviour through the lens of prediction error minimisation, active inference perspectives assert that an agent will often select exploratory, information-seeking action responses over those with more probable expected outcomes (Parr & Friston, 2019). Here, one can minimise the uncertainty that is predicted to exist in an environment, through selective attention, sensory attenuation, and strategic motor adjustments (Friston et al., 2010; Friston, Adams, et al., 2012; Brown et al., 2013; Parr & Friston, 2019). Such epistemic active inference is a common feature of visuomotor behaviour (Friston et al., 2015), with more exploratory gaze strategies typically displayed under uncertain task conditions (Beesley et al., 2015; Tong et al., 2017; Domínguez-Zamora et al., 2018; Walker et al., 2019).

In sum, sensorimotor control depends on an array of context-sensitive mechanisms, which regulate how an agent samples, processes, and acts upon environmental cues. Examination of these predictive functions could enhance our understanding of various clinical conditions (Behrens et al., 2007; Friston et al., 2014; Teufel & Fletcher, 2016).

1.4. Sensorimotor Differences in Autism: a review of potential mechanisms

A key implication of Bayesian and predictive processing theories of autism is that differences in the weighting of prior beliefs and/or prediction error will lead to impaired sensorimotor functions (Pellicano & Burr, 2012; Lawson et al., 2014; Van de Cruys et al., 2014; Palmer et al., 2017). However, movement-related difficulties in autism could arise from a variety of neurobiological and computational mechanisms, and it is clear that predictive processing atypicalities can materialise differently across tasks and sensorimotor functions, depending on contextual and individual factors. Consequently, when evaluating the precise causes of movement-related difficulties in autism, researchers should study action control in a *holistic* and *systematic* manner, using well-established models of the human sensorimotor system.

This review will conceptualise sensorimotor control using Land's (2009) framework. This model provides a comprehensive overview of the processes that underlie natural visually-guided movements and their interactions with various brain structures and environmental factors. The reasons for selecting this framework were twofold. Firstly, it explicitly defines the contributions of four distinct biological systems and illustrates their relations to precise neural networks and processing pathways (see *Section 1.4.1*).

By scrutinising and triangulating evidence from each these interconnected systems, one can examine which mechanisms are intact and which functions are atypical in autism. Second, Land also describes how visuomotor integration may vary under different types of actions. This all-encompassing level of detail enables investigation into the considerable inter-task variability that has emerged in clinical sensorimotor research. As a result, one can systematically evaluate a number of key mechanisms, including those implicated in Bayesian and predictive processing theories of autism.

Crucially, simple computational models of autism (e.g., Brock, 2012; Pellicano & Burr, 2012; Van Boxtel & Lu, 2013) lend themselves to chronic (i.e., persistently recurring) prediction-related differences in action control, which should reliably emerge across interconnected sensorimotor networks. Conversely, any task- or system-specific differences in action control would be independent of these generic impairments, and may implicate hierarchical, context-sensitive functions (e.g., precision modulation, Friston et al., 2013; Lawson et al., 2014). The section below aimed to decipher between these possibilities, by examining the aetiology of autism-related differences in visual, gaze, motor and schema functions. However, before these finer mechanistic enquiries are addressed, a short overview of Land's conceptual framework is provided.

1.4.1. Conceptual Framework

Land's (2009) model identifies four distinct sensorimotor systems that underpin visually-guided actions (Figure 1.2). These systems each have unique, interconnected functions that facilitate natural bodily movements and daily living behaviours. Specifically, the *visual system* processes dynamic sensory cues from the surrounding environment and monitors action using continuous feedback information. Conversely, the role of the *gaze system* is to locate and fixate task-relevant information through coordinated movements of the eyes, head, and trunk. The *motor system* is then responsible for carrying out limb movements and using information supplied through vision and proprioception to modify actions. These interacting functions are controlled by the *schema system*: a supervisory unit which dynamically governs the flow of activity between sensory inputs, internal states, and motor outputs. It does this by selecting top-down internal models (i.e., schemas) that drive cortical activity across various interconnected neural pathways to specify what sensory information is required, where gaze should be directed, and what action(s) will ultimately be undertaken.

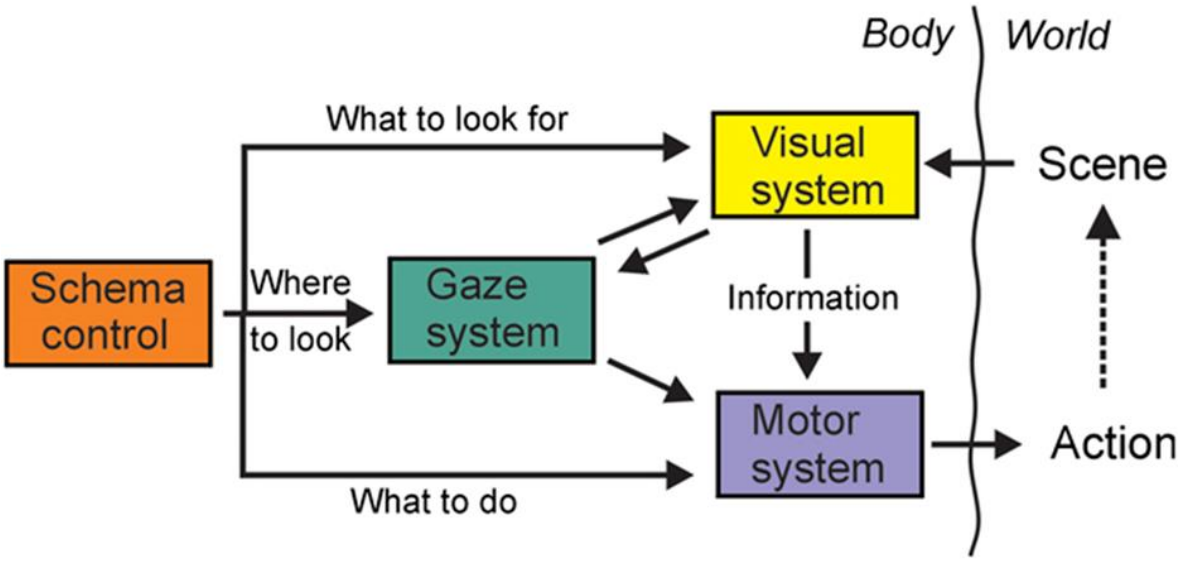

Figure 1.2. Schematic Illustration of the Conceptual Framework, copied from Land (2009) with permission from Cambridge University Press (copyright 2009).

Land argues that top-down processes dominate visuomotor control; however, his conceptual model also illustrates the role of sensory feedback from the surrounding scene (Figure 1.2). Here, salient incoming information can override top-down signals and attract attention in a stimulus-driven manner (see Corbetta et al., 2008). Individual differences in these processing functions can be readily detected using empirical tools like eye-tracking, electromyography (EMG), and motion capture technology (see *Section 1.6*). In recognising the context-sensitive nature of these underlying control operations, Land stated that the role of interacting visuomotor systems will vary between certain task types. These included single action events (e.g., lifting an object), continuous production loops (e.g., steering a car), storage-action alternations (e.g., completing a jigsaw), and multiple action sequences (e.g., playing a game in tennis). From an active inference perspective, these subtle variations in movement control reflect context-sensitive alterations in predictive processing, with an agent's sensorimotor response said to be dynamically adjusted according to current action preferences and top-down beliefs (see *Section 1.3*). So, when combined with computational explanations of human behaviour, Land's model variants permit the formulation of new, empirically-falsifiable hypotheses for autism research (see Chapters 2-4).

In fact, much of Land's (2009) model is congruent with active inference perspectives. While discrete in their theoretical proposals, both theories allude to the dynamic integration of top-down and bottom-up sensory information. Active inference provides a biologically-plausible means through which internal models can regulate visual, gaze, and motor operations (i.e., predictive coding). Here, corticospinal predictions based on high-level action representations are supposedly transmitted downstream to lower processing levels. The resultant 'error' between top-down and bottom-up signals should then directly modulate an agent's dynamic sensorimotor response (via reflex arcs; Adams et al., 2013; Shipp et al., 2013) and visual sampling behaviours (via attentional adjustments; Feldman & Friston, 2010; Friston, Adams, et al., 2012). Importantly, these processes are said to follow Bayesian model principles; so the action plans that are expected to optimally minimise future prediction errors will be preferentially selected and performed (see Parr & Friston, 2019). On this basis, it seems that the two theoretical frameworks offer well-founded conceptualisations of sensorimotor control that can complement each other in the present analyses. The sections below will therefore attempt to synthesise these perspectives, by examining multi-system operations from both a computational and behavioural standpoint.

Before one can develop this line of original, theory-driven empirical enquiry, it is prudent to first evaluate the existing literature in the field. Accordingly, this review will examine current autism research findings from each of the visuomotor sub-systems illustrated in Figure 1.2. Specifically, it will explore the degree to which *visual*, *gaze*, *motor*, and *schema* functions are suboptimal in autism, before identifying precisely which mechanisms prove intact or atypical in previous datasets. By scrutinising action control in this structured and theoretically-driven manner, and by considering the role of atypical active inference within each distinct function, one can broadly characterise the basis of sensorimotor differences in autism. This will aid the development of both empirical studies and prospective practical interventions.

1.4.2. The Visual System

The role of the visual system is to supply task-critical sensory information that can facilitate a motor action (Figure 1.2). Concerned research must not only focus on the retrieval of visual data, but also on how this information is processed by the brain.

These functions have become key topics of investigation, due to the widespread vision-related issues that emerge in autistic people (see Bogdashina, 2003) and their potential impact on sensorimotor control (Hannant et al., 2016). For example, studies have highlighted differences in: visual search (e.g., O'Riordan et al., 2001), spatial attention (e.g., Wainwright-Sharp & Bryson, 1993; 1996), binocular rivalry (e.g., Robertson et al., 2013), gestalt processing (e.g., Brosnan et al., 2004), depth cue integration (e.g., Bedford et al., 2016), and perceptual adaptation (e.g., Pellicano et al., 2007). It must be said that various counter-evidence exists in these overlapping domains and that methodological limitations have restricted our ability to make definitive conclusions (for review, see Simmons et al., 2009). Furthermore, it is clear that most basic *low-level* visual functions are unaffected in autistic people (e.g., contrast sensitivity, visual acuity, flicker detection; Koh et al., 2010; Tavassoli et al., 2011). Consequently, perceptual atypicalities are unlikely to stem from any domain-specific impairment in the visual system and its accompanying levels of sensitivity.

In spite of these existing theoretical disputes, some areas of consensus has been achieved. Indeed, perhaps the most reliable findings in autism research concern those relating to visual search (Simmons et al., 2009). Relative to neurotypical individuals, autistic people consistently show superior performances in Embedded Figures (e.g., Shah & Frith, 1993), Block Design (e.g., Venter et al., 1992), and Feature Search (e.g., O'Riordan et al., 2001) tasks. Here, individuals demonstrate enhanced abilities to detect and process 'target' visual cues, which are presented among an array of 'distractor' items. These functions are underpinned by well-established neurological pathways, such as the dorsal and ventral visual streams (Land, 2009), where autism-related differences in functional connectivity have notably been observed (Villalobos et al., 2005). However, it is unlikely that the wide-ranging perceptual differences in autism are confined to these system-specific neural pathways (Simmons et al., 2009). As with the broad socio-behavioural characteristics of autism, the precise neurobiological origins of these unique visual traits thus remain poorly defined (Joseph et al., 2009).

In recent years, research has started to focus on computational mechanisms of perception, which explain individual differences in visual functions using biologically-plausible models of hierarchical processing networks. Studies suggest that noisy and ambiguous activity patterns from across retina are interpreted using predictive models of the world, as formalised in multiple theoretical explanations (e.g., Rao & Ballard,

1999; Baldi & Itti, 2010; Brown & Friston, 2012). Indeed, various neurotypical visual functions have proven to be 'Bayes-optimal' in this regard (Jacobs, 1999; Murray et al., 2002; Weiss et al., 2002; Knill & Saunders, 2003; Adams et al., 2004; Stocker & Simoncelli, 2006; Sato & Kording, 2014), with incoming sensory signals weighted against prior beliefs according to their relative precision (see *Section 1.3*).

Crucially, Bayesian theories of autism propose a reduced influence of prior models on autistic visual processing (Brock, 2012; Pellicano & Burr, 2012). Though evidence from movement-based tasks is currently lacking, such prediction-related differences have indeed been documented at a perceptual level. For instance, autistic people show atypical integration of sensory information with prior estimates in the context of time-interval judgments (Karaminis et al., 2016), depth perception (Bedford et al., 2016), and visual illusions (Happé & Frith, 2006; Van der Hallen et al., 2015). In these settings, autistic participants appear to preferentially process bottom-up sensory information over non-veridical top-down cues, in a manner that supports Bayesian hypotheses (Pellicano & Burr, 2012). However, autism-related differences do not emerge for *most* perceptual illusions (Van der Hallen et al., 2015; Chouinard et al., 2018) or in tasks that implicate long-term 'structural' priors (Croydon et al., 2017; Lieder et al., 2019; Van de Cruys et al., 2021). Furthermore, biases away from top-down visual cues do not always manifest in autistic visuo*motor* behaviours (Ropar & Mitchell, 1999; Brosnan et al., 2004). These inconsistencies challenge simple computational theories of autism (see Table 1.1) and highlight the importance of examining visual processing alongside other sources of sensorimotor information (e.g., proprioceptive and haptic cues).

Notably, while most Bayesian perspectives predict an *increased* dependence on incoming sensory information in autism, studies suggest that autistic people may rely *less* on visual feedback than neurotypical individuals (Masterton & Biederman, 1983; Jones & Prior, 1985; Glazebrook et al., 2009; Haswell et al., 2009). Such findings are not necessarily at odds with computational models though, as agents often replace visual feedback with alternative sources of incoming sensory data (e.g., proprioception; Land, 2009). Indeed, autistic participants appear to rely almost exclusively on proprioceptive, rather than visual feedback in prism-induced reaching tasks (Masterton & Biederman, 1983). Furthermore, atypicalities in proprioceptive and vestibular processing have been found to co-occur in autism during visually-occluded actions, and are associated with impaired motor skill performances (Siaperas et al., 2012).

Since these low-level tactile and proprioceptive inputs appear to be intact in autistic individuals (Fuentes et al., 2009; Gowen & Hamilton, 2013), the above patterns of data likely reflect differences in the *modulation* of sensorimotor information (e.g., aberrant weighting of prediction errors: Lawson et al., 2014; Van de Cruys et al., 2014).

Overall, it therefore appears that autism-related differences in the visual system implicate higher-level processing mechanisms (Gowen & Hamilton, 2013). Basic low-level perceptual functions seem to be intact in autistic individuals, yet the integration of dynamic visuomotor information is often impaired during action-based tasks (Hannant et al., 2016). From a predictive processing perspective, these findings lend support for proposals of suboptimal precision control and/or error modulation in autism (Friston et al., 2013; Lawson et al., 2014; Van de Cruys et al., 2014; Palmer et al., 2017). However, given the clear inconsistencies observed between studies in the field, thorough investigation into the specificity and generalisability of predictive control deficits is still required (Schuwerk et al., 2016). To do this, future research should assess sensorimotor control *holistically*, by examining the co-ordinated contributions of visual, proprioceptive and motor systems during active inference behaviours.

1.4.3. The Gaze System

The human gaze system controls the process of directing visual fixation through a scene in the service of ongoing perceptual, cognitive and behavioural activity (Henderson, 2003). Though often considered part of vision, Land (2009) advocates the treatment of gaze control as a separate, albeit related, operational system due to its distinct neurobiological underpinnings and functions. Specifically, the role of the gaze system is to overtly bring sensory cues onto the fovea of the eyes, not just via ocular movements, but also through those of the head and trunk (Land, 2009). These active visual sampling behaviours are underpinned by highly-distributed neurological networks, which reciprocally connect frontal eye fields to the parietal lobes, cerebellum, and (pre-) motor regions of the brainstem (Corbetta et al., 1998; Gaymard et al., 2003; Leigh & Zee, 2006). Structural and functional abnormalities in these circuits are well-reported in autistic people (see Brenner et al., 2007), as are atypical head movements (e.g., Martin et al., 2018) and suboptimal postural control (e.g., Molloy et al., 2003; Chang et al., 2010). This makes gaze functions potentially valuable indicators of neurophysiological and/or computational dysfunction in autism.

Atypical foveation of visual objects and semantic stimuli have been displayed in various research domains. A notable study by Wang *et al.* (2015) examined eye-tracking responses to 700 natural scene images and found that autistic people show a smaller overall number of gaze fixations than neurotypical controls. Here, individuals not only focused on 'salient objects of circumscribed interest' (as in Sasson et al., 2008; 2011), they also exhibited delayed saccade latencies and stronger image centre biases (S. Wang et al., 2015). Such visual sampling discrepancies align with reported difficulties in attention (e.g., "tunnel vision"; Rincover & Ducharme, 1987; Burack, 1994) and exploratory gaze behaviours (e.g., Mottron et al., 2007). Crucially though, they cannot solely be explained by low-level saliency information (e.g., pixel- and object-based features; S. Wang et al., 2015), indicating that these differences may originate from impaired oculomotor control (see Brenner et al., 2007). Given the significant downstream effects on attention and movement coordination, these gaze-based operations are potentially crucial limiters of autistic sensorimotor behaviour.

Nevertheless, a recent meta-analysis by Johnson and colleagues (2016) found that the fundamental control of fixations appears to be preserved in autistic people, and that there is minimal evidence for deficits in saccade initiation or gaze disengagement. Indeed, studies of reflexive, visually-guided eye movements suggest that the functional metrics of basic oculomotor control are generally typical in autism (Minshew et al., 1999; Takarae, Minshew, Luna, Krisky, et al., 2004; Luna et al., 2007; D'Cruz et al., 2009; Pensiero et al., 2009; Johnson et al., 2012; 2016). Furthermore, mappings of neuronal organisation between the frontal eye fields and central cortical regions appear unaffected in autism, according to clinical neuroimaging studies (e.g., Hadjikhani et al., 2004).

Conversely, it must be noted that that *endogenous* (i.e., volitional) saccade and pursuit eye movements are often less accurate and more variable in autistic participants (Goldberg et al., 2002; Takarae, Minshew, Luna, Krisky, et al., 2004; Takarae, Minshew, Luna, & Sweeney, 2004; Luna et al., 2007; Stanley-Cary et al., 2011; Johnson et al., 2012; Crippa et al., 2013; Schmitt et al., 2014), particularly when gaze responses require top-down internal models (see Johnson et al., 2016). For example, Goldberg and colleagues (2002) found autism-related impairments in generating anticipatory saccades, even though basic abilities to shift and disengage gaze fixations were preserved. When compared to neurotypical participants, autistic people were less

inclined to make eye movements that *preceded* highly-predictable changes in target position. They also demonstrated a comparatively reduced inhibition of reflexive, goal-inappropriate eye movements; findings which have since been replicated in multiple working memory studies (e.g., Minshew et al., 1999; Manoach et al., 2004; Luna et al., 2007; Thakkar et al., 2008; Mosconi et al., 2009). However, notable counterevidence exists for these effects, with autistic people showing intact predictive saccade abilities in various low-level gaze tracking experiments (e.g., von Hofsten et al., 2009; Aitkin et al., 2013; Ego et al., 2016). Together, results indicate that fundamental oculomotor control is not broadly impaired in autism, and that atypical gaze responses implicate higher-order processing networks (Neumann et al., 2006; Johnson et al., 2016).

To study higher-level attentional mechanisms further, one should explore the links between perception and oculomotor control (Brenner et al., 2007). The close interplay between these sensory processing operations is illustrated in Figure 1.2, with both *visual* and *gaze* systems said to be underpinned by shared internal models (Land, 2009; see active inference perspective: Friston, Adams, et al., 2012). Notably, studies have shown that autistic people fixate on atypical regions of the face during social tasks (Klin et al., 2002; Pelphrey et al., 2002; Dalton et al., 2005; Neumann et al., 2006; Jones et al., 2008; von Hofsten et al., 2009). Although such effects are inconsistent (Van Der Geest et al., 2002; Freeth et al., 2010; Sawyer et al., 2012; see Senju & Johnson, 2009), they raise the possibility that gaze-specific atypicalities are causing the core perceptual and/or socio-communicative difficulties exhibited in these settings (see Brenner et al., 2007). However, such arguments lack empirical support, as many autism-related perceptual differences still exist when attention and/or low-level saliency information is experimentally controlled (e.g., Neumann et al., 2006; Ewing et al., 2013). Moreover, while presenting clear differences in the *interpretation* of sensory information during visual search and illusion-based tasks, autistic participants do not always show atypical gaze responses in these domains (Joseph et al., 2009; Chouinard et al., 2018). Consequently, it appears that system-specific deficits in oculomotor control are unlikely to be driving wider processing biases in autistic people.

From a neurological perspective, gaze- and vision-based differences in autism may still share common mechanistic origins. Indeed, the extraction and processing of goal-relevant sensory cues could be disrupted by cerebellar, parieto-collicular or dorsal stream dysfunction (Takarae, Minshew, Luna, & Sweeney, 2004; Brenner et al., 2007;

Johnson et al., 2016). Current gaze findings are not entirely consistent with pathway-specific disruptions in these regions though (Mottron et al., 2007; Ego et al., 2016), and such precise networks are unlikely to account for the diverse range of autistic visual characteristics (Simmons et al., 2009). Nevertheless, imbalances in excitation-inhibition activity (i.e., *divisive normalisation*: Schwartz et al., 2007) have been identified across cortico-cerebellar circuits (Rubenstein & Merzenich, 2003; Yizhar et al., 2011; Ramaswami, 2014; Rosenberg et al., 2015). These synaptic imbalances may disrupt the elimination of goal-irrelevant sensory signals (Beck et al., 2011), and have been shown to account for heterogeneous autistic gaze behaviours (Vattikuti & Chow, 2010). However, excitation-inhibition differences are situation-specific (C. J. Palmer et al., 2018), and a lack studies have investigated these mechanisms in sensorimotor control tasks. Future studies are thus required in action-based protocols.

According to Land (2009), internal action models will supervise the detection and retrieval of goal-relevant visual information (see Figure 1.2), with the role of bottom-up mechanisms said to be limited in volitional gaze behaviours. Such top-down processes have long been the focus of autism research theory (e.g., Happé & Frith, 2006; Mottron et al., 2006). However, traditional conceptual frameworks generally prove limited in explaining heterogeneous, *autism-specific* visual sampling behaviours (Simmons et al., 2009) and are increasingly being substituted by computational perspectives (see *Section 1.2.2*). Indeed, predictive processing models offer novel, empirically-supported hypotheses concerning autistic gaze control: namely that visual sampling behaviours will be more limited and detail-focused in uncertain sensory conditions (Palmer et al., 2017). Such proposals relate to active inference models of attention (e.g., Feldman & Friston, 2010), which posit that humans selectively sample expected and/or uncertain sensory cues in an attempt to minimise prediction error. Observed autism-related differences in exploratory gaze behaviour (Sasson et al., 2008; 2011), divisive normalisation (Rosenberg et al., 2015), attentional habituation (e.g., Ramaswami, 2014; Tam et al., 2017; Vivanti et al., 2018), and predictive eye movements (Goldberg et al., 2002; D'Cruz et al., 2009; Greene et al., 2019) lend initial support for these hypotheses. Further research is needed though, to better understand which specific processing functions are implicated during autistic sensorimotor operations.

Overall, atypical gaze behaviours appear to be a pervasive feature of autism which coincide, and likely interact, with perceptual characteristics of the condition. Empirical

evidence offers notable support for predictive processing models of autism, however research is currently lacking from movement-based tasks. When evaluating these models in the future, it is crucial that investigations examine active inference formulations of visual sampling behaviour, with predictive gaze patterns considered an integral part of successful sensorimotor performances.

1.4.4. The Motor System

Upon receiving sensory information, the motor system is responsible for executing and controlling the invariant bodily movements that underpin goal-directed actions (Land, 2009). Such functions implicate well-defined circuits in frontal premotor and motor cortices, as well as parietal and subcortical regions of the brain (Rizzolatti & Luppino, 2001). Research has shown that poorer sensorimotor performances in autism are often driven by atypical limb kinematics (e.g., Fabbri-Destro et al., 2009; Whyatt & Craig, 2013a; Chen et al., 2019; Foster et al., 2019), raising the possibility that movement-based difficulties reside in these primary motor networks (Trevarthen & Delafield-Butt, 2013). Reliable autism 'motor signatures' are identifiable in simple reach-and-throw actions (Crippa et al., 2015), object interactions (Cavallo et al., 2021), computer tablet gameplay (Anzulewicz et al., 2016), and movement imitation tasks (Vabalas et al., 2020; see also: Guha et al., 2016). However, generalised movement difficulties cannot be *entirely* accounted for by basic motor system dysfunctions (Dziuk et al., 2007). Moreover, machine learning classifications are significantly enhanced when eye-tracking data are also included (Vabalas et al., 2020). Therefore, evidence suggests that autistic motor control is impaired by *non-specific* neurobiological mechanisms (i.e., functions that also regulate perception, attention and/or learning abilities).

When interpreting the cause of atypical action kinematics in autism, Cook and colleagues (2013) consider that both peripheral and central nervous functions may be involved. Motor impairments could conceivably stem from abnormal muscle tone (Maurer & Damasio, 1982), heightened neural noise (Torres et al., 2013; Torres & Denisova, 2016; Noel et al., 2020), aberrant autonomic regulation (Song et al., 2016; Patriquin et al., 2019), cortico-cerebellar neuropathology (Rogers et al., 2013; Trevarthen & Delafield-Butt, 2013; Jaber, 2016), and various other biological processes (see Torres et al., 2013). Of note here, is the growing evidence that autistic motor control is overpowered by signal variability and noise (Gowen & Hamilton, 2013;

Torres et al., 2013; Torres & Denisova, 2016). Such low-level system corruptions are typically minimised by predictive encoding mechanisms, which modulate sensory information according to statistically likely events (Teufel & Fletcher, 2020).

Crucially, probabilistic state estimations are often represented *before* a movement is completed; however, there is increasing evidence that this prospective mode of control is impaired in autistic individuals. Indeed, early descriptions of an absence in "anticipatory postures" (Kanner, 1943) have since been validated by sophisticated analyses and measurement techniques, such as EMG (e.g., Schmitz et al., 2003), machine learning (e.g., Crippa et al., 2015; Cavallo et al., 2021), and force impedance analysis (e.g., David et al., 2009; 2012). For instance, autistic children have shown suboptimal programming of initial motor outputs and sustained fingertip force coordination during precision grip tasks (David et al., 2009; 2012; Mosconi et al., 2015; Z. Wang et al., 2015). Such motor dysfunctions seemingly derive from atypical feedforward control and/or a failure to flexibly adapt behaviour to changing task demands (see discussions in: David et al., 2012; Z. Wang et al., 2015). Consequently, autism-related differences in movement execution may derive from suboptimal prospective control functions in the central nervous system.

Active inference theories claim that the feedforward, context-sensitive regulation of neuromuscular activity occurs via spinal reflex arcs in the motor periphery, which quash prediction error across the nervous system (Adams et al., 2013; Shipp et al., 2013). Indeed, computational studies have shown that the prospective control of a motor response is reflective of 'Bayes-optimal' predictions about the world (e.g., Hudson et al., 2007; Vilares & Kording, 2011; Kwon & Knill, 2013). If these mechanisms are disrupted in autism, as proposed in predictive processing theories (see *Section 1.2.2*), then actions will be overly reliant on incoming sensory information. Such effects have been observed by Schmitz *et al.* (2003), who found that anticipatory EMG responses in the forearm musculature were attenuated in autistic people during voluntarily-unloaded lifting. When compared to neurotypical controls, autistic participants displayed unstable action kinematics and more reactive modes of control, findings which have since been supported by neurological studies (e.g., Martineau et al., 2004; Thillay et al., 2016). Consequently, there is growing evidence that autistic people are less inclined to use predictions to optimise their movements (see Cannon et al., 2021).

Nonetheless, many of the above findings are limited by small sample sizes and high inter-individual variability. While this corresponds with the 'spectrum-like' nature of autism, such heterogeneity may be caused by confounding factors relating to an individual's developmental trajectory, task motivation, communicative skills, and/or cognitive abilities (Fournier et al., 2010). Similarly, as autism is frequently accompanied by additional clinical diagnoses (e.g., ADHD, DCD, general anxiety disorders: Simonoff et al., 2008), it is likely that motor behaviours are being influenced by co-occurring conditions or neurodevelopmental atypicalities. These confounding variables present a major limitation for research in the field, and have constrained our mechanistic understanding to date (Whyatt & Craig, 2013b).

To account for these sample limitations and potentially confounding factors, academics advocate the use of trait-based empirical approaches (Landry & Chouinard, 2016). Here, one can explore how specific, conceptually-driven outcome variables correlate with autistic-like traits across large neurotypical samples (see *Section 1.6.3*). Such non-clinical evidence has shown that higher levels of autistic-like traits correspond with attenuated sensorimotor predictions during object lifting (Buckingham et al., 2016) and reduced uncertainty-related scaling of reaching movements in the rubber-hand illusion (Palmer et al., 2013; 2015). Though these studies provide notable support for Bayesian and predictive processing theories of autism, their observed effects were statistically weak, and may not necessarily emerge in clinically-diagnosed populations (Buckingham et al., 2016). Similarly, the small magnitude of these effects are unlikely to explain the large performance differences that are generally observed in most sensorimotor studies (Coll et al., 2020). Therefore, future research is required to combine trait-based analyses with more traditional between-group comparisons, to better clarify the role of predictive motor atypicalities in autistic movement behaviours.

Overall, studies of the motor system show clear and consistent differences in autistic action kinematics and prospective movement control. Though pathway-specific motor impairments cannot solely explain the poor praxis and daily living skill outcomes associated with autism, alterations in active inference present a likely candidate for these 'shared' movement difficulties. Nevertheless, limitations in previous research prevent decisive conclusions from being made, and future studies must aim to decipher precisely which regulatory mechanisms are implicated in autism.

1.4.5. The Schema System

The sections above highlight clear autism-related differences in visual, gaze, and motor functions; but it is clear that sensorimotor difficulties do not reside from any system-specific impairments in these domains. Notably, Land (2009) proposes that these interlocking functions are governed by a central 'supervisory' unit, the *schema system*, which controls visuomotor operations via reciprocal top-down neural messaging. Supposedly, these signals convey a set of goal-directed action instructions (*schemas*), which bias the flow of activity between sensory inputs, internal states, and neuromuscular outputs (Norman & Shallice, 1986; Land, 2009). From a neurological perspective, these movement plans appear to be represented in the cerebellum and frontal lobes of the brain (Wolpert et al., 1998; Miller & Cohen, 2001; Cerminara et al., 2009; Land, 2009). Given the wide-ranging atypicalities observed in these regions, and across interacting sensorimotor systems, it is therefore possible that the ability to generate and/or implement internal action models is impaired in autistic people.

Despite presenting a largely distinctive conceptualisation of natural behaviours, most computational hypotheses of autism lend clear theoretical support for this notion. Active inference theory asserts that humans preferentially select motor plans that minimise future prediction error, or *expected free energy*, in a manner circumvents the need for a physical schema system altogether (Friston et al., 2006; Friston, 2011). This self-evidencing process is instead cast as maximising Bayesian model evidence under generative models of the world (Parr & Friston, 2019), and it is these mechanisms that are specifically proposed to be suboptimal in autistic people (see *Section 1.2.2*). Moreover, internal models will be dynamically adjusted over time, based on precision-weighted modulation of prediction error (see *Section 1.3*). Predictive processing theories imply that these adaptive functions are aberrant in autistic people (Lawson et al., 2014; Van de Cruys et al., 2014; Palmer et al., 2017), meaning that action plans may be updated differently over the course of motor development and learning. Therefore, these computational processes present key candidates that could explain the visual, gaze, and motor differences observed in autistic populations.

Importantly though, research suggests that the generation of internal action models is not chronically impaired in autism (Gowen & Hamilton, 2013). Autistic participants typically control and adjust movements based on prior information and experience, as

evidenced in numerous motor adaptation protocols (Gidley-Larson et al., 2008; Haswell et al., 2009; Izawa et al., 2012; Hayes et al., 2018). These findings are notable, as they indicate that participants can form and update action representations in a statistically-optimal manner. Though seemingly at odds with most computational theories of autism, such observations have gained support from cognitive studies, where typical probabilistic learning rates are displayed (Barnes et al., 2008; Brown et al., 2010; Manning et al., 2017). However, it must be noted that statistically-driven learning responses are suboptimal in *some* experimental settings (e.g., Mostofsky et al., 2000; Gordon & Stark, 2007; Jeste et al., 2015; Robic et al., 2015; Thillay et al., 2016; Vivanti et al., 2018). Consequently, it is possible that certain *context-specific* action representations are affected.

Indeed, it is well established that some autistic people have difficulties adjusting their action behaviours between different situational contexts. Adverse responses to unexpected environmental change and uncertainty are particularly common in autism (Rutter, 1978), and seemingly correlate with sensorimotor impairments (Dyck et al., 2006; Gomot et al., 2011; MacDonald et al., 2013). Neuromodulatory responses to salient and repeated sensory cues are also atypical, as evidenced in numerous clinical studies (Courchesne et al., 1984; Kleinhans et al., 2009; Jeste et al., 2015; Thillay et al., 2016; Ewbank et al., 2017; Goris et al., 2018). These neurophysiological profiles associate with autistic-like traits in general populations (Ewbank et al., 2014) and can be computationally accounted for using hierarchical predictive coding models (Friston, 2005; Garrido et al., 2009; Lawson et al., 2014; Auksztulewicz & Friston, 2016). Moreover, atypical surprise responses are shown in autistic motor programming (Nazarali et al., 2009) and gaze habituation behaviours (Vivanti et al., 2018), albeit with large sample heterogeneity. Therefore, the generation of context-sensitive action representations may be suboptimal in some autistic people.

Context-sensitive processing mechanisms also implicate the *implementation* of action models, with the role of top-down information said to vary between tasks and conditions. Active inference states an individual will select motor policies that minimise estimates of future prediction error (Friston et al., 2010; Friston, 2011; Parr & Friston, 2019), with expected precision modulating how sensory information is sampled, learned from, and acted upon (see *Section 1.3*). These higher-level precision estimates are represented in the ACC (Behrens et al., 2007; den Ouden et al., 2010; Bland &

Schaefer, 2012), a brain region highlighted as atypical in multiple clinical studies (Haznedar et al., 1997; Thakkar et al., 2008; Di Martino et al., 2009; Dichter et al., 2009). Consequently, it is perhaps unsurprising that autistic people often have difficulties in action planning (see Gowen & Hamilton, 2013), especially in tasks that require dynamic internal modelling (e.g., tower-building and object-transfer procedures; Ozonoff et al., 1991; Hughes et al., 1994; Hughes, 1996).

Recently, these dynamic active processes have been studied using double-step saccade paradigms (e.g., Johnson et al., 2013; Mosconi et al., 2013). In these oculomotor tasks, participants must shift their gaze towards a peripherally-located target cue, which is systematically displaced during their goal-directed eye movement. Such intrasaccadic target displacements are used to elicit a degree of gaze positional error, which is typically reduced in a progressive, prediction-driven manner over time (McLaughlin, 1967; Wong & Shelhamer, 2012). Importantly, autistic participants display atypical adaptation profiles in these tasks that correlate with levels of sensorimotor impairment (Johnson et al., 2013; Mosconi et al., 2013). Since these individuals are likely to be capable of adjusting their sensorimotor behaviours according to prospective, goal-relevant task information (van Swieten et al., 2010; Aitkin et al., 2013; Ego et al., 2016; Ansuini et al., 2018), these results lend support for the notion of aberrant prediction error *modulation* in autism (e.g., Friston et al., 2013; Van Boxtel & Lu, 2013; Lawson et al., 2014; Van de Cruys et al., 2014).

Moreover, while adaptive sensorimotor learning outcomes are often displayed by autistic people (Gowen & Hamilton, 2013), consistent evidence suggests that these occur via atypical processing mechanisms (Mostofsky et al., 2000; Müller et al., 2004; Haswell et al., 2009; Sparaci et al., 2015; Foster et al., 2019). For instance, when learning new motor sequences, autistic individuals show elevated functional activity in the primary sensorimotor and premotor cortex (Müller et al., 2004). These neural regions are generally active during the early stages of neurotypical skill acquisition (Toni et al., 1998); however, they persist during later phases of adaptation in autistic individuals (Müller et al., 2004). Relatedly, autistic people display persistently elevated receptiveness to recent sensory information during statistical learning (Lawson et al., 2017). In predictive processing terms, this prolonged over-reactivity to salient cues reflects an unusually heightened encoding of prediction errors, indicating that precision-modulated gain control may be aberrant in these individuals (Lawson et al.,

2014; Palmer et al., 2017). So, while the functional ability to use internal action models is preserved in autism, alterations in context-sensitive predictive processing may prevent stable representations of the world from being built and/or updated effectively.

Nevertheless, existing evidence is limited by a lack of data from complex and/or unconstrained motor skills. Indeed, most of the aforementioned studies have employed simple laboratory-based tasks, such as button-pressing and reaction time paradigms (e.g., Müller et al., 2004; Lawson et al., 2017). Due to methodological constraints, these protocols often necessitate restricted movements and artificially-stable external conditions. However, in unconstrained 'real world' environments, action behaviours must adapt to complex, interacting, and fluctuating sensory inputs (Land, 2009; Friston et al., 2010; Palmer et al., 2017; Hayhoe & Matthis, 2018). Consequently, the generalisability of current data is significantly limited, and future research is required in naturalistic, movement settings (Cannon et al., 2021).

Overall, evidence supports the notion that autistic sensorimotor difficulties reside in context-sensitive processing mechanisms, which affect the dynamic formation and implementation of internal action models. Indeed, though probabilistic motor representations can be generated accurately in autistic people, the process by which this occurs and adjusts over time consistently proves atypical. However, research is still needed in naturalistic sensorimotor tasks. Such enquiry will not only improve our understanding of movement-based difficulties, but could also shed light on the fundamental mechanisms that underpin various autistic-like traits and behaviours.

1.4.6. Conclusions

Atypical sensorimotor control appears to be a core feature of autism, although the nature of these differences will largely depend on the task and individual involved. The aetiology of these functional issues is currently unclear, but researchers believe that atypicalities in Bayesian inference and/or predictive processing could play a causal role. At present, evidence for these proposals is mixed, due to inconsistencies in task requirements, participant characteristics, and analysis techniques. Furthermore, studies are limited by small sample sizes, artificial lab-based protocols, and various potentially confounding variables (e.g., cognitive impairments, developmental factors, co-occurring disorders). Nevertheless, consistent autism-related differences in visual, gaze, and motor functions are displayed, particularly in uncertain environmental

conditions. While these atypicalities are unlikely to reflect any pathway-specific disruptions in the visuomotor system, they may share a common computational origin, which impacts on the integration of sensory data and generative action models.

On this basis, predictive processing theories offer notable promise for prospective research in this field. Indeed, by providing formalised and empirically falsifiable hypotheses that focus on shared computational phenotypes, these frameworks can explain the heterogeneous, multi-factorial aetiologies of autism-related daily living difficulties. Scientific investigations must now decipher specifically how sensorimotor control differs in autistic people, through examining predictive processing during naturalistic, unconstrained movement tasks. To account for the integrative, context-sensitive nature of active inference, one should examine behaviour across multiple sensorimotor systems. This holistic, multi-systems approach will help us better understand and manage daily living difficulties in autistic people.

1.5. Aims of the Thesis

The aim of this project was to examine the aetiology of sensorimotor impairments in autism. Specifically, this thesis assesses various potential mechanisms that may underpin movement-based difficulties in autistic people, before considering how these functions can be targeted, or enhanced, in future applied practice. On the basis of the above literature review, this research particularly focuses on Bayesian and predictive processing theories of autism. These computational accounts present novel, practically-significant implications for sensorimotor behaviour, as they imply that daily living difficulties stem from atypicalities in predictive action control (i.e., impairments in active inference, prior beliefs, and hierarchical neural gain transmission; Table 1.1). Such enquiry aimed to not only further our theoretical understanding of autism, but to also assist in the development of effective, evidence-based practical interventions.

Given the recent emergence of computational theories in the field (see *Section 1.2.2*), Chapter 2 investigates the relationship between autism and predictive sensorimotor control. Specifically, this initial work focuses on the simple daily living skill of object lifting, where prediction-related functions are both well-defined and empirically-quantifiable (see *Section 1.6.1*). *Study 1* describes a trait-based analysis of the general population, which was undertaken within the unique context of the size-weight illusion.

By integrating this established paradigm with contemporary methodologies from vision research and clinical neuroscience, one could explore associations between autistic-like traits and various predictive sensorimotor functions. Any significant trait-related covariates were then re-inspected for accuracy and consistency in a large pre-existing dataset (Buckingham et al., 2016). *Study 2* examined these same object lifting behaviours and variables within clinically-diagnosed autistic individuals. Here, one could decipher specifically which predictive mechanisms are intact and which appear atypical in autism, to evaluate the efficacy of different theoretical hypotheses. This combined study approach improves the generalisability of results, while circumventing a number of potential confounds and methodological limitations (see *Section 1.6.3*).

Next, Chapter 3 considers the precise computational underpinnings of autistic sensorimotor impairments. Here, the autism-related processing styles highlighted in *Study 2* are scrutinised using a naturalistic experimental approach. Specifically, *Study 3* adopted an immersive visuomotor interception task, where dynamic manipulations of environmental uncertainty and volatility were used to assess key active inference mechanisms (e.g., the use of prior beliefs and precision weighting functions). Since autistic people commonly struggle with performing these type of skills in the 'real-world' (Green et al., 2002; Vanvuchelen et al., 2007; Gowen & Hamilton, 2013; Whyatt & Craig, 2013b; Ament et al., 2015; Chen et al., 2019), this analysis refines our mechanistic understanding of functional daily living difficulties in this population.

Finally, to assist in the development of future evidence-based practice, Chapter 4 evaluates potential approaches for reducing sensorimotor difficulties in autistic people. This analysis explores whether the computational mechanisms highlighted in Chapters 2-3 can be optimised through the use of systematic informational cues (e.g., advanced instructions or environmental manipulations). To do this, *Study 4* examined differences in autistic sensorimotor control following the provision of explicit probabilistic cues within immersive virtual reality. Here, findings illustrate whether computational atypicalities result from dynamic, potentially malleable functions (e.g., relating to the extraction of goal-relevant environmental cues), or inherent, neurobiologically constrained mechanisms that are implicit and inflexible in nature. Such enquiry provides a crucial starting point for strategies aiming to combat movement-related difficulties in autism. From here, various evidence-based practical interventions can be developed (see discussion and critical evaluation of approaches in Chapter 5).

1.6. Methodology

To better understand the complex and often under-studied difficulties that are faced by autistic people in sensorimotor tasks, a comprehensive investigatory approach is required. Here, lived experiences of autistic people must be integrated with specialist insight from neurology, psychiatry, neuroscience, education, psychology, as well as basic biological sciences (Robledo et al., 2012). Accordingly, this thesis will employ a number of novel interdisciplinary study methods, as detailed below.

1.6.1. Object Lifting Studies

Contrary to the reductionist approaches employed in many previous investigations, Chapter 2 examines predictive sensorimotor control *holistically* using a well-established object lifting paradigm. In these studies, participants were presented with objects that varied in physical size and/or mass, which they were then required to grasp, lift, and hold at a comfortable height. To achieve these actions, internal generative models are combined with visual and haptic feedback, as discussed in *Section 1.3*. Though such integration is usually regarded 'optimal', it can produce a well-defined, non-veridical perceptual effect in this setting: smaller objects feel heavier than equally-weighted larger ones (the '*Size-Weight illusion*'; Charpentier, 1891).

Importantly, these illusory effects emerge, at least partly, from an agent's prior expectations (that larger objects will normally be heavier than smaller ones: Brayanov & Smith, 2010; Buckingham, 2014; Saccone & Chouinard, 2019). Limb movements and sensory sampling behaviours will also depend on these predictive action models (Figure 1.2). This provides a unique opportunity to study predictive processing across multiple interacting perceptual and sensorimotor systems, in a manner that entails minimal motivation and socio-communicative requirements. Such characteristics are particularly advantageous in autism research, and contrast with the bulk of existing studies in this field (Haker et al., 2016). Moreover, the ability to efficiently regulate fingertip motor forces is influential in various daily living skills that are known to be impaired in autistic people (e.g., dressing and writing; Fuentes et al., 2009). Therefore, findings offer significant practical implications for the autism community.

Studies 1 and *2* systematically examined the use of prior expectations across each of Land's conceptualised sensorimotor systems (2009**;** Figure 1.2). Specifically, prior

expectations based on *visual* cues (i.e., object size; Gordon et al., 1991) were assessed using numerical ratings of predicted heaviness (as in Buckingham & Goodale, 2013), while participants' use of bottom-up proprioceptive information was derived from pre-lift hand kinematics (e.g., grasp phase dynamics; Hamilton et al., 2007). Various prediction-related *gaze* (e.g., search rate behaviours) and *motor* (e.g., peak grip and load force profiles) outcomes were also examined, using mobile eye-tracking and force transducer analysis (as in Johansson et al., 2001; Buckingham et al., 2016). Finally, motion capture data detailed the degree to which predictions bias one's overall lifting *actions* (as in Johansson & Westling, 1988). If predictive processing is broadly impaired in autism, then clinically-related differences should have emerged across multiple sensorimotor modalities. Conversely, if autistic movement control is associated with context-sensitive processing mechanisms, then one would have seen inconsistencies, or independence, between these modalities (see *Section 1.4.1*)

1.6.2. 'Vision-in-Action' Paradigms

To examine the precise mechanisms that underpin autistic sensorimotor impairments (Chapter 3), *Studies 3-4* focused on a complex, multi-system fundamental movement skill. This took the form of an interceptive visuomotor task, as autistic people generally have difficulties performing this type of skill (Green et al., 2002) and such actions can be readily 'deconstructed' to an individual, mechanistic level (Whyatt & Craig, 2013b). Although multiple sensorimotor modalities were, again, explored (with reference to Figure 1.2), the role of the gaze system was particularly informative as to what control processes were being employed. Indeed, mobile eye-tracking provides objective, accurate measures of visuomotor attention (Hamner & Vivanti, 2019), in a manner which has successfully elucidated the mechanistic basis of other neurodevelopmental conditions (for example from DCD research, see Wilson et al., 2013).

Nevertheless, unconstrained whole-body movement experiments can be difficult to control (Farley et al., 2019) and are often performed in environments that are overwhelming for autistic people (Yanardağ et al., 2010). This presents significant methodological and ethical concerns. Therefore, based on previously-defined empirical approaches (e.g., Diaz et al., 2013; Binaee & Diaz, 2019; Mann et al., 2019), interceptive actions were performed in immersive virtual-reality (VR). This not only permitted precise control over task-relevant variables (e.g., ball flight trajectory,

background noise); it also afforded systematic, unconstrained manipulations of sensory and/or environmental information (e.g., uncertainty and volatility statistics). Furthermore, by offering a more stable 'safe space' for participants, this virtual setting could reduce potentially-overwhelming sensory and social stimuli from the surrounding research environment (Bradley & Newbutt, 2018).

1.6.3. Clinical and Non-Clinical Approaches

To avoid potential confounds relating to sensorimotor control, a combination of trait- and clinically-based study designs were employed. Autistic-like traits are said to be continuous and normally-distributed in general populations, with clinical ASD viewed to reside at the extreme end of this continuum (Baron-Cohen et al., 2001; Ruzich et al., 2015). Recent etiological approaches advocate studies that cross the diagnostic divide, by identifying correlates of autism that merge into the general population (e.g., Robinson et al., 2011). This reduces the influence of numerous extraneous variables (Landry & Chouinard, 2016), with rates of developmental delay, cognitive impairment, and many co-occurring conditions higher in autistic people (Simonoff et al., 2008).

In this regard, the present thesis often takes a two-stage investigative approach. At first, relationships are explored between sensorimotor outcomes and non-clinical levels of autistic-like traits, as indexed using validated questionnaires (e.g., the Autism Spectrum Quotient, AQ: Baron-Cohen et al., 2001). Such trait-based analysis permits the identification of *autism-specific* processing mechanisms which are less influenced by clinically-related confounds. Thereafter, more conventional between-group comparisons are conducted, which examine how these specific autism-related mechanisms differ between autistic and neurotypical samples. This combined investigative approach has successfully established a number of behavioural, neurological, and sensory characteristics of autism in previous research projects (e.g., Almeida et al., 2013; Cooper et al., 2013; Poljac et al., 2013; Robertson & Simmons, 2013; Ewbank et al., 2014).

Chapter 2

Sensorimotor functions depend on various interlocking systems and processing pathways, which are coordinated by predictive action models (Friston et al., 2010). To optimally control movements, predictions are computed from prior expectations and incoming sensory data, before being transmitted hierarchically across the cerebral cortex (Shipp et al., 2013). It is proposed that autistic individuals display chronic attenuations in this use of prior information (Pellicano & Burr, 2012; Sinha et al., 2014; Van de Cruys et al., 2014). These 'simple' Bayesian hypotheses draw on wide-ranging empirical evidence, with autistic individuals having been shown to display reduced anticipatory postural adjustments (Schmitz et al., 2003), atypical error-based gaze adaptation (Mosconi et al., 2013), and impaired motor learning capabilities (Gidley-Larson & Mostofsky, 2006). Furthermore, anatomical and functional abnormalities are commonly displayed by autistic participants in neural regions said to drive predictive control, such as the cerebellum (Courchesne, 1997; Fatemi et al., 2002; Allen & Courchesne, 2003; Fatemi et al., 2012), ACC (Dichter et al., 2009) and basal ganglia (Hollander et al., 2005). Therefore, it is proposed that sensorimotor difficulties in autism may be caused by generic impairments in the ability to make and/or use predictions (e.g., Pellicano & Burr, 2012; Sinha et al., 2014).

However, research has shown that various prediction-dependent processes are *not* chronically impaired in autism (Gidley-Larson et al., 2008; Tewolde et al., 2018), and findings are often task- or context-sensitive (Palmer et al., 2017; Cannon et al., 2021). For example, recent object lifting studies (Buckingham et al., 2016; Arthur et al., 2019) have explored how sensorimotor prediction correlates with autistic-like traits in large neurotypical populations. These studies examined the degree to which participants predictively lift 'heavy-looking' objects (e.g. large objects) with greater fingertip force rates than 'lighter-looking' ones (e.g. small objects; Buckingham et al., 2016)—a type of sensorimotor prediction generated in the dorsal premotor cortex (Chouinard et al., 2005). Here, although participants with higher autistic-like traits showed reduced sensorimotor prediction when interacting with different-sized objects (Buckingham et al., 2016), such effects did not replicate when objects differed in material properties (Arthur et al., 2019). These studies suggest that predictive processing atypicalities in autism may be driven by task- or context-specific mechanisms, rather than from any chronic attenuations in the use of prior knowledge.

Sensorimotor control depends on various context-sensitive mechanisms, which are proposed to dynamically modulate cortical gain across hierarchical neural networks (Friston, 2005; Adams et al., 2013; Shipp et al., 2013). Top-down signals are typically downregulated when uncertainty about one's prior beliefs is high, to ensure that unbiased sensory cues can be processed (Yu & Dayan, 2003; Kwon & Knill, 2013). Notably, such context-sensitive neurobiological responses appear to be diminished in autistic individuals (Ewbank et al., 2017; Lawson et al., 2017), prompting suggestions that autism may be characterized by inflexibilities in how predictive processing is adjusted according to environmental statistics (Lawson et al., 2017; Palmer et al., 2017). These arguments are supported by recent findings in the rubber-hand illusion (Palmer, Paton, et al., 2015) and object lifting (Arthur et al., 2019), where participants with higher autistic-like traits display a lower degree of uncertainty-driven adjustments in gaze and motor control. However, it remains unclear whether sensorimotor difficulties in autism are underpinned by *chronic* attenuations in the use of prior information, or *context-sensitive* mechanisms relating to how this prior information is integrated with environmental statistics.

This chapter examines how predictive sensorimotor control differs in autistic individuals across two object lifting experiments. *Study 1* examined a large neurotypical sample, exploring the correlations between autistic-like traits and various measures related to sensorimotor prediction. By adopting this initial trait-based approach, potential autism-related confounds relating to differences in cognitive ability and co-occurring disorders can be minimised (Landry & Chouinard, 2016). This initial experiment was then followed by a second study, which analysed how prediction-related sensorimotor variables differ between neurotypical individuals and participants with a clinical diagnosis of ASD. In both studies, participants lifted objects that differed in physical size and mass (Figure 2.1), before reporting how heavy they felt on a numerical scale. Various multi-modal indices of perception, action, and sensory sampling behaviour were then assessed, to decipher which prediction-based behaviours are specifically impaired or intact in autism (Ego et al., 2016). This multimodal approach would permit examination into whether autism-related sensorimotor atypicalities reflect chronic, domain-general attenuations in predictive control, or context-sensitive patterns linked to specific neurobiological pathways.

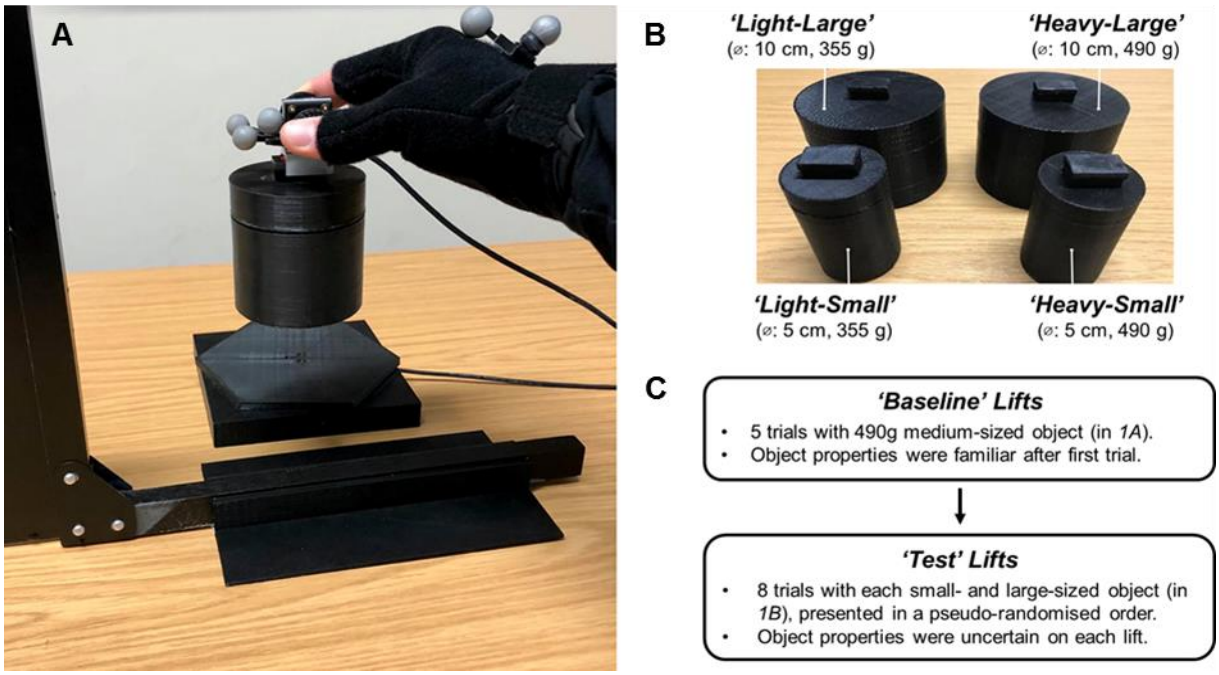

Figure 2.1. The experimental set-up for object lifting trials (**A**), the four 'test' objects lifted by participants (**B**), and a schematic overview of the testing session (**C**) in *Studies 1* and *2*. Objects were concealed by a manual clapper-board prior to each trial. Following an auditory tone (trial onset), participants reached and lifted objects with their thumb and forefinger to a comfortable height above the table. Objects were held steady until hearing a second auditory tone (trial offset), before being placed back on the platform. These procedures were repeated for 'baseline' and subsequent 'test' trials, with various prediction-related sensorimotor measures obtained.

To examine predictive processing at a perceptual level, numerical heaviness ratings were averaged for each object. Here, prior expectancies bias perception in a non-veridical 'anti-Bayesian' manner (Brayanov & Smith, 2010), with small objects typically perceived to feel heavier than equally-weighted larger ones (Charpentier, 1891). Any attenuations in the use of prior expectations would result in a reduced magnitude of this perceptual illusion. To examine mechanisms relating to active inference, peak grip (pGFR) and load (pLFR) force rate differences between the initial lifts of the large and smaller objects were calculated, alongside resulting action kinematics. Here, tendencies to underestimate and overestimate lifting force can be derived from unexpectedly heavy and unexpectedly light object lifts. If prior beliefs are chronically diminished, then similar motor profiles would be shown for the large and small objects

(i.e., reduced pGFR and pLFR difference scores). To supplement this multimodal analysis, participants' gaze patterns were also monitored, with predictive processing hypotheses having direct implications for visual sampling behaviours (Palmer et al., 2017), and shorter, more frequent fixations signalling inefficiencies or impairments in predictive sensorimotor control (Murray & Janelle, 2003; Wilson et al., 2013).

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2.1. Study 1: Associations between sensorimotor prediction and non-clinical autistic-like traits

2.1.1. Introduction

The aim of *Study 1* was to investigate the associations between sensorimotor prediction and autistic-like traits, using an exploratory, non-clinical approach that would be minimally affected by co-occurring disorders and cognitive ability (Simonoff et al., 2008). Specifically, a large general population were examined, where autistic-like traits tend to vary in a normally-distributed manner (Baron-Cohen et al., 2001). Since co-occurring sensorimotor conditions are far less prevalent in neurotypical samples (Simonoff et al., 2008), this analysis would shed light on *autism-specific* sensorimotor correlates, in a way that is unaffected by small sample sizes and clinically-related confounds (see discussions in: Landry & Chouinard, 2016 and *Section 1.6.3*). In a SWI paradigm akin to the present study, individuals with greater autistic-like traits proved less inclined to utilise prior information in their lifting movements (Buckingham et al., 2016). However, these relationships were weak and did not replicate when objects differed in material properties (instead of size cues; Arthur et al., 2019). Accordingly, this study examined whether the observed associations between autistic-like traits and sensorimotor prediction transfer across different sensory modalities and conditions.

The present study scrutinised the use of predictions at both chronic (i.e. context-independent) and context-sensitive hierarchical levels. Tendencies to underestimate and overestimate lifting force are subject to distinct, situation-specific processing operations (Jenmalm et al., 2006). For example, when lifting a mug of tea, prior

uncertainty about the weight of the mug may have little effect on pGFR overestimation tendencies, as the consequence of prediction error is relatively minor (i.e. unnecessary energy expenditure, increased effort). Conversely though, as underestimation can lead to detrimental effects (i.e. slips or drops), it would be expected that high grip force 'safety margins' are used under uncertain conditions (Hadjiosif & Smith, 2015). Therefore, individuals may utilise the same overall expectation (e.g. that larger mugs will weigh more than smaller ones) in a distinct, context-sensitive manner.

On the basis of simple Bayesian theories (e.g., Brock, 2012; Pellicano & Burr, 2012) and previous research in the SWI (Buckingham et al., 2016), it was hypothesised that participants with higher autistic-like traits would show chronic attenuations in sensorimotor prediction. This would be reflected in negative correlations between levels of autistic-like traits and indices of the perceptual SWI, pGFR and pLFR differences, movement initiation velocities, and gaze fixation durations.

2.1.2. Methods

2.1.2.1. Participants

Eighty-nine neurotypical participants (46 male, 43 female; 23 ± 3 years; 90% right-handed; see *Appendix A1*), who did not report any cognitive disabilities or neurological disorders, were recruited to take part in this study. Participants were excluded if they reported any conditions known to affect sensorimotor control, including ASD, meaning that one individual with DCD and two with musculoskeletal injuries were excluded. To ensure that analyses were not influenced by 'clinically significant' trait characteristics, participants were excluded if they exhibited total scores ≥ 32 ($n = 4$; as recommended by Baron-Cohen et al., 2001). As such, the study was robust to clinically-related confounds (Landry & Chouinard, 2016). Remaining participants ($n = 82$) exhibited AQ scores ranging from 5–31 (mean: 15.87 ± 6.39), values which are consistent with large, representative neurotypical populations (Baron-Cohen et al., 2001). The study received approval from the School of Sport and Health Sciences Ethics Committee (University of Exeter) and informed consent was obtained from all participants in accordance with British Psychological Society guidelines. All participants were naïve to the study objectives and had normal or corrected-to-normal vision.

2.1.2.2. Apparatus and stimuli

Participants lifted homogenous 7.5-cm tall black plastic cylinders using an aluminium and plastic lifting handle, which was fitted with an ATI Nano-17 Force transducer. Objects differed in physical diameter (small: 5 cm, large: 10 cm) and mass (light: 355 g, heavy: 490 g), presenting a total of four 'test' items (Figure 2.1). An additional medium-sized 'control' object (diameter: 7.5 cm; mass: 490 g) also provided baseline comparisons for grip and load force outcomes, all of which were recorded at 500 Hz. During lifting, participants wore a Pupil Labs mobile eye gaze registration system (Kassner et al., 2014), which calculated gaze positions at 90 Hz (spatial accuracy: 0.60°; precision: 0.08°). The eye-tracking system was calibrated using the manufacturer's built-in screen marker routine prior to data collection and following any displacement of the gaze registration cameras and/or loss of data quality during testing. A manual clapper board concealed objects and restricted visual feedback prior to the onset of each trial (as in Arthur et al., 2019). To enable kinematic analysis, the position of rigid bodies comprised three reflective markers, attached to the lifting handle and to a worn glove, were tracked by an 8-camera optical motion capture camera system at 120 Hz (OptiTrack Flex13, NaturalPoint, Corvallis, Oregon).

To index autistic-like traits, participants completed the 50-item adult AQ (Baron-Cohen et al., 2001; *Appendix E*), a widely used research tool which has proven both valid and reliable in large general populations (Woodbury-Smith et al., 2005). The AQ assesses five sub-traits associated with autism, namely: attention to detail, attention switching, imagination, communication, and social skills. Participants self-reported whether they 'definitely agree', 'slightly agree', 'slightly disagree' or 'definitely disagree' with 50 itemized statements that assess each of these subscales. This provides an overall score out of 50, whereby higher numbers reflect greater autistic-like traits.

2.1.2.3. Procedures

All measures of autistic-like traits were completed before the lifting protocol. Thereafter, participants repeated a previously described set of standardized lifting procedures, both for 'baseline' and 'test' trials (Figure 2.1; see Arthur et al., 2019 for more detail). Specifically, during both conditions, participants lifted objects from a seated position with the thumb and forefinger of their dominant hand, and held them steady at a comfortable height above the table surface. The onset and offset of each

trial were signalled by two computer-generated auditory tones, each separated by 4 s. Participants were instructed to lift objects in a ‘smooth, controlled and confident manner’, and to ‘gently place the object back on its starting platform’.

Each session began with five ‘baseline’ trials, and was followed by 32 ‘test’ trials (Figure 2.1), where each object was lifted eight times in one of three pseudorandomized orders. These predetermined trial sequences presented objects in an uncorrelated, entropic order, but guaranteed that each ‘heavy’ item was lifted at least once before any ‘light’ trials. Such precautions would minimize order effects (Maiello et al., 2018), while ensuring initial ‘test’ lifts were unexpectedly heavy or light, relative to baseline trials. After each lift, participants verbally reported a numerical judgement about how heavy the object felt, with larger numbers instructed to represent heavier weights. Importantly, no constraints were placed on these values to minimise ratio scaling biases (as in Buckingham et al., 2016).

2.1.2.4. Data analysis

Perceived heaviness scores: Heaviness ratings were normalized to a *z*-score distribution to permit inter-individual analyses. To quantify the magnitude of the SWI, where small objects are erroneously perceived to weigh more than equally weighted larger ones (Charpentier, 1891), average values for the larger objects were subtracted from those of the smaller ones (Buckingham et al., 2016). Conversely, to quantify detection of real weight changes, averages for the heavy objects were subtracted from lighter objects.

Force data: Extracted force data were smoothed using a 14-Hz Butterworth filter, with forces perpendicular to the surface of the handle defined as grip force and resultant vectors of the tangential forces interpreted as load force. To determine peak force rates, data were differentiated with a 5-point central difference equation. From here, broad size-related prediction errors were assessed for grip (pGFRdiff) and load (pLFRdiff) force rate outcomes, through subtracting values from the first ‘test’ lift of the smaller objects from those of the larger objects (Buckingham et al., 2016). To isolate more context-specific mechanisms, sensorimotor prediction for small and heavy objects were also assessed separately. To index underestimation of force, pGFR from the first test trial of the small heavy object was subtracted from that of the final baseline lift. Conversely, to index overestimation, pGFR exhibited during this final baseline trial

was subtracted from the first large heavy test trial. This analysis was conducted on pGFR, and not pLFR, following inspection of trial-by-trial lifting profiles, which suggested that prediction-related differences were more sensitive for this measure. For all of these outcomes, higher index values would indicate a greater degree of sensorimotor prediction (as in Buckingham et al., 2016; Arthur et al., 2019).

Gaze data: Visual fixations were extracted from the gaze data using Pupil Player software (Kassner et al., 2014). Fixations were defined as gaze that remained on a location, within 1° of visual angle (as recommended by Salvucci & Goldberg, 2000). To illustrate participant's visual sampling behaviours, the total number and average duration of fixations were recorded for baseline trials and for the first lift of each object, with any brief fixations (<120 ms; Williams et al., 1994) removed from analysis. As attention was mostly directed towards the object in this task (see Supplementary Videos, at https://osf.io/p52h8/), the occurrence of shorter and/or more frequent fixations would signal greater sampling of goal-relevant sensory cues.

Kinematic data: Raw positional data for each infrared marker were smoothed using a dual-pass, zero-phase lag 10-Hz Butterworth filter (Franks et al., 1990), with hand and object velocity then calculated from the average position of each rigid body. These signals were then combined into resultant 3D vectors and differentiated with a 5-point central difference equation to yield velocity values. From here, reach and lift movement phases were segmented for each trial, using a 50mm/s movement threshold (as in Eastough & Edwards, 2007). Specifically, the reach phase began when hand velocity first exceeded a 50 mm/s for three consecutive frames and concluded upon the onset of grip force. The lift phase was determined from the time point where both hand and object velocity first exceeded 50 mm/s until the point where the object reached its maximum vertical position. The maximum velocity of the hand during reach (MRV) and lift (MLV) phases was then recorded, as were the time points where these events occurred (as a percentage of total movement time).

2.1.2.5. Statistical analysis

Statistical analyses were performed using JASP (version 0.12.2), with significance accepted at $p < .05$ and data presented ± standard deviation (SD). Outliers were removed from their respected analysis, with univariate outliers identified as values >3.29 SD above or below the mean ($p < 0.001$) and multivariate outliers ascertained

by extreme Mahalanobis distances ($p < .001$). To assess whether participants experienced the SWI and showed prediction-related motor patterns, separate 2 (small, large) × 2 (light, heavy) repeated-measures ANOVAs were conducted. Average heaviness scores, as well as pGFR and pLFR values from initial lifts, were entered as dependent variables. Planned *t*-tests using the Bonferroni correction probed any significant results, with effect sizes calculated using partial-eta squared (η_p^2).

Pearson's correlation explored relationships between AQ scores, the perceptual SWI, and prediction-related measures of force, movement kinematics, and visual sampling behaviours. Correlational analysis was favoured over between-group comparisons to provide greater statistical power (Mitchell & Jolley, 2013), in a manner that is consistent with previous studies in the field (Buckingham et al., 2016; Lawson et al., 2017). Holm-Bonferroni corrections (Holm, 1979) were then used to adjust for multiple comparisons, and Bayes factors (BF_{10}) were obtained to illustrate the strength of evidence in favour of the alternative/null hypotheses. In accordance with recommended statistical conventions (e.g., van Doorn et al., 2021), a symmetric Cauchy prior with a width parameter of 0.707 was selected for these analyses, with moderate support for the alternative model set at $BF_{10} > 3$ and strong support indicated by $BF_{10} > 10$.

There were no statistical violations relating to normality, homoscedasticity, or linearity. However, one participant's heaviness ratings (remaining $n = 81$), and five participants' force data (remaining $n = 77$), were excluded following detection of univariate outliers in the associated outcome measures ($p < .001$). Additionally, eight participants were removed from kinematic analysis (remaining $n = 74$) and 22 from gaze analysis (remaining $n = 60$) due to poor data quality and/or outliers.

2.1.3. Results and Discussion

A repeated measures ANOVA was conducted with average heaviness scores for each 'test' object (small-light, small-heavy, large-light, large-heavy) entered as dependent variables. ANOVA revealed significant effects of size and mass on perceived heaviness (Size: $F(1,81) = 1150.86$, $p < .001$, $\eta_p^2 = 0.93$, $BF_{10} = 3.22 \times 10^{33}$; Mass: $F(1,81) = 1395.16$, $p < .001$, $\eta_p^2 = 0.95$, $BF_{10} = 2.13 \times 10^{48}$). Average scores for smaller 'test' objects were greater than those for larger ones ($p < .001$, $BF_{10} = 1.44 \times 10^{45}$) and scores for heavier objects were greater than those for the lighter ones ($p < .001$, BF_{10}

= 9.34×10^{48}). Together, effects show that both illusory and physical differences in mass were detected. However, correlation analysis showed that there were no significant associations between AQ scores and heaviness ratings (SWI: $r = 0.13$, $p = .25$, $BF_{10} = 0.27$; real weight: $r = -0.17$, $p = .14$, $BF_{10} = 0.40$; Figure 2.2.A). This reinforces observations that prior expectations influence weight perception comparably across the general autism phenotype (Buckingham et al., 2016).

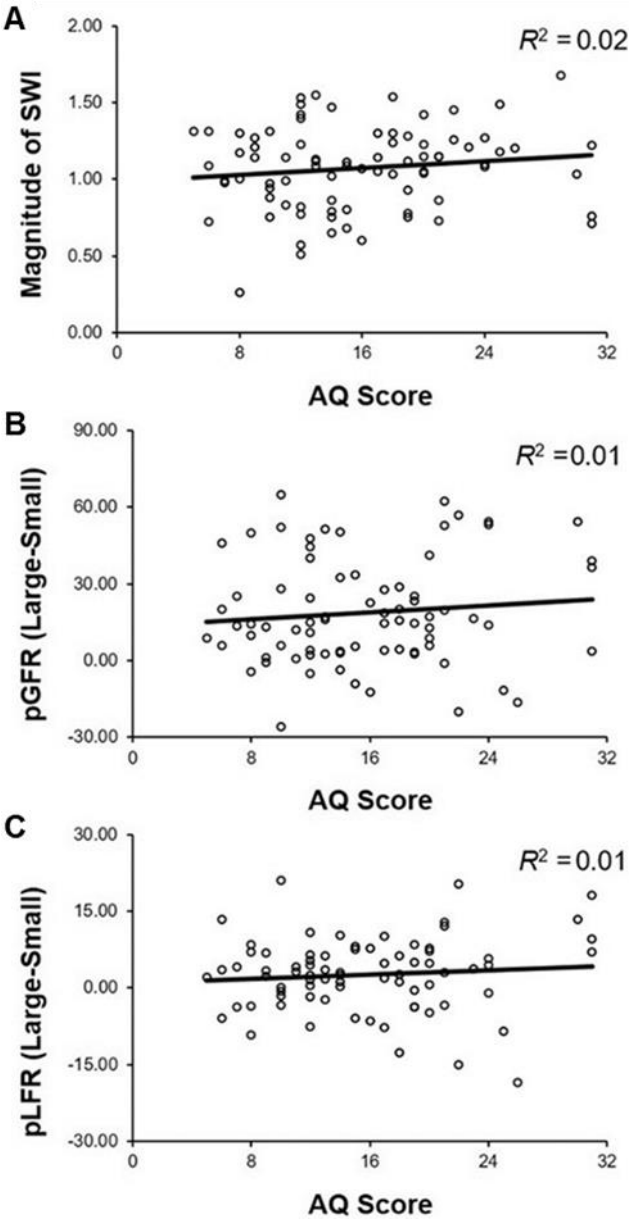

Figure 2.2. Scatter plots highlighting associations between autistic-like traits (AQ scores) and the magnitude of the perceptual Size-Weight Illusion (SWI; **A**), prediction-related differences in peak Grip Force Rate (pGFR; **B**) and peak Load Force Rate (pLFR; **C**) in *Study 1*. No significant relationships emerged (all $p > 0.05$).

Next, ANOVAs examined pGFR and pLFR profiles from the initial lifts of 'test' objects. These revealed no significant effects for object mass on pLFR ($F(1,77) = 1.03$, $p = .31$; $\eta_p^2 = 0.01$, $BF_{10} = 0.18$) and marginal effects on pGFR ($F(1,77) = 4.03$, $p = .05$, $\eta_p^2 = 0.05$, $BF_{10} = 1.01$). However, strong effects for size emerged (pGFR: $F(1,77) = 62.03$, $p < .001$, $\eta_p^2 = 0.45$, $BF_{10} = 1.10 \times 10^9$; pLFR: $F(1,77) = 9.24$, $p = .003$, $\eta_p^2 = 0.11$, $BF_{10} = 12.96$), with force rates lower when lifting the smaller compared to larger objects (pGFR: $p < .001$, $BF_{10} = 4.06 \times 10^8$; pLFR: $p = .003$, $BF_{10} = 8.53$). This indicates that the object lifting paradigm elicited size-related expectation biases on initial 'test' lifts. Interestingly, however, the magnitude of these predictive biases was not significantly related to AQ values (p's > .37; Figure 2.2), with Bayes factors reflecting strong evidence for null trait-based effects (pGFRdiff: $r = 0.10$, $p = .37$, $BF_{10} = 0.21$; pLFRdiff: $r = 0.09$, $p = .43$, $BF_{10} = 0.19$). Furthermore, no significant correlations emerged between AQ scores and lifting kinematics (Table 2.1; p's > .24, all BF_{10} values < 0.30). These results highlight a lack of relationship between autistic-like traits and the use of prior expectations at a motor level, a pattern of data which has now emerged in the context of both *size*- and *material*-based object heaviness cues (Arthur et al., 2019).

Table 2.1. Bivariate Correlations between Autistic Quotient Scores and Sensorimotor Outcomes in *Study 1*.

	Mean (SD)	***R***
Force Measures		
pGFRdiff (N/s)	18.70 (20.95)	0.10
pLFRdiff (N/s)	2.61 (7.26)	0.09
pGFR Underestimation (N/s)	21.49 (28.62)	-0.25*
pGFR Overestimation (N/s)	6.25 (32.30)	0.20
Gaze Measures		
Fixation Number	3.93 (0.55)	0.03
Fixation Duration (ms)	427.03 (115.47)	0.14
Kinematic Measures		
MRV (mm/s)	917.34 (157.83)	-0.11
MLV (mm/s)	341.70 (82.47)	0.14
Time to MRV (%)	37.56 (6.39)	0.03
Time to MLV (%)	35.30 (7.04)	-0.05

*pGFRdiff: differences in peak Grip Force Rate between initial lifts of the large and small 'test' objects; pLFRdiff: differences in peak Load Force Rate between initial lifts of the large and small 'test' objects; MRV: maximum reach velocity; MLV: maximum lift velocity; * denotes significant relationship with AQ scores.*

Gaze patterns were markedly consistent both within- and across-subjects. Specifically, participants tended to fixate upon the stationary object throughout the reach and grasp phases, before using pursuit and saccadic eye movements to track its in-flight lift trajectory. Upon reaching a stable 'hold' position, subsequent object-directed fixations were then maintained until the offset of the trial, when an anticipatory saccade would draw gaze back towards the starting platform (i.e. final object location; see Supplementary Videos at https://osf.io/p52h8/ for illustration). Such gaze patterns are consistent with previous studies (e.g., Johansson et al., 2001), and are said to be 'supervised' by top-down action models (Land, 2009). Interestingly, our data provided strong evidence that AQ scores were unrelated to these search rate behaviours (Fixation number: $r = 0.03$, $p = .85$, $BF_{10} = 0.16$; Duration: $r = 0.14$, $p = .28$, $BF_{10} = 0.28$; Table 2.1). This further supports the lack of associations between autistic-like traits and prediction-controlled sensorimotor behaviour in this task.

To shed light on *context-sensitive* predictive processes, trial-by-trial variations in pGFR responses were examined. Specifically, correlations between AQ scores and baseline-subtracted fingertip force profiles for the 'small-heavy' and 'large-heavy' objects were inspected. Here, no significant relationships were found between pGFR overestimation and AQ scores ($r = 0.20$; $p = .08$, $BF_{10} = 0.62$), suggesting that participants comparably increased force rate for larger 'test' objects. Results did, however, provide anecdotal support for an inverse relationship between AQ and pGFR underestimation values ($r = -0.25$, $BF_{10} = 1.47$), although such effects were non-significant when accounting for multiple comparisons ($p = .03$, Table 2.1).

The fact that prediction-based effects emerge in *some*, but not *all* trials, suggests that autism-related movement atypicalities may originate from context-sensitive mechanisms. Elevated pGFR profiles for unexpectedly heavy objects (in high-AQ participants) could represent a strategy aimed at minimising the likelihood of task errors (i.e., slips or drops, Cashaback et al., 2017). Such an argument lends support for proposed associations between autism and volatility processing (Lawson et al., 2017), as these compensatory behaviours are often deployed when environmental uncertainty is perceived to be high (Hadjiosif & Smith, 2015). Though evidence is clearly inconclusive, it would therefore be premature to rule out any context-sensitive relationships between autistic-like traits and sensorimotor prediction at this point.

2.1.4. Exploratory Analysis

Study 1 highlighted inverse relationships between AQ and pGFR underestimation, however these correlations were weak and inconclusive. This exploratory analyses evaluated the reliability and generalisability of these results, by examining whether such statistical associations emerge in a previously recorded dataset (Buckingham et al., 2016) and/or in participants' movement kinematics (peak lifting velocities).

2.1.4.1. Analysis of Existing Data

First, a re-inspection of Buckingham *et al.*'s data (2016; retrieved from: https://osf.io/2cmdu/) was undertaken. In this previous work, a comparable object lifting protocol and neurotypical sample were analysed (n = 88, age = 22 ± 3 years). Contrary to *Study 1*, a significant relationship between AQ scores and fingertip force outcomes was observed. Participants with higher autistic-like traits showed reduced pGFR differences between small and large objects (Figure 2.3). It was concluded that these individuals were less inclined to incorporate prior information into their motor programmes. However, on closer inspection, it is unclear whether these effects reflect generic attenuations in the use of sensorimotor prediction, as originally believed. Indeed, relationships between AQ scores and anticipatory motor profiles were only significant for unexpectedly-heavy object lifting trials in *Study 1* and such context-dependent effects could conceivably be driving the correlations that are presented in Figure 2.3.

To explore this possibility, this analysis investigated whether associations between AQ scores and fingertip force profiles in Buckingham *et al.* (2016) reflect chronic variations in the use of prior beliefs or context-specific processing atypicalities (i.e., attenuations in *either* force under- or over-estimation). Although there were no baseline trials in this previous work, a 400g medium-sized object (diameter: 7.5 cm) was included in the SWI protocol which could be compared with equally-weighted small (diameter: 5 cm) and large (diameter: 10 cm) cylinders. As such, pGFR and pLFR data were extracted from initial trials of each object, and index scores could then be computed for underestimation and overestimation profiles respectively. Underestimation scores were calculated by subtracting 'small' from 'medium' force rates, while first-lift values from the 'medium' object were subtracted from those of the 'large' object to index overestimation. Higher values would signify greater tendencies to under- or over-estimate force, while lower scores would highlight reductions in the use of prior beliefs.

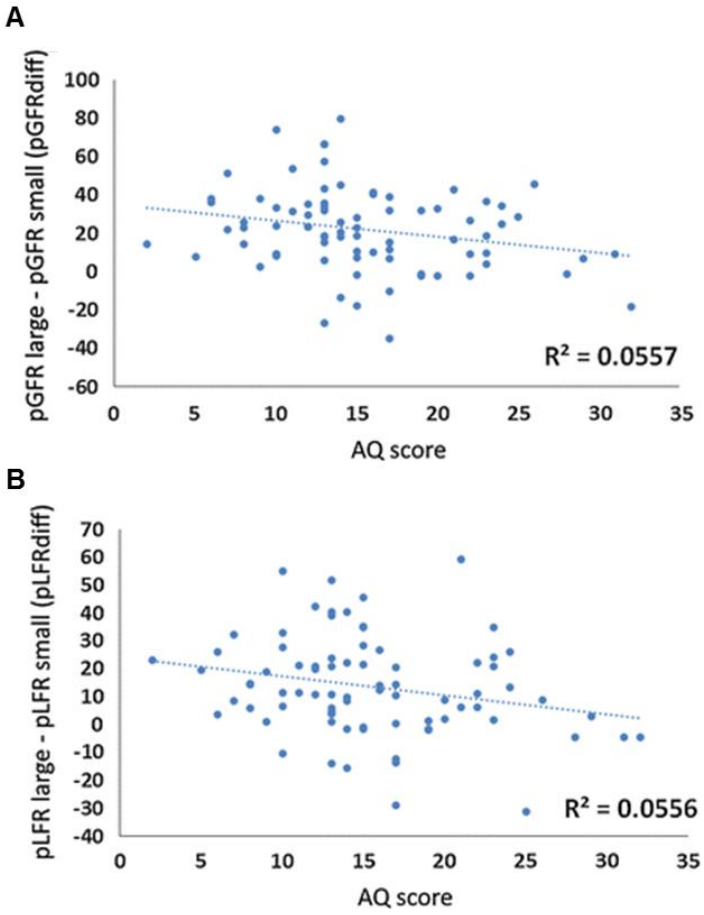

Figure 2.3. Scatter plots highlighting the previously reported relationships between AQ scores and prediction-related differences in peak Grip Force Rate (**A**) and peak Load Force Rate (pLFR; **B**). Copied from Buckingham *et al*. (2016), with permission from Springer Nature (open access).

Bayesian correlation analysis provided only anecdotal support for the previously-reported relationships between high AQ scores and attenuated sensorimotor prediction (pGFRdiff: r = -.24, BF_{10} = 1.23; pLFRdiff: r = -.24, BF_{10} = 1.23). Furthermore, there was a lack of relationships between AQ and overestimation tendencies in this dataset (pGFR: r = 0.11, BF_{10} = 0.22; pLFR: r = 0.07, BF_{10} = 0.16). Interestingly, though, analyses highlighted strong evidence for an association between AQ scores and pGFR underestimation tendencies (r = -.37, BF_{10} = 34.89), and moderate evidence in favour of trait-based pLFR underestimation effects (r = -.32, BF_{10} = 8.73). Consequently, the novel context-sensitive effects that emerged in *Study 1* not only replicate in this previous dataset; they appear to be driving the weak prediction-related associations that were originally recorded in this prior investigation.

2.1.4.2. Post-Hoc Kinematic Analysis

To further scrutinise these context-specific motor differences, post-hoc tests examined their influence on participants' movement kinematics. Any underestimation of lifting force should result in a marked slowing of movement (Jenmalm et al., 2006). So, using the same approach employed in the force analyses of *Study 1*, MLV values from initial lifts of the 'small-heavy' object were subtracted from those in the final 'baseline' trial, to provide an underestimation score. As expected, participants generally displayed slower lifting movements in this initial, unexpectedly-heavy trial (Figure 2.4.A), which confirmed that force underestimation impacted on participants' action kinematics. These kinematic profiles were inversely related to AQ scores (Figure 2.4.B), although support was only anecdotal in this data (r = -.24, p = .04, BF_{10} = 1.14). As such, results provide further support for the notion that autism-related atypicalities in sensorimotor prediction may result from context-sensitive processing mechanisms (e.g., in precision weighting: see Friston et al., 2013; Lawson et al., 2014; 2017; Palmer et al., 2017).

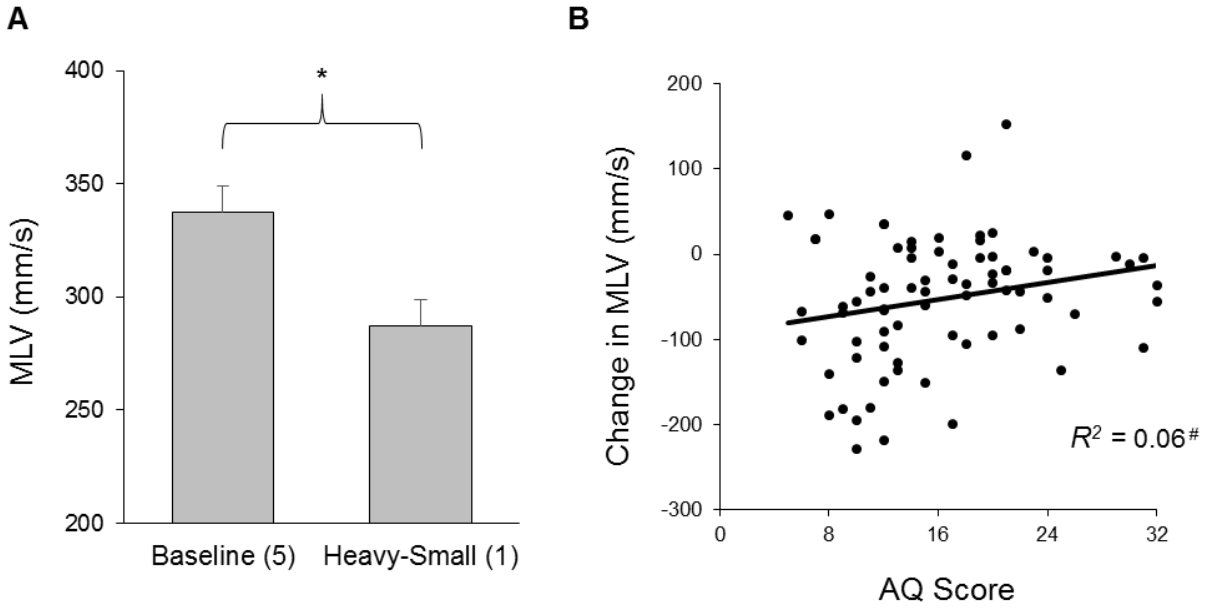

Figure 2.4. Changes in Maximum Lift Velocity (MLV; **A**) from the final 'Baseline' trial to the initial 'Heavy-Small' trial, and scatter plot highlighting the relationship between Autism Spectrum Quotient (AQ) scores and the magnitude of these changes (**B**). *Denotes significant difference between trials (t(73) = 6.30, p < .001, BF_{10} = 6.11*10^5); # shows a significant correlation between included co-variables (p < .05).

2.1.5. Interim Summary

This study showed that the broad use of sensorimotor prediction during object lifting is not associated with autistic-like traits, either at a perceptual or visuomotor level. However, higher autistic-like traits consistently correspond with reduced force underestimation tendencies, indicating that prediction-related atypicalities are evident in *some* (but not all) task conditions. These results support links between autism and context-sensitive predictive processing mechanisms (e.g., precision modulation), which required investigation in participants with a clinical diagnosis of ASD.

2.2. Study 2: Predictive sensorimotor control in autistic individuals.

2.2.1. Introduction

Following the novel findings presented *above*, *Study 2* examined how predictive sensorimotor control manifests in individuals with a clinical diagnosis of autism. To do this, a conventional between-groups design was employed, whereby a number of key prediction-related variables were compared between autistic and non-autistic participants. Given the context-sensitive associations highlighted between AQ scores and predictive processing in *Study 1*, this study specifically focused on how participants utilise sensorimotor predictions under different environmental conditions.

Using the same object lifting protocol as illustrated in Figure 2.1, pGFR and pLFR differences were again inspected, along with changes in gaze search rate between baseline and 'test' trials. Such analysis would probe the degree to which participants adjust sensorimotor control according to variations in environmental uncertainty. Indeed, previous research has shown that neurotypical participants increase gaze search rate when they are more uncertain about an object's mass (Arthur et al., 2019). This response likely illustrates an increased sampling of ambiguous, goal-related visual cues (i.e., to reduce free energy: Friston, Adams, et al., 2012). However, the degree to which an individual adjusts these gaze behaviours is inversely related to levels of autistic-like traits (Arthur et al., 2019). Consequently, it was hypothesised that autistic participants would show reduced pGFR underestimation and diminished uncertainty-related changes in search rate, when compared to neurotypical controls.

2.2.2. Methods

2.2.2.1. Participants

33 participants with a clinical diagnosis of ASD, recognized according to DSM-V or ICD-10 criteria (WHO, 2012; American Psychiatric Association, 2013), were recruited for this study (see *Appendix A2)*. Initially, four participants were removed from the study, after reporting co-occurring conditions known to affect sensorimotor control (DCD: $n = 3$; musculoskeletal injury $n = 1$). Remaining participants ($n = 29$: 19 male, 10 female; 21 ± 3 years; 25 right-handed) demonstrated a broad range of autistic-like traits, as confirmed from Social Communication Questionnaire responses (SCQ: Berument et al., 1999; total scores: 18.46 ± 5.91), which correspond with previously reported clinical values (Schuwerk et al., 2016). Although all Social Responsiveness Scale scores exceeded the clinical 'cut-off' of 11, three participants scored below the recently recommended SCQ threshold of 12 (Schanding et al., 2012). However, as the presence of a formal ASD diagnosis was the criterion variable for group assignment, and none of our reported effects were altered by excluding these low SCQ cases, these participants were still included in the primary analysis (as in Schuwerk et al., 2016).

To permit between-group comparisons, an individually-matched group of neurotypical participants (19 male, 10 female, 21 ± 3 years; 25 right-handed), selected based on age, gender and dominant hand, were also tested. These individuals did not report any conditions known to affect sensorimotor control, including ASD, and did not participate in *Study 1*. As expected, this group displayed significantly lower self-reported autistic-like traits than their autistic counterparts ($t(56) = 12.32$, $p < 0.001$, $BF_{10} = 2.33 \times 10^{14}$), and there were no group differences for age or handedness. All participants were naïve to the study objectives and had normal or corrected-to-normal vision. The study received approval from the School of Sport and Health Sciences Ethics Committee (University of Exeter) and informed consent was obtained from all participants in accordance with British Psychological Society guidelines.

2.2.2.2. Materials and Procedures

The experimental set-up, recording equipment, and protocol were identical to *Study 1* except for a few adjustments. Firstly, as well as reporting how heavy an object felt, participants also verbally rated how heavy they predicted each object would be *prior to* the lifting protocol (as in Buckingham & Goodale, 2013). Once again, no constraints

were placed on these verbally reported scores, except that higher numbers should reflect heavier predicted weights. As with perceived heaviness, these values were subject to *z*-score normalisation and then compared between individuals, to illustrate whether prior expectations were different between groups.

Second, to index autistic-like traits, participants completed the shortened version of the Social Responsiveness Scale (SRS-S), a 16-item questionnaire which has proven reliable and valid in clinical populations (Sturm et al., 2017; *Appendix F*). The SRS-S measures four subscales, namely: the use of language, social information processing, capacity for reciprocal responses, and stereotypic/repetitive behaviours. Items are rated from 0 (never true) to 3 (almost always true) to yield a total SRS-S score. To supplement these self-reported data, the SCQ (Berument et al., 1999) was completed by parents or guardians for the ASD group. The SCQ is a widely used and validated clinical assessment tool, which indexes aptitudes in social responsiveness, verbal communication, and restricted repetitive stereotyped behaviours.

Finally, to reflect the refined investigative approach taken in this study, kinematic outcomes were not examined during the task. Instead, only force-based motor variables were analysed, so as to limit family-wise error rate and potential clinically-related confounds. Kinematic markers were replaced by coloured tape, which could be identified from the 'world' eye-tracking camera footage to segment the onset and offset of each trial. Such procedures were undertaken using a custom algorithm in MATLAB, with trial onset representing the first frame in which the handle tape became visible.

2.2.2.3. Data Analysis

Outcome measures relating to perceived heaviness (SWI score), fingertip force production (pGFR and pLFR) and gaze behaviour (fixation number/duration) were the same as those that were assessed in *Study 1*. To additionally monitor context-sensitive gaze adjustments in this experiment, an additional index score for search rate was computed for baseline trials and for the first lift of each 'test' object. This measure was calculated as in previous research (Arthur et al., 2019), by dividing the total number of fixations across a trial by their average duration. Here, fixations were extracted and defined using the same process as in *Study 1*. As fixations are mostly directed towards the object in this task, higher search rate values (i.e., shorter, more frequent fixations) would likely illustrate greater sampling of this uncertain, goal-relevant sensory cue.

2.2.2.4. Statistical Analysis

Pearson's correlation analysis explored relationships between sensorimotor outcomes and autistic-like trait scores (as in *Study 1*); however, independent *t*-tests were also used to compare between groups in this study. As before, ANOVAs assessed the effects of size and mass on perceived heaviness scores and fingertip lifting forces (pGFR and pLFR), with main effects of group additionally examined in this context. Here, any significant effects were examined with planned *t*-tests, and non-spherical data were adjusted using the Greenhouse-Geisser correction. Holm-Bonferroni corrections (Holm, 1979) adjusted for multiple comparisons. Two autistic participants were unable to verbally report perceived heaviness, so they and their matched neurotypical controls were excluded from these analyses (remaining $n = 54$). Two participants displayed extreme pGFR and pLFR values (>3.29 SD; remaining $n = 54$) and three participants showed poor quality gaze data (remaining $n = 52$), leading to the subsequent exclusion of these cases and their matched controls. Remaining data showed no statistical violations relating to normality, homoscedasticity, or linearity.

2.2.3. Results and Discussion

To first assess whether groups made similar cognitive predictions about object weight prior to their lifting trials, participants provided numerical ratings for how heavy they predicted each object would be, based on their visual appearance alone. A mixed-model ANOVA revealed a significant main effect of size for these scores, with larger objects predicted to be heavier than equally-weighted smaller ones ($F(1.69,84.69) = 61.03$, $p < .001$, $\eta_p^2 = 0.55$, $BF_{10} = 1.61 \times 10^{21}$). Importantly, there were no significant Group × Size interactions ($F(1.69,84.69) = 0.79$, $p = .44$, $\eta_p^2 = 0.02$, $BF_{10} = 0.26$), and ratings were unrelated to both SCQ ($r = 0.23$, $p = .27$, $BF_{10} = 0.44$) and SRS-S scores ($r = -0.10$, $p = 0.49$, $BF_{10} = 0.22$). As such, results suggest that both groups had equivalent prior expectations of object weight prior to the lifting protocol.

ANOVAs then assessed the degree to which these predictions influenced perceived heaviness ratings. As before, they revealed significant main effects of size ($F(1,52) = 537.70$, $p < .001$, $\eta_p^2 = 0.91$, $BF_{10} = 2.19 \times 10^{26}$) and weight ($F(1,52) = 426.77$, $p < .001$, $\eta_p^2 = 0.89$, $BF_{10} = 8.59 \times 10^{21}$). However, no Group × Size interactions were observed ($F(1,52) = 0.17$, $p = .69$, $\eta_p^2 = 0.003$, $BF_{10} = 0.18$), with both groups rating small objects

as heavier than larger ones (Figure 2.5). Similarly, no Group × Mass effects emerged ($F(1,52) = 1.73$, $p = .20$, $\eta_p^2 = 0.03$, $BF_{10} = 0.26$), and relationships between autistic-like traits and SWI scores were non-significant (SRS-S: $r = -0.10$, $p = .49$, $BF_{10} = 0.22$; SCQ: $r = -0.16$, $p = .47$, $BF_{10} = 0.33$). This suggests that autistic people integrate prior heaviness expectations with incoming sensory information in a typical, 'anti-Bayesian' manner during this task (Brayanov & Smith, 2010).

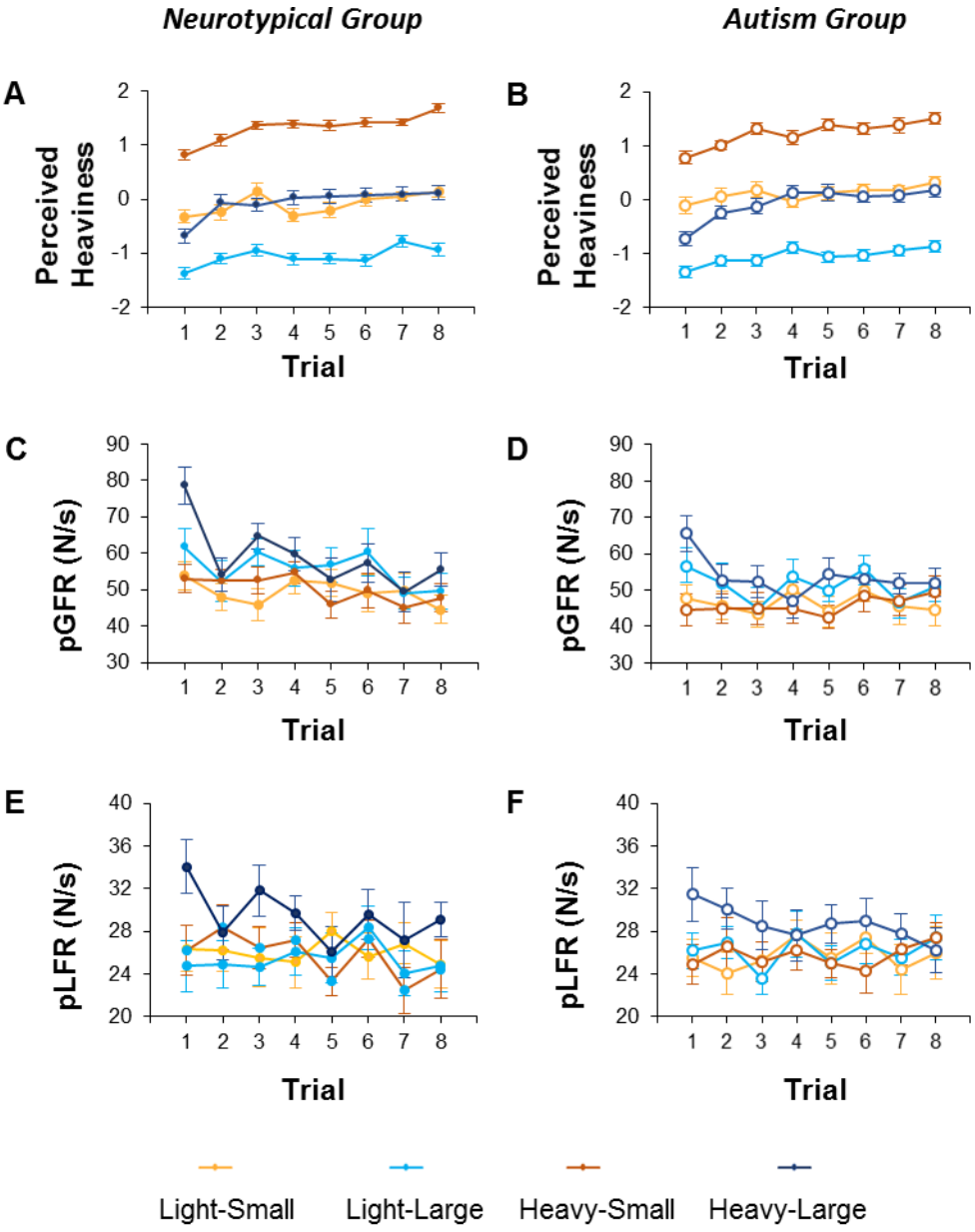

Figure 2.5. Trial-by-trial averages (± SEM) for normalised perceived heaviness ratings (**A-B**), peak grip force rate (pGFR; **C-D**), and peak load force rate (pLFR; **E-F**) in *Study 2*. Filled circles represent neurotypical values, empty circles represent autistic group.

To examine the use of these predictions at a motor level, pGFR and pLFR values from the first lift of each test object were compared between groups. ANOVA showed significant effects for both size (pGFR: $F(1,52) = 61.05$, $p < .001$, $\eta_p^2 = 0.54$, $BF_{10} = 2.98 \times 10^8$; pLFR: $F(1,52) = 12.14$, $p = .001$, $\eta_p^2 = 0.19$, $BF_{10} = 8.35$) and mass (pGFR: $F(1,52) = 6.07$, $p = .02$, $\eta_p^2 = 0.11$, $BF_{10} = 1.30$; pLFR: $F(1,52) = 12.75$, $p < .001$; $\eta_p^2 = 0.20$, $BF_{10} = 11.42$]. However, pGFRdiff ($t(52) = 0.47$; $p = .64$; $BF_{10} = 0.30$) and pLFRdiff ($t(52) = 0.25$; $p = .80$; $BF_{10} = 0.28$) were not significantly different between groups (Table 2.2), suggesting that neurotypical and ASD groups scale fingertip forces equivalently according to prior expectations of object mass (Figure 2.5). Furthermore, analysis generally showed no significant associations between autistic-like traits and either pGFRdiff (SRS-S: $r = -0.14$, $p = .31$, $BF_{10} = 0.28$; SCQ: $r = -0.33$, $p = .12$, $BF_{10} = 0.25$) or pLFRdiff (SRS-S: $r = -0.002$, $p = .99$, $BF_{10} = 0.17$). Although Bayes factors provided moderate evidence for an inverse correlation between pLFRdiff and SCQ scores ($BF_{10} = 3.23$; as in Buckingham et al., 2016), Pearson's correlation coefficient was non-significant when accounting for multiple comparisons ($r = -0.47$, $p = .02$). Therefore, results show that both autistic and non-autistic participants scale fingertip forces according to prior expectations of object heaviness.

Table 2.2 Group Averages (SD) in *Study 2*.

	ASD Group	***NT Group***
Demographic Measures		
Age	21.28 (3.63)	21.31 (3.30)
SRS-S Total	19.03 (6.24)	3.86 (0.24)*
Perceptual Measures		
Predicted Weight Score	1.31 (1.07)	1.52 (0.94)
SWI Score	1.24 (0.41)	1.18 (0.35)
Sensorimotor Measures		
pGFRdiff (N/s)	29.73 (29.18)	33.54 (30.31)
pLFRdiff (N/s)	7.19 (16.15)	6.22 (11.80)
pGFR Underestimation (N/s)	16.18 (20.00)	8.84 (18.93)
pGFR Overestimation (N/s)	4.88 (22.40)	16.71 (23.23)

SRS-S: Social Responsiveness Scale- shortened; SWI: Size-Weight Illusion; pGFR: peak Grip Force Rate; pLFR: peak Load Force Rate; *denotes significant group difference ($p < .05$).

Interestingly, there were no significant group differences in either pGFR overestimation ($t(52) = 1.91$, $p = .06$, $BF_{10} = 1.20$) or underestimation ($t(52) = 1.38$; $p = .17$; $BF_{10} = 0.60$; Table 2.2). These findings were perhaps unsurprising, given the inconclusive nature of data in *Study 1*, and are reinforced by null correlations between pGFR underestimation and SRS-S scores ($r = -0.24$; $p = .23$; $BF_{10} = 0.48$). However, analysis did provide moderate evidence for a correlation between pGFR underestimation and SCQ scores ($r = -0.52$, $p = .01$, $BF_{10} = 6.62$). It is also likely that the low neurotypical group underestimation values (8.84 ± 18.93 N/s) are obscuring any autism-related group differences that may exist in this dataset (see Jarrold & Brock, 2004 for discussion of 'floor effects' in autism research). Therefore, though it is unclear how autistic underestimation profiles distinguish from neurotypical values, the earlier trait-based associations (Table 2.1) do appear to replicate in clinically diagnosed populations.

Finally, changes in gaze search rate were monitored between the final four 'baseline' trials (i.e. where objects were familiar and unexpected outcomes were unlikely) and the first lifts of each 'test' object (i.e. where such environmental statistics were more uncertain; as in Arthur et al., 2019). ANOVA revealed a significant Group × Uncertainty interaction ($F(1,50) = 4.62$, $p = .04$, $\eta_p^2 = 0.09$, $BF_{10} = 6.38$). As expected, neurotypical participants showed significant increases in search rate between 'baseline' and 'test' trials ($t(25) = 3.42$, $p = .002$, $BF_{10} = 17.48$), an effect likely driven by an increase in short, object-driven fixations. Such visual sampling adaptations may represent a heightening of bottom-up attentional control under more uncertain conditions (Yu & Dayan, 2003; Vossel et al., 2014). Interestingly though, corresponding changes in the ASD group were not significantly different from zero ($t(25) = 0.74$, $p = .47$, $BF_{10} = 0.27$; Figure 2.6). This reduced sensitivity to uncertainty aligns with data from the rubber-hand illusion, where autistic individuals have been shown to demonstrate inflexible adjustments in reaching kinematics (Palmer, Paton, et al., 2015). Nevertheless, changes in search rate were only marginally related to self-reported autistic-like traits (SRS-S scores: $r = -0.30$; $p = .03$, $BF_{10} = 1.56$) and did not significantly correlate with SCQ scores ($r = 0.35$, $p = .11$, $BF_{10} = 0.89$). Therefore, though data provide cautious, preliminary evidence for a reduced distinction between stable and uncertain conditions in autism, further empirical scrutiny is required.

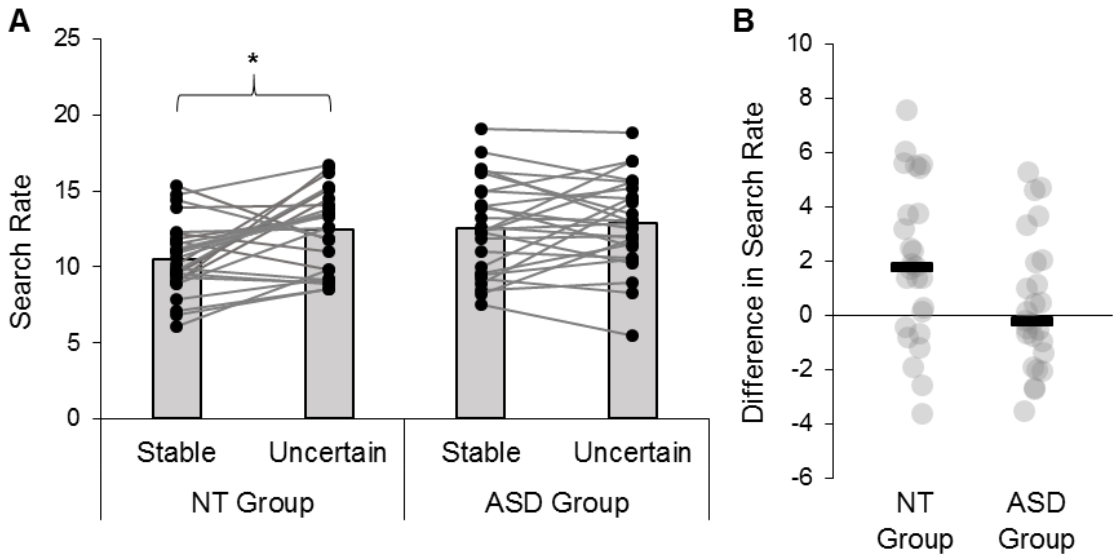

Figure 2.6. Changes in gaze search rate between stable (Baseline lifts 2–5) and uncertain (initial 'test' lifts) trial conditions for neurotypical (NT) and autism (ASD) groups in *Study 2*. Bars represent group averages, lines and circles represent individual cases. *denotes significant difference between conditions ($p < 0.01$).

2.2.4. Exploratory Analysis

In *Study 2*, the ASD group appeared to display reduced uncertainty-related increases in gaze search rate compared to their neurotypical counterparts (Figure 2.6). Such gaze adjustments also correlate with levels of autistic-like traits in both the general public (Arthur et al., 2019) and in clinical populations (*Study 2*). To investigate these context-sensitive effects further, the raw fixation data obtained in *Study 2* were re-inspected. Here, exploratory analyses aimed to clarify whether observed changes in search rate resulted from: a) an increase in fixation frequency and/or b) a shortening of fixation durations. Separate ANOVAs were conducted, with both fixation number and duration entered as dependent variables. Significant group-by-condition interaction effects occurred for fixation number ($F(1,50) = 7.73$; $p = .01$; $\eta_p^2 = = .13$; $BF_{10} = 4.03$) but not duration ($F(1,50) = 1.20$; $p = .28$; $\eta_p^2 = = 0.02$; $BF_{10} = 0.61$). As illustrated in Figure 2.7, neurotypical participants showed significant increases in the number of fixations between 'stable' and 'uncertain' trials ($p = .003$; $BF_{10} = 15.03$), whereas minimal changes were displayed by autistic participants ($p = .46$; $BF_{10} = 0.27$).

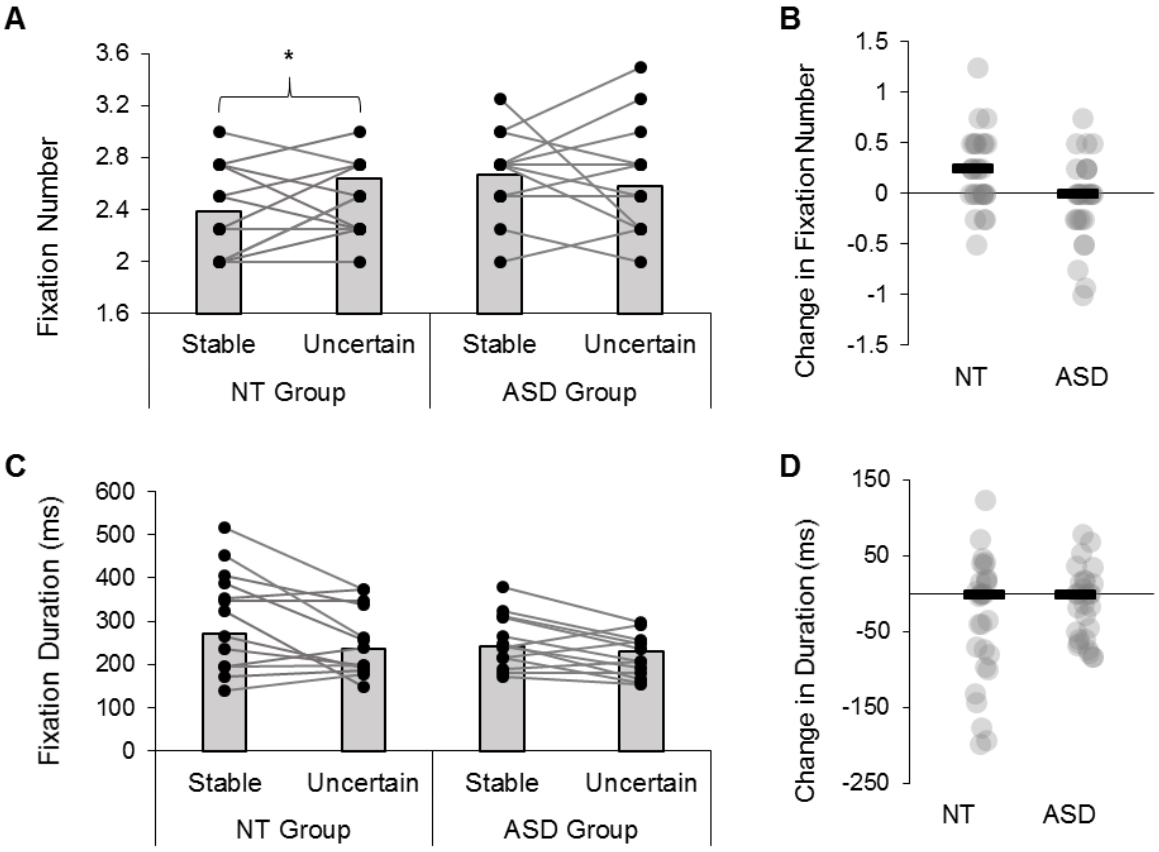

Figure 2.7. Changes in gaze fixation number (**A, B**) and duration (**C, D**) between stable (baseline lifts 2–5) and uncertain (initial 'test' lifts) conditions for neurotypical (NT) and autism (ASD) groups. Bars represent group averages, lines and circles represent individual cases. *denotes significant difference between conditions ($p < 0.01$).

These increases in fixation frequency likely reflect an increased sampling of the lifting object, as this represented a highly uncertain action stimuli. Such an assumption was reinforced upon visual inspection of the gaze data, which indicated that almost all fixations were directed towards goal-relevant cues (i.e., the object and lifting platform; see Supplementary Videos at https://osf.io/p52h8/). However, to specifically test this hypothesis, the proportion of fixations made to the object and platform were manually detected from each trial. This analysis was performed for the neurotypical group *only*, with any task-irrelevant fixation trials (0.02%) being excluded. As predicted, neurotypical subjects increased the number of object-directed fixations between stable and uncertain trials ($t(25) = 3.32$; $p = .003$, $BF_{10} = 14.04$), but showed null differences in the number of platform-directed fixations ($t(25) = .23$; $p = .82$, $BF_{10} = 0.21$).

2.2.5. Interim Summary

During the task of object lifting, autistic people appear to integrate prior expectations and sensory information in a manner that is consistent with neurotypical individuals. Contrary to 'simple' Bayesian and predictive processing theories, autism-related attenuations in the use of prior knowledge were not detected in participant's perceptual experiences, motor responses, or visual sampling behaviours. However, while neurotypical participants appear to readily adjust the sampling of goal-relevant visual information under different trial conditions, autistic participants did not distinguish between 'stable' and 'uncertain' trials in their gaze behaviour. These subtle differences in sensorimotor control may highlight a broader atypicality relating to the hierarchical modulation of environmental uncertainty and/or volatility in autism.

2.3. Discussion

This chapter investigated the aetiology of sensorimotor difficulties in autism, using a multimodal object lifting paradigm. *Study 1* first explored associations between predictive sensorimotor control and autistic-like traits in a non-clinical population, then *Study 2* assessed how specific movement-related mechanisms differ in autistic individuals. In both experiments, participants' actions were strongly driven by prior expectations, and the generic employment of these sensorimotor predictions did not appear implicated in autistic people.

Contrary to 'simple' Bayesian theories (e.g., Brock, 2012; Pellicano & Burr, 2012) and evidence of abnormal cerebellar functioning in clinical populations (Courchesne, 1997; Fatemi et al., 2002; Allen & Courchesne, 2003; Fatemi et al., 2012), the studies did not find any chronic autism-related attenuations in the use of prior information. Instead, autistic participants appeared to both *make* typical predictions about an object's likely mass, and then *use* these predictions to control their actions. For example, when lifting heavy-looking objects, both autistic and neurotypical participants showed equivalent increases in fingertip force rates (Figure 2.5). These results align with the null trait-based effects observed in *Study 1* (Table 2.1) and in previous non-clinical object lifting research (Arthur et al., 2019). They also add to various studies that have shown typical,

or even enhanced, prediction-related functions in autistic individuals (Mostofsky et al., 2004; Gidley-Larson et al., 2008; Ego et al., 2016; Tewolde et al., 2018).

Such findings are noteworthy as they suggest that autism is unlikely to be characterised by generic impairments in the ability to make and/or use predictive action models. These observations are clearly at odds with proposals of chronically diminished priors (Pellicano & Burr, 2012) and inflexible weighting of prediction errors (Van de Cruys et al., 2014) in the disorder. Indeed, according to these 'simple' computational perspectives, one would have expected autism-related atypicalities to emerge consistently across sensorimotor systems, since predictions about object weight are shown to influence perception, motor activity, visual sampling behaviours, and action kinematics (Johansson & Westling, 1988; Gordon et al., 1991; Johansson et al., 2001; Buckingham, 2014). However, it was clear that such effects did not occur in these studies, where broad expectation-driven action and visual sampling behaviours were consistently displayed by autistic participants (Figure 2.5). These null findings may have significant applied implications, as various skill interventions rest on an individual's ability to develop, refine, and automate self-generated action models (Körding et al., 2007; Haker et al., 2016). Given the substantive impact that sensorimotor difficulties are likely to have on autistic people's independence (Jasmin et al., 2009), social activities (Brandwein et al., 2015), and health-related behaviours (Scharoun et al., 2017), these findings offer potentially fruitful avenues for both researchers and practitioners in the field.

Results correspond with wide-ranging clinical evidence that autism-related atypicalities in sensorimotor prediction are context-dependent (e.g., von Hofsten et al., 2009; Tewolde et al., 2018; see Cannon et al., 2021). Although no broad processing impairments were displayed by autistic participants in this task, anticipatory motor atypicalities have previously been observed in other object interaction protocols (e.g., bimanual lifting; Schmitz et al., 2003). Such contextual irregularities have been the focus of recent work, which argues that autism is characterised by atypicalities in how predictive processing is *adjusted* under different conditions (Lawson et al., 2017; Palmer et al., 2017). According to these perspectives, such between- and within-study inconsistencies would be expected, as any atypicalities are contingent upon highly variable environmental statistics (uncertainty, volatility; Palmer et al., 2017). This is cautiously supported by the present data, where autism-related tendencies to over- but

not underestimate pGFR were inconsistently displayed. However, given the inconclusive nature of these interpretations, further empirical scrutiny is required.

Recent neurological evidence suggests that sensorimotor difficulties are caused by differences in the regulation, or connectivity, of neurobiological networks (Villalobos et al., 2005; Mostofsky et al., 2009; Fournier et al., 2010; Gowen & Hamilton, 2013). From a computational perspective, this research supports context-sensitive, hierarchical models of autism, which posit that predictive atypicalities stem from aberrant neuromodulatory functioning (Friston et al., 2013; Lawson et al., 2014; 2017). According to these perspectives, autism-related atypicalities will be more frequent under uncertain task conditions, where ambiguous prior information is typically downregulated relative to more reliable sensory evidence (e.g. from visual feedback and proprioception; Maloney & Zhang, 2010; Tong et al., 2017). Indeed, these 'typical' context-sensitive patterns of behaviour were apparent in *Study 2*, where neurotypical participants exhibited marked changes in gaze search rate (i.e. visual sampling) under more uncertain trials (Figures 2.5 & 2.6). Interestingly, such distinctions were not shown by the ASD group, suggesting that autistic participants display reduced, uncertainty-related adjustments in sensorimotor control (Palmer, Paton, et al., 2015).

However, these findings must be interpreted with caution, as visual sampling atypicalities could implicate various interrelated cognitive and attentional mechanisms. Indeed, despite being a key tenet of predictive processing theories (Palmer et al., 2017), it is entirely possible that the precise, context-sensitive differences in gaze behaviour observed in *Study 2* are indicative of wider autism-related atypicalities (e.g. in executive functioning: Ozonoff & McEvoy, 1994; attentional styles: Happé & Frith, 2006; anxiety: White et al., 2009). Therefore, it currently remains unclear how prior inputs are mechanistically integrated with sensory and environmental information in autism. Although data consistently showed that the use of prior information does not appear to be chronically attenuated (and these studies were able to qualitatively discern trials where prior uncertainty was relatively low or high), future studies should aim to statistically compute and/or experimentally manipulate the uncertainty and reliability of sensory cues. To do this, researchers should focus on outcomes relating to sensorimotor integration, as context-sensitive representations of prior and sensory uncertainty are said to modulate the connectivity of neurobiological action systems (Friston et al., 2013). Specifically, studies could use complex, multi-system movement

tasks, such as interceptive motor skills, where prediction-related visuomotor patterns are both well established and integral to successful performance (Fiehler et al., 2019).

Overall, *Studies 1* and *2* provide clear, consistent evidence that autistic individuals can typically control their lifting actions according to predictions about an object's weight. These 'predictive' profiles are implemented across various sensorimotor systems (e.g. cognition, gaze patterns, motor control), and are shaped by an individual's prior knowledge and experience. Future research is required to examine how these prediction-related mechanisms are integrated and altered under different probabilistic conditions, to help us better understand and manage sensorimotor difficulties in autism. Indeed, the above studies cautiously suggest that context-sensitive functions relating to hierarchical precision weighting and estimates of environmental uncertainty may be atypical. However, prospective studies must examine the role of these mechanisms in underpinning autistic sensorimotor impairments, using naturalistic tasks in which individuals typically exhibit movement-related difficulties.

Chapter 3

In this chapter, the precise computational origins of autistic sensorimotor impairments are investigated using a novel experimental approach. Since the exploratory findings of Chapter 2 identified potential atypicalities in context-sensitive predictive control, this work focuses on key regulatory functions that modulate active inference during dynamic movement tasks. Specifically, analyses examine whether difficulties in hand-eye coordination are underpinned by aberrant precision weighting and/or volatility processing, as proposed by recent theories of autism (Friston et al., 2013; Lawson et al., 2014; 2017). By studying an interceptive skill in which autistic people often display motor coordination issues, this chapter begins to elucidate the mechanistic underpinnings of various practical difficulties that are routinely faced within the autism community. Such empirical scrutiny develops our understanding of why autistic people experience these sensorimotor impairments and which specific functions could be targeted to optimise daily living skills in the future.

To pursue this novel line of enquiry, it is important to examine naturalistic and unconstrained action responses. Indeed, studies in the field are frequently criticised for using artificially controlled and/or simplistic task deigns (Wulf & Shea, 2002; Stevenson et al., 2009; Bejjanki et al., 2016; Noel et al., 2020). However, most 'real-world' skills require dynamic processing operations to be performed, that integrate complex and changeable sensory cues (Körding et al., 2007; Franklin & Wolpert, 2011; Hayhoe & Matthis, 2018). As such, the generalisability of previous results onto applied interventions can often prove limited (Wulf & Shea, 2002). Although *Study 1* and *2* examined object interaction behaviours that are prevalent within numerous daily living operations (Ernst, 2009), this stable and controlled laboratory task involved relatively simplistic and constrained upper-limb movements (with limited degrees of freedom and multi-system coordination). As such, a paradigm shift was needed at this stage.

Accordingly, *Study 3* examined an interceptive motor skill that has been proven to rely on complex and dynamic information processing (Diaz et al., 2013; Binaee & Diaz, 2019; Mann et al., 2019). Specifically, a simulated racquetball game was performed within VR, where a variety of context-sensitive, prediction-related measures could be obtained. Visuomotor responses in this task closely resemble those in 'real-world' environments (Diaz et al., 2013), so analyses could be conducted in an ecologically-

valid manner. However, when compared to traditional methods, VR protocols afford unique levels of control over dynamic experimental conditions (see *Section 1.3.2*). As such, probabilistic uncertainty was systematically manipulated over time, and context-sensitive action responses were scrutinised in an unconstrained laboratory setting. This innovative empirical approach required a number of new, interdisciplinary concepts and techniques to be developed (see *below*). Nevertheless, the highly controlled and scientifically-grounded methodologies gave rise to novel, empirically-reliable data that advances our understanding of autistic sensorimotor difficulties.

The study below has been published as: Arthur, T., Harris, D., Buckingham, G., Brosnan, M., Wilson, M., Williams, G., & Vine, S. (2020). An examination of active inference in autistic adults using immersive virtual reality. *Scientific Reports, 11,* 20377.

3.1. Study 3: An examination of active inference in autistic adults using immersive virtual reality.

3.1.1. Introduction

Autism is diagnosed according to atypicalities in social interaction, communication, and behavioural flexibility. However, one particular source of daily living difficulty for many autistic people concerns impaired visuomotor coordination abilities (Jasmin et al., 2009; Gowen & Hamilton, 2013). Performance-related difficulties on standardised motor assessments are commonly displayed by autistic people (Fournier et al., 2010; Gowen & Hamilton, 2013; Coll et al., 2020), with particular impairments shown in interceptive skills like catching or hitting a ball (Green et al., 2002; Whyatt & Craig, 2013b; Ament et al., 2015; Chen et al., 2019). These differences emerge at a kinematic level (Glazebrook et al., 2006; Whyatt & Craig, 2013a; Chen et al., 2019), for which autistic people show noisy, inflexible, and uncertain movement patterns (Cook et al., 2013; Torres et al., 2013; Torres & Denisova, 2016; Foster et al., 2019). The degree of impairment in motor tasks correlates with an individual's socio-behavioural traits (MacDonald et al., 2013) and daily living competencies (Jasmin et al., 2009). Research into the source of these sensorimotor difficulties could thus develop both our scientific understanding of autism, and our capacity to manage its various clinical features.

Studies have shown that movement is coordinated using probabilistic models about the world (*predictions*), which are derived from incoming sensory evidence and prior expectations (Vilares & Kording, 2011; Adams et al., 2013). When performing an action like hitting a tennis ball, the brain will regulate motor responses (e.g., movement kinematics) and sampling behaviours (e.g., gaze responses) according to incoming sensory cues and prior beliefs (e.g., about gravity, ball bounciness: Diaz et al., 2013). Such dynamic sources of information are weighted according to their uncertainty, or *precision*, which is directly proportional to learning rate (Behrens et al., 2007). These precision-weighted predictions not only serve to optimise perceptual functions, they also represent a set point that an individual can act towards in their movements (Friston, Samothrakis, et al., 2012; Adams et al., 2013; Shipp et al., 2013). Any deviations away from near-optimal processing could result in sensorimotor impairment.

Notably, various researchers have highlighted the role of impaired predictive processing in autism (see Palmer et al., 2017). Though conflicting in their precise explanations, most 'simple' computational frameworks attest to an attenuated influence of prior expectations on autistic perception and action (Brock, 2012; Pellicano & Burr, 2012). These accounts can explain heterogeneous socio-behavioural traits and neurological abnormalities displayed in autistic people (see clinically-focused review: Haker et al., 2016). Furthermore, proposed differences in predictive processing align with a range of autism-related sensorimotor atypicalities (Van de Cruys et al., 2014), including: impaired movement planning (Hughes, 1996; Nazarali et al., 2009), reduced anticipatory motor adjustments (Schmitz et al., 2003; Chen et al., 2019), suboptimal movement initiation kinematics (Glazebrook et al., 2006; Whyatt & Craig, 2013a), slower error-based saccade adaptation (Johnson et al., 2013; Mosconi et al., 2013), and atypical gaze fixation behaviours (Sasson et al., 2008; 2011). However, prediction-related difficulties only emerge under some task conditions (see Cannon et al., 2021), with autistic people demonstrating intact visual motion prediction (von Hofsten et al., 2009; Tewolde et al., 2018), anticipatory lifting forces (*Study 1*), and non-social ocular tracking abilities (Aitkin et al., 2013; Ego et al., 2016). These inconsistent findings undermine proposals that prior expectations are generically attenuated in autism.

Instead, recent theories argue that autism is characterised by atypicalities in context-sensitive processing functions, which determine how predictive control is hierarchically adjusted according to environmental statistics (e.g., uncertainty, volatility; Lawson et

al., 2014; 2017; Palmer et al., 2017). In contrast to the simple frameworks discussed above, these mechanisms implicate how an individual *dynamically* models the world, through precision-related modulation of cortical gain (Lawson et al., 2014). Here, autistic daily living difficulties are not perceived to result from 'one-level' attenuations in the use of prior expectations; they are proposed to stem from mechanisms that contextually regulate prediction error across multi-level neural networks. These hierarchical functions not only determine the precision of prior beliefs, they also model how environmental probabilities fluctuate over time. Indeed, estimations about environmental (in)stability implicate how an individual samples and learns about sensory information (Behrens et al., 2007; Mathys et al., 2011; 2014), with even minor abnormalities likely to impair the formation of stable, statistically-optimal predictive models (Lawson et al., 2014). As a result, autistic people may consistently interact with the world as if it is uncertain or volatile, a hypothesis supported by studies of probabilistic learning (e.g., Robic et al., 2015), neural habituation (e.g., Ewbank et al., 2017; Goris et al., 2018), and pupil diameter responses (e.g., Lawson et al., 2017).

When interpreted alongside active inference perspectives, these hierarchical frameworks present novel, empirically-falsifiable predictions about behaviour. Optimal sensorimotor control rests on dynamic adjustments in the sampling and weighting of sensory information, with physical actions said to 'fulfil' predictions and/or reduce their uncertainty (Friston, Samothrakis, et al., 2012; Adams et al., 2013; Shipp et al., 2013). Here, the use of generative models is seen to minimise future prediction errors (or Bayesian surprise), based on estimates of hidden world states. When uncertainty in prior expectations is high or environmental volatility increases (e.g., when conditions become more unpredictably-changeable), individuals tend to rely more heavily on incoming sensory feedback and will adjust their visual search strategies accordingly (Beesley et al., 2015; Walker et al., 2019; *Study 1*). Alternatively, when sensory information is more uncertain, more emphasis will be placed on longstanding prior expectations and 'top-down' attentional processes (Vilares & Kording, 2011; Tong et al., 2017; Helm et al., 2020). Such Bayes-optimal adjustments have been demonstrated in neurotypical cue combination (Stocker & Simoncelli, 2006; Körding et al., 2007), interceptive timing (Miyazaki et al., 2005), movement planning (Hudson et al., 2007; Kwon & Knill, 2013), and visuomotor integration (Körding & Wolpert, 2004; Stevenson et al., 2009; see Vilares & Kording, 2011 for review).

Though current research is limited, recent evidence from the rubber-hand (Palmer et al., 2015) and size-weight (*Study 1*) illusions suggests that autistic people display inflexibilities in active inference. When compared to neurotypical controls in these studies, autistic participants were less inclined to adjust visual search and movement kinematics under non-veridical, uncertain conditions. Importantly, these differences in context-sensitive processing were not accompanied by any generic attenuations in the use of prior expectations (Palmer, Paton, et al., 2015; *Study 1*). These results provide clear support for recent hierarchical frameworks of autism (Lawson et al., 2014; 2017; Palmer et al., 2017). However, neither study experimentally manipulated or quantified environmental statistics over time, meaning that causal links must be made with caution. Moreover, movement-related *impairments* were not examined in either lab-based task, limiting their utility in the development of practical interventions.

The present work examined how movement is dynamically controlled during multi-sensory interceptive actions, where autistic people often display performance impairments (Green et al., 2002; Vanvuchelen et al., 2007; Whyatt & Craig, 2013a; Ament et al., 2015; Chen et al., 2019). To this end, this study adopted an immersive virtual racquetball task (Diaz et al., 2013; Mann et al., 2019) which monitored how predictive control is adjusted between different volatility conditions. Here, the use of VR facilitated systematic, unconstrained manipulations of environmental uncertainty, allowing us to decipher precisely which predictive processing mechanisms are implicated in autism. Specifically, VR enabled us to artificially alter whether the 'bounciness' of an approaching ball remained stable or unpredictably-changeable (volatile) over time, before measuring how sensorimotor behaviours were adjusted. Atypical predictive processes usually manifest most clearly in uncertain or volatile conditions, as suboptimal probabilistic expectations will impair abilities to distinguish random sensory noise from actual environmental changes (Van de Cruys et al., 2014; Lawson et al., 2017). Accordingly, it was hypothesised that autistic participants would show impaired interceptive performances, particularly under volatile conditions.

In this task, both the timing and location of anticipatory eye movements are affected by prior expectations and incoming visual information (Diaz et al., 2013; see also Hayhoe et al., 2012). Specifically, anticipatory saccades move gaze ahead of the ball to its expected future location, with the subsequent fixation point proving directly proportional to both its early-flight trajectory and, crucially, its predicted elasticity profile

(Diaz et al., 2013; Mann et al., 2019). These sampling behaviours appear fundamental in the retrieval of post-bounce position information, with unexpected and computationally 'surprising' changes in ball bounciness leading to poorer subsequent gaze pursuit (Hayhoe et al., 2002). It was hypothesised that autistic participants would be less inclined to use a predictive gaze strategy than their neurotypical counterparts, and would show later pre-bounce saccades, shorter fixations around the bounce point, and a reduced distinction between expected and unexpected gaze tracking responses. Furthermore, on the basis that autistic people may be hypersensitive to environmental change (Lawson et al., 2017), it was hypothesised that the ASD group would show greater changes in these measures between stable and volatile task conditions.

Predictions are also used to guide an individual's interceptive motor response (Binaee & Diaz, 2019; Mann et al., 2019). Typically, movement onset times are flexibly adjusted according to previous ball trajectories and spatiotemporal conditions (Cesqui et al., 2015; Mann et al., 2019), via top-down signalling and precision-mediated sensory attenuation (Friston, Samothrakis, et al., 2012; Adams et al., 2013; Shipp et al., 2013). Research from constrained motor tasks indicates that movement onset kinematics are suboptimal in autism (Schmitz et al., 2003; Glazebrook et al., 2006; Whyatt & Craig, 2013a), with further scrutiny required in unconstrained movement skills. Moreover, for dynamic and naturalistic actions, the optimal regulation of movement rests on context-sensitive mechanisms (Adams et al., 2013). During uncertain conditions, for example, neurotypical adults have been shown to increase joint stiffness and restrict multi-effector redundancy (Burdet et al., 2001; O'Sullivan et al., 2009). Though such 'fixing' of joint angles is less efficient, and would usually be associated with more novice-like movement profiles (i.e., reduced movement degrees of freedom; Bernstein, 1967), it likely represents an active attempt to reduce uncertainty from signal-dependent noise (O'Sullivan et al., 2009). Given that autistic people are proposed to interact with the world as if it is generally uncertain or volatile (Lawson et al., 2017), it was hypothesised that the ASD group would show greater 'fixing' of joint angles than the neurotypical group (i.e., reduced range of motion and hand displacement; see Table 3.1). In line with previous studies (Palmer, Paton, et al., 2015; *Study 1*), autistic participants were also expected to display inflexible motor kinematics, as evidenced by reduced between-condition adjustments in swing onset time and peak hand velocity.

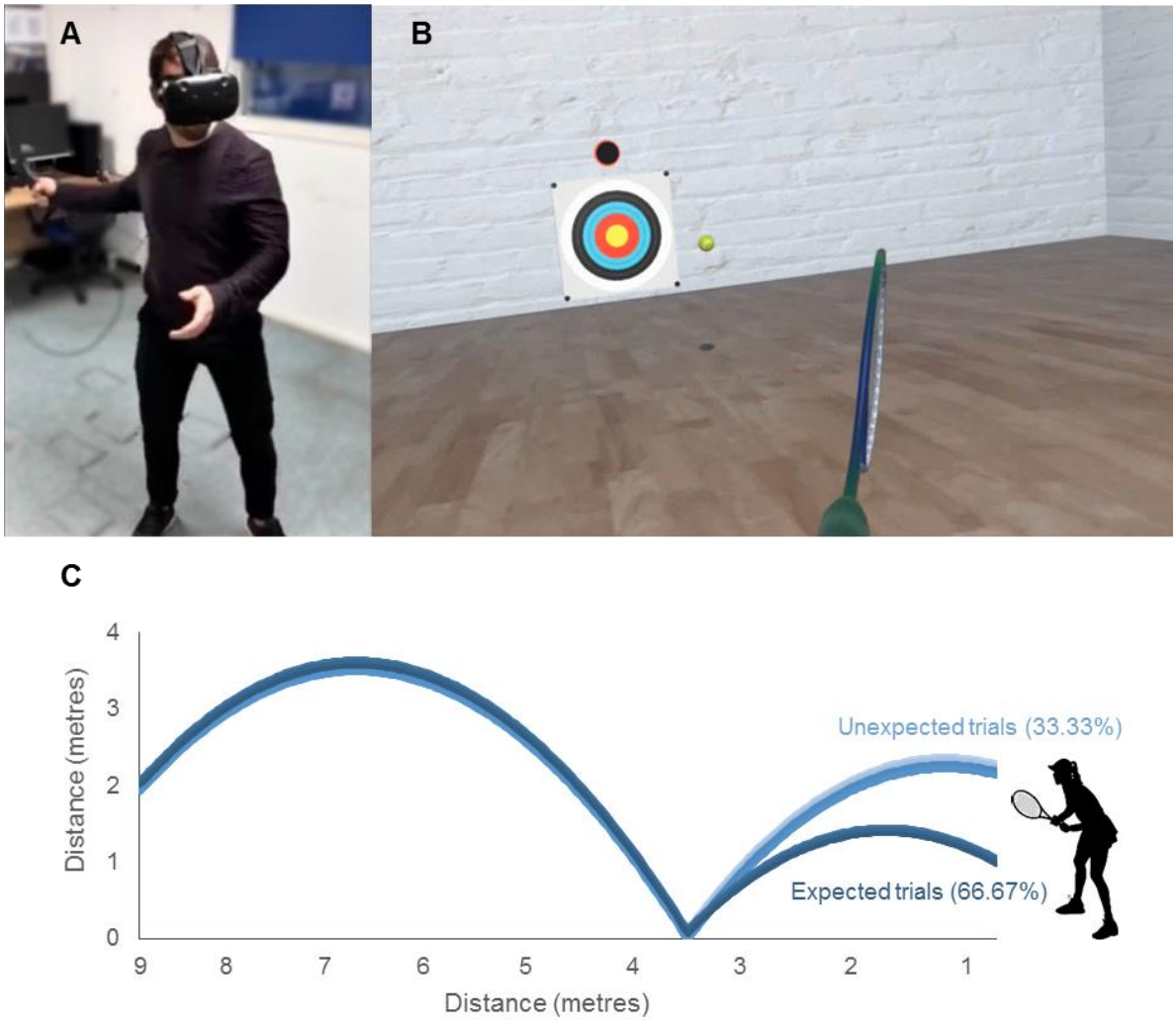

Figure 3.1. The Virtual Racquetball task in *Study 3*. An illustration of the experimental set-up (**A**), example gameplay footage (**B**), and a side-view of ball trajectory distributions (**C**). Note: for all trials, virtual balls stayed fixed on the midline of the room and followed the same pre-bounce speed and trajectory. Differences between expected and unexpected trials were consigned to ball elasticity manipulations only. See Supplementary Videos at: https://osf.io/ewnh9/.

3.1.2. Methods

3.1.2.1. Participants

Ninety participants visited the laboratory (33 female, 78 right-handed, age: 22 ± 4 years). Thirty of these individuals had a formal diagnosis of ASD, while the remaining sample (*n* = 60) were age-matched neurotypical individuals (ASD group: 21 ± 5 years;

NT group: 22 ± 4 years; $t(88) = .70$, $p = .70$, $BF_{10} = 0.25$). A large neurotypical sample was recruited to provide sufficient power for correlational analysis (see *Appendix A3*). All autistic participants reported that they had received their diagnosis from a qualified clinician according to DSM-IV (American Psychiatric Association, 2013) or ICD-10 (World Health Organisation, 2012) criteria, and completed both the 26-item Autistic Quotient (AQ-26; Austin, 2005) and Social Communication Questionnaire (SCQ; Berument et al., 1999) to corroborate clinical presentation of autistic-like traits.

Although diagnosis status was not independently verified in this study, a broad range of SCQ scores were displayed by the ASD group that are consistent with normative clinical values (mean: 18.34 ± 5.72; see Barnard-Brak et al., 2016). Participants self-reported normal or corrected-to-normal vision and were excluded if they reported any history of musculoskeletal or neurological disorders, leading to the removal of two cases (ASD: $n = 1$; NT: $n = 1$). Neurotypical participants also completed the AQ-26 (range: 37-80, mean: 55.17 ± 9.77; $n = 59$) to permit correlational analyses across the whole sample (i.e., the 'broader autism spectrum'; Landry & Chouinard, 2016). All participants were naïve to the experimental aims and had no prior experience of playing VR-based racquet sports. Informed consent was obtained in accordance with British Psychological Society guidelines, and the study received approval from the School of Sport and Health Sciences Ethics Committee (University of Exeter, UK) and Department of Psychology Ethics Committee (University of Bath, UK).

3.1.2.2. Apparatus and stimuli

A virtual environment, simulating an indoor racquetball court, was developed using the gaming engine Unity (Unity Technologies, San Francisco, CA). This simulated environment (see Figure 3.1) spanned 15 metres in length and width, and contained a series of concentric circles projected onto the front wall as an aiming target. Above this target was an additional concentric circle, representing the starting location where virtual balls were launched from in each trial (launch height: 2 m). The floor resembled that of a traditional squash court, with participants instructed to start behind the 'short line' (located 9 m behind front wall, .75m from the midline; as in Diaz et al., 2013). To ensure consistency in this starting position, a 1 m^2 service box was marked on the laboratory floor with reflective tape, and an experimenter checked that participants were stood in this square prior to all experimental trials.

The virtual environment was presented to participants on an HTC Vive head-mounted display (HTC Inc., Taoyuan City, Taiwan; Figure 3.1), a high-precision, consumer-grade VR system which has proven valid for small-area movement research tasks (field of view: 110°, accuracy: 1.5cm, jitter: 0.5mm, latency: 22ms; Niehorster et al., 2017). Two 'lighthouse' base stations recorded movements of the headset and hand controller at 90Hz. The headset also included an inbuilt Tobii eye-tracking system, which uses binocular dark pupil tracking to monitor gaze at 120 Hz (spatial accuracy: 0.5-1.1°; latency: 10ms, headset display resolution: 1440 x 1600 pixels per eye). Gaze was calibrated over five virtual locations prior to each condition, and upon any obvious displacement of the headset during trials.

Participants then attempted to hit balls towards the projected target circles using a virtual racquet (Figure 3.1), operated by the Vive hand controller. Virtual balls were 5.7 cm in diameter, and resembled the visual appearance of a 'real-world' tennis ball. The visible racquet in VR was 0.6 x 0.3 x 0.01 m, although its physical thickness was exaggerated by 20 cm for the detection of ball-to-racquet collisions (see discussion of tunnelling effects: Diaz et al., 2013; Mann et al., 2019). One neurotypical participant was excluded from analyses following frequent loss of headset tracking during their session (remaining n = 86).

3.1.2.3. Procedures

On arrival to the laboratory, participants provided written informed consent and completed the autistic-like trait questionnaires. Next, they were fitted with the VR headset and presented with a view of the simulated racquetball court. Participants completed six familiarisation trials and the inbuilt VR eye-tracker was subsequently calibrated, before undertaking the stable and volatile conditions. During each trial, individuals were instructed to hit virtual balls towards the centre of the projected target. Balls were launched from the front wall, following 3 auditory tones, and passed exactly through the room's midline, bouncing 3.5 m in front of the prescribed starting position. Right-handed participants started 0.75 m to the left of this midline, and left-handers 0.75 to the right of this point, meaning that all shots were forehand swings.

Participants were informed that the ball would bounce once, but that they were free to hit the ball before or after it reached them. Task instructions simply stated that they should aim to hit as many balls as possible to the middle of the front target. No further

information relating to ball elasticity, trajectory or probabilistic manipulations were provided. Virtual balls followed the same pre-bounce trajectory and speed (vertical speed: -9 m/s at time of bounce; Figure 3.1), which were both consistent with the effects of gravity (-9.8 m/s^2). Although bounces were accompanied by auditory feedback, no visual, proprioceptive, or verbal feedback were provided upon making contact with the ball. Instead, a neutral 'pop' sound was incorporated, so as to minimise the influence of motivation and communicative requirements.

To manipulate environmental volatility in each condition, this study systematically varied ball elasticity over time (Figure 3.1). Specifically, in expected trials, ball elasticity was congruent with its visual 'tennis ball-like' appearance, and set at 65%. Conversely, in unexpected trials, elasticity was increased to 85%, an abrupt change in 'bounciness' that is easily detectible to participants (Diaz et al., 2013). By selecting such unnatural ball elasticity profiles, and by adjusting these without the participant's knowledge (Hayhoe et al., 2002; Diaz et al., 2013), it was anticipated that post-bounce ball trajectory would deviate substantially from any 'real-world' prior distributions. This would then permit unique control over participant's experience of expected and unexpected events, through probabilistically contrasting order sequences (available at https://osf.io/ewnh9/).

Specifically, in the stable condition, balls were presented in 'predictable' serial orders (e.g., three unexpectedly-bouncy balls would follow three expected ones, and so on), with the likelihood of facing a 'normal' ball (i.e., expected event) remaining fixed at 66.67%. In the volatile condition, these ball probabilities were unstable, switching irregularly between highly- (83%), moderately- (67%) and non-predictive (50%) in blocks of 6, 9, or 12 trials. Importantly, conditions contained the same number of expected (n = 30) and unexpected (n = 15) trials in 'high-interference, non-repeating schedules' (Hebert et al., 1996), meaning that the difference between blocks was consigned to environmental volatility only (i.e., differences in how labile the context is perceived to be).

To permit precise within- and between-condition comparisons, three expected and three unexpected 'test' trials were situated within each block. These trials had identical prior probability distributions (66.67% of preceding trials contained expected ball trajectories) and identical previous trial histories (n – 1 were all expected trials). To

ensure that bouncy balls remained computationally surprising in the stable condition, unexpected 'test' trials were taken from within the final nine trials, in which the order sequences had recently been changed.

The experiment began with a practice set of six trials, whereby balls were projected from the target without a bounce (so that ball elasticity remained unknown to participants). Thereafter, upon calibration of the eye-tracking system, experimental conditions were performed in a counterbalanced order. Each condition contained 45 trials and was separated by a short break, with a total of 96 trials performed by each participant.

3.1.2.4. Data analysis

To index task performance, the proportion of trials in which participants made contact between the ball and racquet (*interception rate*, %) were recorded. Thereafter, positional data for the hand controller were extracted from the Vive system, and smoothed using a dual-pass, zero-phase Butterworth filter (at 10 Hz; Franks et al., 1990). The contact point between the racquet and ball (referred to as: *ball contact frame*) were derived from the last data point before ball exhibited an abrupt change in direction of its trajectory. Trials where participants missed the ball were also included in analyses. In these instances, the reference ball contact frame represented the last data point in which the ball's depth position exceeded that of the racquet. Trials where participants used a backhand swing, as opposed to a forehand swing, were noted at the time of data collection and removed from kinematic analysis.

To capture aspects of swing kinematics, a number of measures linked to motor proficiency were calculated, namely: swing onset time, peak velocity of the hand, maximum hand displacement from the head, and swing Range of Motion (ROM; see Table 3.1). Specifically, swing onset time was defined from the first frame at which forward motion of the racquet began, while swing offset corresponded with the ball contact frame. The foreswing, representing the forward phase of the hand movement before ball contact (Rodrigues et al., 2002), was defined between swing onset and swing offset. Velocity of the hand controller was calculated as the square root of the sum of squared vector differentials, where peak velocity and the timepoint of peak velocity (ms, relative to ball contact frame) was identified during the foreswing phase. Higher peak velocities, which occur close to ball contact, are indicative of more

proficient motor control (see Reid et al., 2013). Normalised maximum hand displacement from the headset denoted the span of the arm from the body during the swing. This was operationally defined as the distance between the headset and hand controller position in the transverse plane (divided by body height in meters). Swing ROM (°) was calculated as the angular deviation of the hand controller during the foreswing. Angular deviation was defined in the transverse plane, with angles of 0° representing minimal rotation. Reductions in maximum hand displacement and/or swing ROM values would signal greater 'fixing' of movement degrees of freedom (H. A. Palmer et al., 2018), a motor strategy which could be used to reduce action uncertainty (O'Sullivan et al., 2009).

Table 3.1. Description of Kinematic Outcome Measures in *Study 3*.

Variable	***General Description***	***Operationalised Definition***
Swing Onset Time	Moment when the racquet first started moving towards the ball.	The first timeframe in which forward motion of the VR hand controller was detected (relative to trial onset).
Peak Velocity of the Hand	The highest speed that the hand reached when moving towards the ball.	The maximum differential position of the VR hand controller shown between frames following swing onset (expressed in m/s)
Time of Peak Hand Velocity	The moment when the hand reached its highest speed.	The time at which Peak Velocity of the Hand occurred, relative to ball contact.
Maximum Hand Displacement	The furthest distance that the hand deviated away from the body during the swing.	The maximum distance that occurred between the VR headset and controller in the transverse plane following swing onset (normalised by participant body height).
Swing Range of Motion	The total arc travelled around the body by the hand during the swing action.	The total angular deviation (°) of the hand controller from the VR headset that occurred in the transverse plane.

A single unit vector corresponding to cyclopean gaze direction was extracted from the inbuilt eye-tracking system, with features defined according to head-centred, egocentric coordinates (i.e., vertical and horizontal coordinates). Both this extracted gaze vector, and the ball's head-centric position were then plotted with respect to 2D direction in space, to provide relative 'in-world' angular orientation metrics (see gaze-

head and gaze-ball angles: Table 3.2). Here, yaw angles represented rotation about a vertical axis that is in-line with gravity, and pitch values index angular deviance from a plane originating at eye-height that is parallel to the floor plane (Diaz et al., 2013; Mann et al., 2019). All trials were segmented from the moment of ball release until the time point corresponding to ball contact frame. Gaze values were passed through a three-frame median filter, before being smoothed by a second-order, zero-lag Butterworth filter (Fooken & Spering, 2019). In line with recent recommendations (e.g., Cesqui et al., 2013; 2015), different cut-off frequencies were applied for saccade identification (50 Hz) and analysis of positional tracking features (15 Hz). Trials with >20% missing data, or where eye-tracking was temporarily lost (>100 ms) were excluded.

Angular velocities (°/s) and accelerations (°/s^2) of gaze-in-world vectors were calculated from the distance between samples of the filtered signal. Saccades were identified from portions of data where gaze acceleration was more than five times its median absolute acceleration (Mann et al., 2019). To avoid erroneous detections (e.g., due to pursuit or tracker-noise artefacts), gaze velocity had to exceed 40°/s for five consecutive frames and had to be at least 20% greater than that of the ball, with time periods preceded or followed by missing data also excluded. If this acceleration criteria failed to identify any pre-bounce saccades, trials were manually inspected using a 30°/s velocity threshold (Cesqui et al., 2015). Onset and offset times were determined from these signals using acceleration minima and maxima (Fooken & Spering, 2019). A spatial dispersion algorithm was then used to extract gaze fixations (Krassanakis et al., 2014). These were defined from portions of data where velocity was < 30°/s (Diaz et al., 2013), using a 3° spatial dispersion threshold and a minimum required duration of 100 ms (Salvucci & Goldberg, 2000). This method excluded phases of smooth pursuit and instead highlighted periods in which gaze became stable within a 3° area.

Upon identification of saccades and fixation periods, various prediction-related gaze metrics were calculated (see Table 3.2). As we were interested in the final predictive saccade made before the ball had bounced, the latency (i.e., median onset time, relative to bounce) and amplitude (i.e., mean deviance between the final and initial gaze position) of this gaze event were recorded. Moreover, the fixation position at the moment of bounce was extracted (expressed as gaze-head pitch angle), in addition to the average gaze-ball pitch after this timepoint. To assess the degree of gaze tracking prediction error, average gaze-ball pitch was converted into *z*-scores for each

participant, with mean expected test scores subtracted from their corresponding unexpected test trial values. This presented a *UE-E gaze tracking difference* score, whereby higher scores would signal a greater difference between expected and unexpected trials (i.e., greater behavioural surprise following an unexpected event).

Table 3.2. Description of Gaze Metrics in *Study 3*.

Variable	***General Description***	***Operationalised Definition***
Gaze-head angle	Where gaze was being directed in space, relative to the head.	Angular orientation of the gaze vector in 2D space, with respect to the VR headsets in-world position (expressed as pitch and yaw,°)
Gaze-ball angle	Where gaze was being directed in space, relative to the ball.	Angular deviation in 2D space between the gaze vector and the ball's head-centric position (expressed as pitch and yaw, °).
Anticipatory pre-bounce saccade onset time	The moment when gaze suddenly shifted ahead of the ball before it bounces.	The median onset time of participants' final pre-bounce saccade (recorded in ms, relative to when the ball had bounced).
Anticipatory pre-bounce saccade amplitude	How far gaze moved when it was being suddenly shifted ahead of the ball (see above).	The change in gaze-head pitch angle (°) that occurred between the onset and offset of participants' final pre-bounce saccade.
Bounce fixation duration	How long gaze remained steady for, around the time when the ball was bouncing.	The average duration of gaze fixations that occurred at the time of, or immediately prior to, the ball bouncing on a trial (expressed in ms).
Bounce fixation location	Where gaze was directed around the time when the ball was bouncing.	The average gaze-head pitch angle (°) of fixations that occurred at the time of, or immediately prior to, the ball bouncing.
Average post-bounce gaze tracking error	How much higher or lower gaze was from the ball, on average, from when it bounced to when it was hit by the racquet.	The average gaze-ball pitch angle (°) shown from the first timeframe after the ball bounces up to the point of racquet-ball contact.
UE-E gaze tracking difference	How much closer gaze was tracking expected as opposed to unexpected balls after they bounced.	Differences in normalised post-bounce gaze tracking error (see above) between expected and unexpected 'test' comparison trials.

Gaze and kinematic data values that were > 3.29 SD away from the mean were classed as univariate outliers ($p < 0.001$) and removed from analysis (see Osborne, 2013). Participants with > 20% of data identified as missing and/or outliers were excluded ($n = 6$). One performance outlier was excluded from analysis, after they failed to intercept the ball on any trials and showed extreme gaze values, potentially due to equipment error and/or a lack of task understanding. Following this case removal, a further two autistic participants were then identified as potential performance outliers (see Figure 3.2). However, since the overall pattern of results was not affected by their inclusion, and such extreme values are consistent with previously documented clinical sensorimotor impairments, these cases remained in the analysis (as recommended in clinical guidelines; Aguinis et al., 2013). Remaining missing data points within the dataset ($n = 80$) were deemed missing completely at random, on the basis of Little's MCAR test ($p > 0.05$). For all variables, normality, linearity, multicollinearity, and homoscedasticity of data were inspected. Cleaned data were analysed using JASP (version 0.12.2), with significance accepted at $p < 0.05$ and data presented ± SD.

Mixed-model ANOVAs assessed the effects of group and condition on all of the metrics relating to performance (interception rate), action kinematics (swing onset time, peak hand velocity, time to peak velocity, maximum hand displacement, ROM) and gaze behaviour (predictive saccade onset time/amplitude, bounce fixation duration/position, average post-bounce gaze tracking error, UE-E gaze tracking difference scores). Any significant differences were examined using two-tailed *t*-tests and all effect sizes were calculated using partial-eta squared. To explore the role of autistic-like traits, Pearson's Correlation analysis explored relationships between all sensorimotor outcomes and AQ-26 scores. As data for interception rate and predictive saccade outcomes violated assumptions of normality, these outcomes were inspected using non-parametric *t*-tests and correlation equivalents (i.e., Mann-Whitney U for group comparisons, Spearman's Rho for correlation analyses). Mixed-model ANOVAs are robust to moderate deviations from statistical normality (Lix et al., 1996), and were still performed for these measures. Non-spherical data were adjusted using the Greenhouse-Geisser correction, and multiple comparisons were accounted for using the Holm-Bonferroni method (Holm, 1979). For all tests, Bayes Factors quantified the strength of evidence for the alternative and null hypotheses (as in *Chapter 1*).

3.1.3. Results

3.1.3.1. Performance Data.

The proportion of successful interceptions revealed a negative skew due to a high number of participants successfully hitting the ball in all trials (*n* = 18; Figure 3.2). However, a range of interception rates were still exhibited, particularly in the autism group (range: 27.78-100%). A mixed-model ANOVA showed that performance levels statistically differed between groups ($F(1,78) = 7.92$, $p = .01$, $np2 = .09$, $BF_{10} = 7.07$), with lower interception rates evident in autistic (86.38 ± 19.20%) as opposed to neurotypical participants (94.69 ± 7.19%). These overall scores were not significantly different between stable and volatile trials ($F(1,78) = 1.13$, $p = .29$, $np2 = .01$, $BF_{10} = 0.18$). However, there was a significant condition-by-group interaction ($F(1,78) = 5.08$, $p = .03$, $np2 = .06$, $BF_{10} = 1.90$), with autism-related performance impairments emerging under volatile conditions (Figure 3.2; $W = 963.00$, $p < .01$, $BF_{10} = 21.50$). Spearman's Rho analysis supported these observations, with AQ-26 scores across the entire sample negatively correlating with interception rate in the volatile ($Rs = -.25$, $p = .02$, $BF_{10} = 35.18$) but not stable trials ($Rs = -.09$, $p = .44$, $BF_{10} = 1.03$).

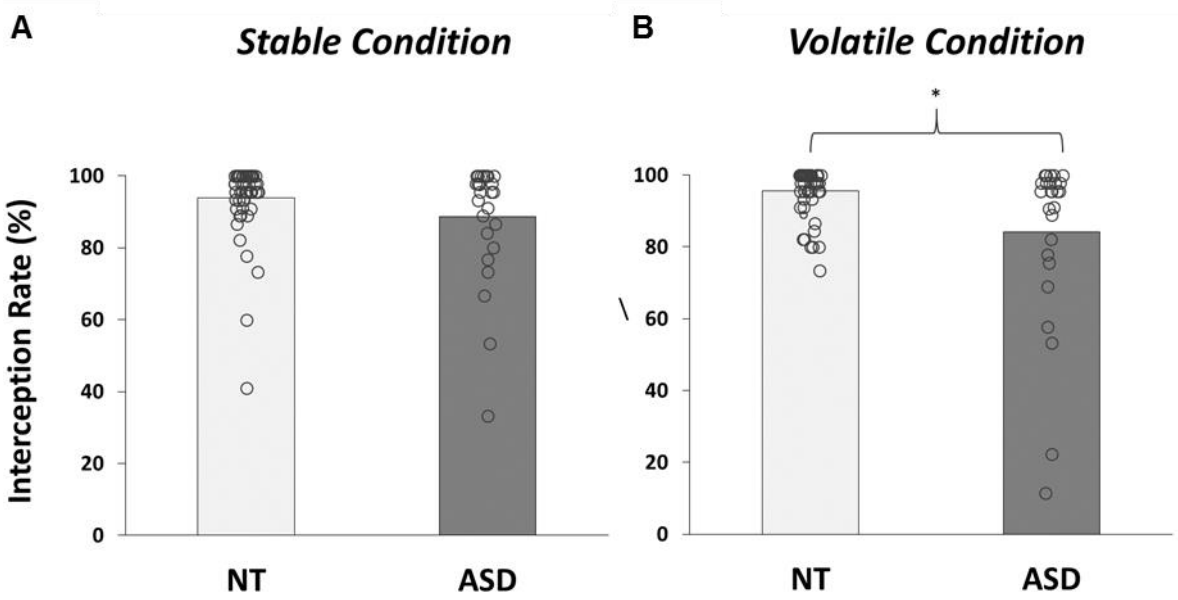

Figure 3.2. Performance data in *Study 3*. The proportion of balls successfully intercepted in stable and volatile conditions for each group. NT: neurotypical; ASD: autism spectrum disorder; *denotes significant group difference ($p < .05$).

3.1.3.2. Kinematic Data.

Next, aspects of swing kinematics were compared between groups and conditions, based on the position of the VR hand controllers. Three participants (ASD: n = 1; NT: *n* = 2) were excluded from this analysis, following detection of univariate outliers or invalid trials (remaining *n* = 77). For peak velocity of the hand, ANOVAs showed a significant effect of group ($F(1,75) = 5.18$, $p = .03$, $np2 = .07$, $BF_{10} = 2.38$) but not condition ($F(1,75) = .04$, $p = .84$, $np2 < .001$, $BF_{10} = .19$), with autistic participants employing slower foreswings than neurotypical individuals ($t(75) = 2.28$, $p = .03$, $BF_{10} = 2.20$). However, the timing of peak velocity was not significantly different between groups ($F(1,75) = 1.79$, $p = .19$, $np2 = .02$, $BF_{10} = .69$), and occurred close to ball contact in both conditions (Table 3.3). Though swing onset times occurred later in volatile trials ($F(1,75) = 4.47$, $p = .04$, $np2 = .06$, $BF_{10} = .74$; Table 3.3), no group differences emerged ($F(1,75) = 1.82$, $p = .18$, $np2 = .02$, $BF_{10} = .76$). Moreover, no significant interactions or correlations were present for these swing onset and peak velocity variables (p's > .23; all $BF_{10} < .50$), except for peak hand velocity, which was inversely related to AQ-26 scores ($R = -.25$, $p = .03$, $BF_{10} = 1.59$). Therefore, autistic participants exhibited slow, novice-like movement kinematics in both task conditions.

Table 3.3. Kinematic Averages (SD) during each Experimental Condition in *Study 3*.

	NT Group		***ASD Group***	
	Stable	*Volatile*	*Stable*	*Volatile*
Swing Onset Time[#]	0.59 (0.10)	0.60 (0.10)	0.55 (0.10)	0.57 (0.08)
Peak Velocity of the Hand*****	10.15 (2.93)	9.96 (3.01)	8.41 (2.79)	8.54 (2.98)
Time of Peak Hand Velocity	-0.04 (0.02)	-0.04 (0.03)	-0.04 (0.02)	-0.04 (0.02)
Max Hand Displacement*****	0.61 (0.06)	0.61 (0.07)	0.55 (0.08)	0.55 (0.07)
Swing Range of Motion***** [#]	83.06 (25.63)	79.94 (27.24)	67.31 (28.01)	65.31 (31.10)

ASD: autism spectrum disorder; NT: neurotypical; *****significantly groups differences ($p < .05$); [#]significant differences between conditions ($p < .05$).

During their foreswing actions, autistic participants kept their hands closer to the body (Maximum Hand Displacement: $F(1,75) = 13.84$, $p < .001$, $np2 = .16$, $BF_{10} = 55.09$) and employed reduced ranges of motion (swing ROM; $F(1,75) = 5.35$, $p = .02$, $np2 =$

.07, BF10 = 1.65) compared to their neurotypical counterparts. For swing ROM, a weak main effect for condition also emerged ($F(1,75) = 4.08$, $p = .047$, $np2 = .05$, $BF_{10} = 1.94$), with average values in both groups reducing between stable and volatile trials ($t(76) = 2.33$, $p = .02$, $BF_{10} = 1.60$). The condition-by-group interaction, however, was non-significant ($F(1,75) = .19$, $p = .66$, $np2 = .003$, $BF_{10} = .37$), with volatility-related changes in swing ROM proving similar between groups. Therefore, autistic participants showed higher, more uncertain-like swing ROM values in *both* stable and volatile conditions (Table 3.3). Relatedly, lower movement degrees of freedom were associated with higher AQ-26 scores across the whole sample, both for maximum hand displacement ($R = -.37$, $p = .001$, $BF_{10} = 27.10$) and swing ROM ($R = -.24$, $p = .03$, $BF_{10} = 1.33$). Nonetheless, changes in swing ROM were highly variable (ΔROM range: -31.17 – 24.08, SD: 10.36°), and there was a lack of condition-related effects for maximum hand displacement ($F(1,75) = .07$, $p = .79$, $np2 = .001$, $BF_{10} = .20$).

3.1.3.3. Gaze Data.

Eye-tracking data from eight participants (ASD: $n = 2$; NT: $n = 6$) were identified as poor quality and were excluded from gaze analyses (remaining $n = 72$). As described previously (Diaz et al., 2013; Mann et al., 2019), participants utilised a prediction-driven gaze strategy (Figure 3.3). Specifically, after pursuing its early-flight trajectory, gaze tended to shift 'predictively' ahead of the ball via large, anticipatory pre-bounce saccades. Gaze then stayed relatively still and focused on a location just above the ball's future bounce position, in what is referred to hereafter as the bounce fixation location. This fixation was generally maintained for ~200 ms (mean: 182.16 ± 63.28 ms) until the ball 'caught up'; when participants would attempt to track the ball onto the racquet through a combination of smooth pursuit and corrective saccades.

Interestingly, these general strategies were favoured by all participants, irrespective of their diagnosis status (Figure 3.3). ANOVAs showed that the timing and amplitude of participants' pre-bounce saccades were not affected by condition or group (p's > .29; all $BF_{10} < 1$; Figure 3.4), nor were they correlated with AQ-26 scores (p's > .24; $BF_{10} < .33$). Moreover, the duration of the subsequent bounce fixation was not significantly affected by volatility, diagnosis status, or levels of autistic-like traits (p's > .06; $BF_{10} < 1.07$). Therefore, anticipatory gaze adjustments were evident in both groups, and these prediction-driven responses proved robust to changing environmental conditions.

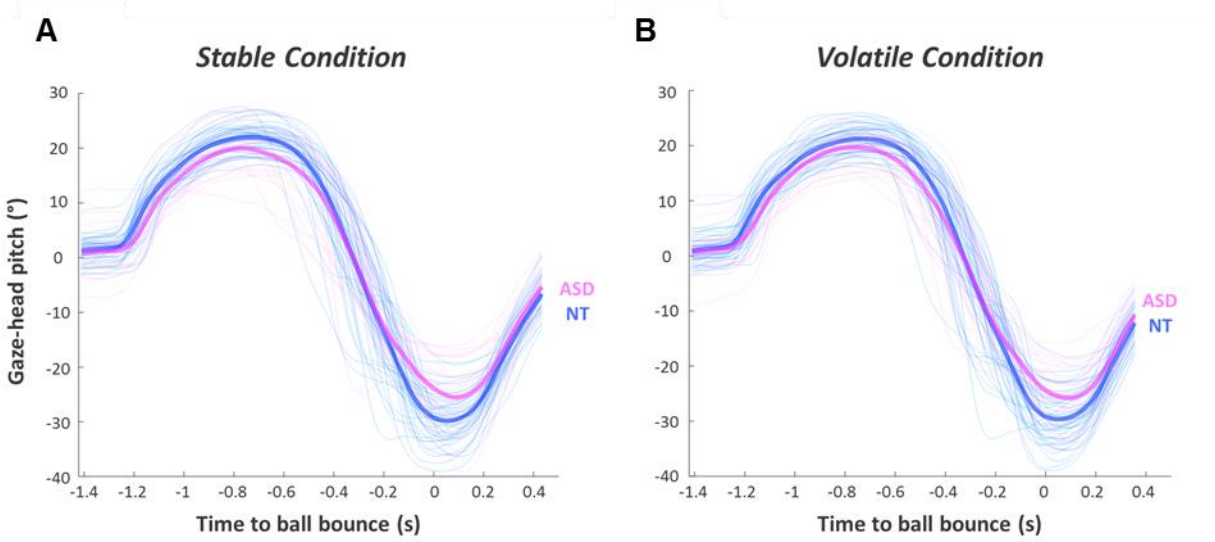

Figure 3.3. Gaze strategies during the virtual racquetball task in *Study 3*. Average pitch of the gaze-in-world vector during stable (**A**) and volatile (**B**) conditions. Pitch represents the vertical angle of a vector which originates from the head at eye-height. Values of zero represent a vector that is parallel to the floor plane, while more positive values indicate that an individual is looking relatively higher in space around the bounce point. Bold lines are group averages, thin lines denote individual cases. NT: neurotypical; ASD: autism spectrum disorder.

Notably, both groups attempted to closely pursue the balls after they had bounced on each trial (Figure 3.3). These tracking behaviours would presumably be impaired if any oculomotor deficits were present. As such, the vertical distance between participant's gaze and the centre of the virtual ball was assessed on a frame-by-frame basis (in angular pitch coordinates), and averaged for the post-bounce portion of each trial. Here, greater deviation values would reflect larger average distances between gaze and ball vectors (i.e., high tracking error; Binaee & Diaz, 2019). However, ANOVA showed no significant main effects (condition: $F(1,70) = .16$, $p = .69$, $np2 = .002$, $BF_{10} = .18$; group: $F(1,70) = 3.63$, $p = .06$, $np2 = .05$, $BF_{10} = 1.36$) or interactions ($F(1,70) = .66$, $p = .42$, $np2 = .01$, $BF_{10} = .43$) for this measure. Moreover, these gaze tracking profiles were unrelated to AQ scores ($R = .19$; $p = .11$; $BF_{10} = .50$). On this basis, it seems unlikely that sensorimotor difficulties were driven by any generic motion tracking deficits or oculomotor impairments in this task (see post-hoc analysis: *Section 3.1.3.3*).

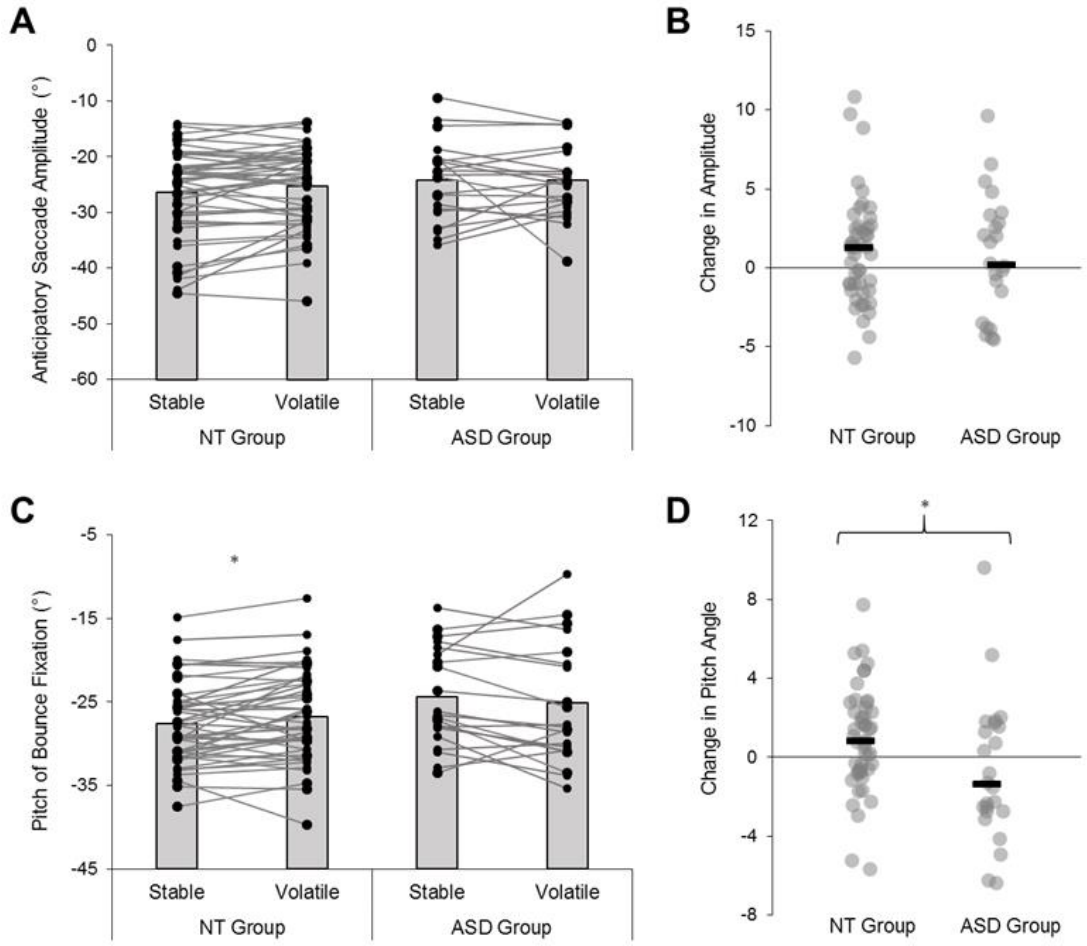

Figure 3.4. The amplitude of anticipatory pre-bounce saccades (**A**) and subsequent gaze fixation locations (**C**) during stable and volatile conditions in *Study 3*. Values represent average angular coordinates of the gaze-in-world vector (°), with between-condition changes illustrated in panels **B** and **D**. NT: neurotypical; ASD: autism spectrum disorder; *denotes statistically significant differences ($p < .05$).

Potential differences in the position of participant's final pre-bounce gaze fixation appeared (see time '0' in Figure 3.3). Typically, people will look higher above the floor when they are expecting more 'bouncy' ball trajectories (Diaz et al., 2013; Mann et al., 2019). Though anecdotal group differences ($BF_{10} = 1.32$) did not reach significance for this metric ($F(1,70) = 3.47$, $p = .07$, $np2 = .05$), there was a significant group-by-condition interaction which required inspection ($F(1,70) = 4.72$, $p = .03$, $np2 = .06$, $BF_{10} = 1.51$). Bounce fixations were higher in autistic than neurotypical participants, but only in stable trials (stable: $t(70) = 2.59$, $p = .01$, $BF_{10} = 4.08$; volatile: $t(70) = 1.12$, $p = .27$,

BF_{10} = 0.44). These context-sensitive effects were caused by volatility-related increases in the neurotypical group ($t(47) = 2.42$, $p = .02$, $BF_{10} = 2.16$; Figure 3.4), who adjusted their fixations under volatile conditions to facilitate the pursuit of bouncier ball trajectories. Autistic participants did not show such between-condition changes ($t(23) = .96$, $p = .35$, $BF_{10} = .32$, Figure 3.4), and instead showed a generally elevated gaze profile around the point of bounce (Figure 3.3). Therefore, as with their swing kinematics (ROM: Table 3.3), autistic participants appeared to display behaviours that are typically affiliated with more uncertain conditions. However, the pitch angle of bounce fixations was unrelated to AQ-26 scores (p's > .13; $BF_{10} < .50$), and the weak anecdotal evidence against the null ($BF_{10} = 1.51$) must be interpreted with caution.

Finally, this study also distinguished gaze tracking responses between expected and unexpected trials. Positional distances between gaze and ball vectors were averaged in the vertical plane for the post-bounce portion of each trial. In this case, analyses focused on probability-matched 'test' trials and subtracted normalised expected values from their unexpected trial equivalents (see *methods*). The resulting UE-E difference scores indexed levels of surprise to unexpected events, with higher scores signalling that participants had tracked expected balls more closely than the salient 'bouncy' ones. Two participants were excluded from this analysis due to missing data on 'test' trials (remaining $n = 70$). Manipulation checks confirmed that UE-E difference scores were significantly greater than zero under stable conditions ($t(69) = 2.61$, $p = .01$, $BF_{10} = 2.98$). So, participants tracked expected balls more closely than unexpected ones for these trials. ANOVAs revealed a significant effect of condition on this measure ($F(1,68) = 6.38$, $p = .01$, np2 = .09, $BF_{10} = 4.37$), with UE-E differences decreasing under volatile conditions ($t(69) = 2.67$, $p = .01$, $BF_{10} = 3.46$). Crucially, there was a significant effect of group on these scores ($F(1,68) = 5.80$, $p = .02$, $np2 = .08$, $BF_{10} = 3.22$). When compared to neurotypical individuals, autistic participants showed generally reduced surprise (i.e., they were tracking unexpectedly bouncy balls with a similar level of accuracy to the more expected ones; Figure 3.5). There were also significant negative relationships between UE-E differences, AQ-26 scores ($R = -.25$, $p = .04$, $BF_{10} = 1.19$) and interception rates ($Rs = .30$, $p = .01$, $BF_{10} = 3.46$). However, no interaction effects emerged for this metric ($F(1,68) = .01$, $p = .92$, $np2 < .001$, $BF_{10} = .27$), illustrating that autistic individuals adapted behaviours typically between conditions.

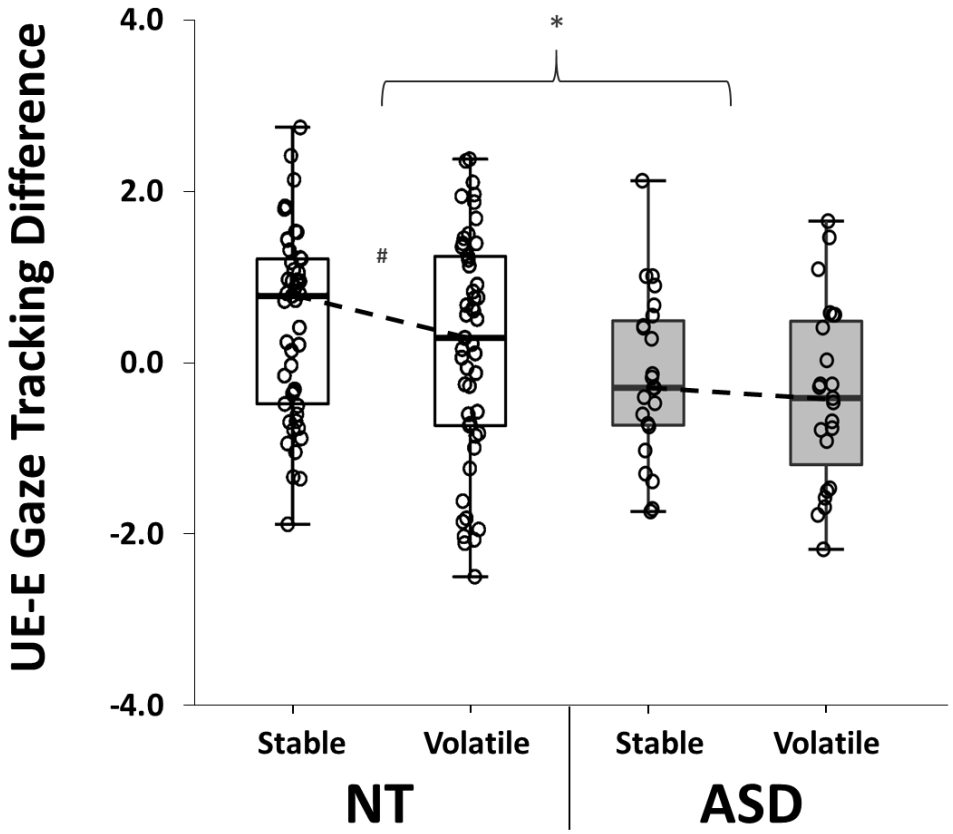

Figure 3.5. Group differences in gaze tracking behaviours between expected (E) and unexpected (UE) test trials in *Study 3*. Higher index values signify more 'prediction-driven' errors in post-bounce gaze pursuit (i.e., greater behavioural surprise when faced with the unexpectedly 'bouncy' balls). NT: neurotypical; ASD: autism spectrum disorder. *denotes significant between-group difference ($p < .05$); #denotes significant change between conditions ($p < .05$).

3.1.3.3. Post-Hoc Analyses of Gaze Tracking Behaviours.

In the results above, it was found that autistic people employ gaze patterns that are typically associated with high-uncertainty conditions. While neurotypical participants tended to pursue expected ball trajectories more closely than unexpected ones, autistic individuals appeared to sample both cues with similar levels of accuracy (Figure 3.5). These differences were not a result of any obvious gaze tracking abnormalities, nor were they accompanied by any alterations in the timing or amplitude of key saccadic eye movements (Figures 3.3 & 3.4). Instead, they likely reflect aberrant surprise responses. However, it is possible that atypical gaze responses stem from underlying

attentional and/or oculomotor impairments that determine one's ability to engage, disengage, and shift attention in coordination with fast-moving sensory cues (Brenner et al., 2007; Johnson et al., 2016). This post-hoc analysis evaluated such a possibility, through a series of exploratory gaze data comparisons.

First, the total number of saccades and fixations were assessed for each trial and averaged for both conditions, before being entered into separate mixed-model ANOVAs. Here, atypically low frequencies might indicate impaired shifting or disengagement of visual attention. Conversely, any inaccuracies in continuous smooth pursuit or goal-directed saccades would likely demand a relatively high frequency of corrective gaze shifts (Hayhoe et al., 2002). Neither of these data patterns emerged, with ANOVAs showing null group (saccades: $F(1,70) = 2.10$, p = .15, $np2 = .03$, $BF_{10} = .83$; fixations: $F(1,70) = .10$, $p = .75$, $np2 = .001$, $BF_{10} = .44$), condition (saccades: $F(1,70) = 1.13$, $p = .29$, $np2 = .02$, $BF_{10} = .37$; fixations: $F(1,70) = .80$, $p = .38$, $np2 = .01$, $BF_{10} = .25$), and interaction effects (saccades: $F(1,70) = .11$, $p = .74$, $np2 = .002$, $BF_{10} = .27$; fixations: $F(1,70) = .10$, $p = .75$, $np2 = .001$, $BF_{10} = .28$). This suggests that autistic and neurotypical participants were shifting their gaze and fixating upon cues at a similar frequency in both conditions.

Next, analysis explored whether autism-related gaze differences simply reflected impaired motion tracking abilities. If this was true, then one would expect particular difficulties to emerge on trials with the greatest ball velocities. As such, the average post-bounce distance (i.e., tracking error) between gaze and ball pitch vectors was extracted from 'bouncy' ball trials *only*. Here, any fundamental motion tracking impairments would result in generally high gaze-ball differences, regardless of whether the high-elasticity ball speeds are expected or uncertain. Bouncy-ball trial values were therefore averaged across both conditions and subsequently compared between groups, using an independent *t*-test. Group differences were not statistically significant in this analysis ($t(70) = .41$, $p = .68$, $BF_{10} = .27$), indicating that autistic and neurotypical participants had similar post-bounce tracking abilities with regards to the fast-moving ball cues (see related results in von Hofsten et al., 2009; Ego et al., 2016).

Overall, this analysis finds little support for the notion that autism-related gaze differences result from broad impairments in attentional and/or oculomotor control. Instead, sensorimotor difficulties are likely related to context-sensitive mechanisms

(e.g., trial-by-trial predictions about ball bounciness, environmental uncertainty, and volatility estimations). Further empirical scrutiny is required, however, before any definitive conclusions can be made.

3.1.3.4. Exploratory Analyses of Gaze Variability.

Autistic participants predictively positioned their gaze at a higher location than neurotypical individuals when the virtual balls were bouncing (Figure 3.3). Such data patterns may be consistent with proposals that autistic people overestimate environmental volatility: agents who perceive that the world is more changeable will increasingly update their long-term predictive models according to recent (high-elasticity) sensory information. Computationally, this would reflect an increase in learning rate (Behrens et al., 2007; Mathys et al., 2011; 2014), though such conclusions require further scrutiny (see discussion).

To initiate this enquiry, this analysis explored the *variability* of participants' gaze fixation behaviours. Specifically, it looked at the standard deviation of bounce fixation locations (pitch angles) shown during each condition. If participant's visual sampling behaviours were being heavily driven by long-term prior expectations, then this trial-by-trial variability should be relatively low. On the other hand, larger standard deviations would indicate that gaze fixations are being strongly influenced by recent sensory data (i.e., highly changeable ball elasticity profiles from preceding trials).

Mixed-model ANOVAs revealed a significant main effect of condition for these standard deviation values ($F(1,70) = 5.63$, $p = .02$, np2 = .07, $BF_{10} = 3.03$). Participants increased pitch variability between stable and volatile conditions (Figure 3.6), as indicative of an increased updating of prior models (i.e., a higher learning rate). While no significant interaction effects emerged for this metric ($F(1,70) < .001$, $p = .99$, $np2 < .001$, $BF_{10} = .27$), the ASD group displayed generally higher trial-to-trial variability than their neurotypical counterparts ($F(1,70) = 38.47$, $p < .001$, $np2 = .36$, $BF_{10} = 3.11*10^5$). This tendency to increasingly update bounce fixation locations is in line with proposals that autistic people are over-reactive to environmental change, and reinforces the potential role of aberrant precision weighting in autism (Lawson et al., 2017). Research may wish to explore this topic further, by using sophisticated computational models of gaze fixation behaviours to study how volatility-based learning parameters change over time.

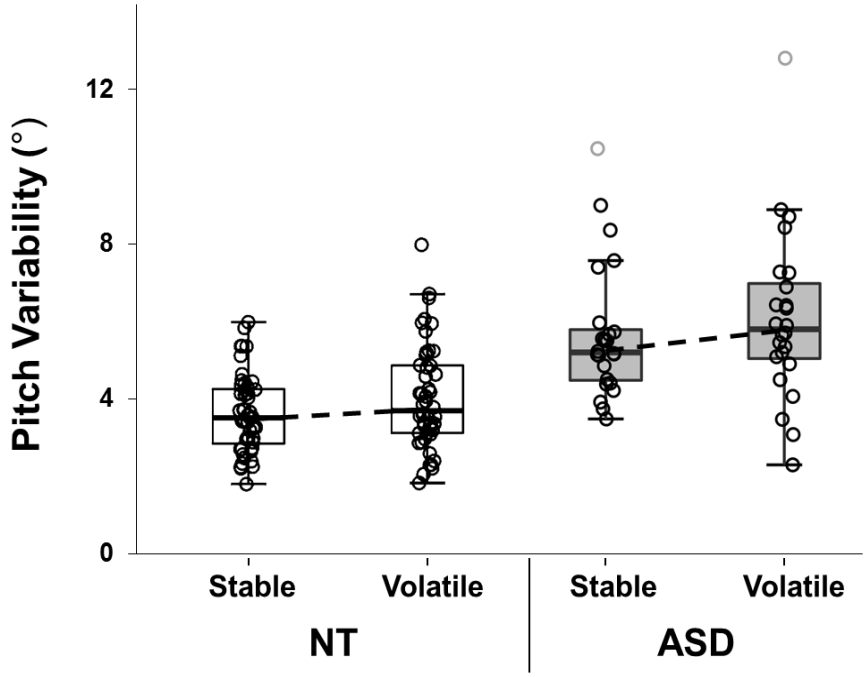

Figure 3.6. Trial-by-trial standard deviation values corresponding to the spatial location (pitch angle) of bounce gaze fixations for each condition in *Study 3*. NT: neurotypical; ASD: autism spectrum disorder. Two extreme values were identified and are represented as light grey circles (removal of these cases does not affected the overall pattern of results).

3.1.4. Discussion

This study examined how sensorimotor control is dynamically adjusted in autism, using a novel and immersive VR paradigm which systematically varied environmental volatility. Here, the frequency with which participants successfully intercepted a virtual bouncing ball was significantly lower in autistic individuals (Figure 3.2), confirming basic impairments in motor skill execution (Green et al., 2002; Vanvuchelen et al., 2007; Whyatt & Craig, 2013a; Ament et al., 2015; Chen et al., 2019). Such performance difficulties were accompanied by atypical swing kinematics (Table 3.3), gaze fixation patterns (Figure 3.3), and levels of behavioural surprise (Figure 3.5). Results support active inference formulations of predictive processing (Palmer et al., 2017), and suggest that the dynamic regulation of sensory sampling and motor control behaviours is fundamentally different in autistic people.

In accordance with predictive processing theories of autism (e.g., Lawson et al., 2014; Van de Cruys et al., 2014), difficulties in sensorimotor performance were more pronounced under volatile conditions (Figure 3.2). Such results align with findings from more constrained prediction-based tasks (e.g., statistical learning and sensorimotor illusion paradigms: Palmer, Paton, et al., 2015; Robic et al., 2015), where autism-related atypicalities emerge under uncertain or unstable probabilistic conditions (see recent review: Cannon et al., 2021). Furthermore, the observed differences in this task appeared specific to autism, and were not a result of any confounding clinically-diagnosed conditions (e.g., identified co-occurring motor disorders). Therefore, this novel, systematic assessment of sensorimotor control extends our computational understanding of autism into more dynamic and unconstrained environments, where optimal behaviours rest on hierarchical, iterative predictive processing.

Autistic participants employed arm swing actions that were lower in peak velocity, closer to the body, and more restricted in ROM (Table 3.3). These profiles are indicative of more novice-like swing mechanics, as actions are typically slower and have reduced degrees of freedom in the early stages of learning (Bernstein, 1967; Reid et al., 2013; H. A. Palmer et al., 2018). Autism-related sensorimotor difficulties may thus reside at the kinematic level (Cook et al., 2013; Torres et al., 2013; Campione et al., 2016; Torres & Denisova, 2016; Chen et al., 2019; Foster et al., 2019). Indeed, atypical peak hand velocities have been consistently reported in clinical visuomotor research (Glazebrook et al., 2009; Cook et al., 2013; Takamuku et al., 2021) and could result from various central and/or peripheral factors, including aberrant predictive action modelling (Cook et al., 2013). However, contrary to the initial hypotheses (and previous work: Glazebrook et al., 2006; Whyatt & Craig, 2013a), kinematic group differences were not significant for any of the movement initiation metrics (Table 3.3). Therefore, when examined in isolation, it is unclear whether these atypical movement kinematics in autism reflect specific differences in predictive processing, or more general impairments in sensorimotor development.

Accordingly, this study next sought to explore the precise mechanisms that drive autistic motor differences. Notably, participants' gaze kinetics were remarkably robust to the highly-changeable probabilistic conditions (Figure 3.3), which reinforces suggestions that a prediction-driven visual sampling strategy is optimal for dealing with dynamic and uncertain cues for this type of task (Diaz et al., 2013; Binaee & Diaz,

2019). The present data shows that autistic individuals also employed this top-down strategy (Figure 3.3) and that they shifted their visual attention and tracked approaching balls similarly to neurotypical individuals. These findings undermine proposals of broad attentional differences (Ozonoff et al., 1991; Happé & Frith, 2006) and/or generic attenuations in the use of prior knowledge (Pellicano & Burr, 2012). Moreover, null group differences were observed in relation to participants' anticipatory pre-bounce saccades, despite these eye movements being directly related to previous trial trajectories and task constraints (Diaz et al., 2013; Cesqui et al., 2015; Mann et al., 2019). Consequently, these results join varied evidence against simple Bayesian theories of autism, and support conclusions that predictive processing abilities are not generically impaired in sensorimotor tasks (Gidley-Larson et al., 2008; Ego et al., 2016; Tewolde et al., 2018; Cannon et al., 2021; see also *Studies 1 & 2*).

Recent research suggests that sensorimotor difficulties in autism may instead stem from context-sensitive mechanisms relating to hierarchical precision modulation and volatility processing (Lawson et al., 2014; 2017; Palmer et al., 2017). In this study, participants displayed subtle adjustments in visual sampling behaviour that were qualitatively consistent with optimal active inference. Specifically, when conditions were more uncertain, individuals appeared to rely less on prior information and more on exploratory attentional cues (Beesley et al., 2015; Walker et al., 2019). This was illustrated in participants' gaze data, where tendencies to track expected balls more closely than unexpected ones were reduced under volatile conditions (Figure 3.5). Participants also adjusted their fixations more variably in these trials (Figure 3.6). Together, such context-sensitive patterns of data match results from psychophysics experiments, where unexpected cues are processed more rapidly under uncertain conditions (e.g., Vossel et al., 2014). The changes observed here reflect volatility-related modulation of precision and learning rate, which increases an individual's responsivity to salient events (Behrens et al., 2007).

Strikingly, the current dataset shows consistent autism-related atypicalities in this context-sensitive modulation of sensorimotor control. Indeed, autistic participants showed differences in swing ROM (Table 3.3), bounce fixation location (**F**igure 3.4 & 3.6), and behavioural surprise (Figure 3.5); metrics which all appeared sensitive to volatility conditions. For each of these measures, the ASD group demonstrated behaviours that are typically associated with high environmental instability. For

instance, differences in gaze tracking between expected and unexpected 'test' trials were significantly reduced (Figure 3.5), indicating dampened surprise to unexpected events (as in recent neurological and behavioural evidence: e.g., Nazarali et al., 2009; Lawson et al., 2017; Goris et al., 2018). Similarly, while neurotypical participants reduced swing ROM during volatile conditions only, autistic participants exhibited low ROM scores across *both* conditions (Table 3.3). These atypical movement profiles can be explained by an increased tendency to 'expect the unexpected' in autism (Lawson et al., 2017), as a greater fixing of joint angles may serve as an active attempt at reducing uncertainty (i.e., through reducing signal-dependent motor noise; O'Sullivan et al., 2009). Therefore, this study supports proposals that autistic people tend to interact with the world like it is highly unstable or uncertain (Lawson et al., 2017).

Atypical volatility processing can explain difficulties with various activities of daily living in autism (Palmer et al., 2017). Participants who showed poorer task performance and higher autistic-like traits in this study tended to sample the world in a more uncertain-like manner. This is unsurprising, as the majority of balls bounced in an 'expected' way, so it would be suboptimal to sample cues as if they are unrelated to long-term prior experience. However, fixation data cautiously suggest that autistic participants predictively positioned their gaze at a higher, more variable location than their neurotypical counterparts (Figures 3.3-3.6), in a manner that benefits the sampling of recent high-elasticity ball trajectories (Diaz et al., 2013). Though it is currently unclear whether these differences resulted from atypical learning rates or compensatory, non-linear adaptations in gaze behaviour (e.g., 'centering' strategies: Heinen et al., 2005), these results reinforce the notion that autistic participants were overestimating volatility, or 'expecting the unexpected', during the task (Lawson et al., 2017).

Nevertheless, the exact source of aberrant uncertainty expectations and volatility modulation in autism remains to be explored (Lawson et al., 2014; Palmer et al., 2017). Contrary to the initial hypotheses, autistic and neurotypical groups appeared to comparably adjust visual sampling and motor kinematics according to environmental (in)stability. These null effects are notable, as recent computational models posit that autistic people are hypersensitive to environmental change, potentially due to dysfunctions in neural excitation and/or modulation (Lawson et al., 2014; Quattrocki & Friston, 2014; Rosenberg et al., 2015; Lawson et al., 2017). Though conflicting with these proposals, such findings align with reinforcement learning data (Manning et al.,

2017), which suggest that atypicalities may be consigned to higher-level processing functions (see also: C. J. Palmer et al., 2018). This study was unlikely to implicate such mechanisms, with visual motion cues about ball-flight dynamics likely occurring in lower hierarchical levels. It is also possible, however, that the autistic group data do not highlight atypicalities in volatility processing at all, but rather a broad, psycho-behavioural intolerance of uncertainty. Indeed, behavioural inflexibility and an insistence on sameness are well-defined autistic-like traits that correlate with motor difficulties (MacDonald et al., 2013). While these traits have been conceptually linked to predictive processing atypicalities (Lawson et al., 2014; Van de Cruys et al., 2014), statistical associations do not consistently materialise (e.g., Tewolde et al., 2018). Therefore, research must establish whether sensorimotor difficulties reflect abnormalities in neuromodulation (e.g., in noradrenergic responsivity, divisive normalisation) or secondary consequences of cognitive and behavioural traits.

A number of study limitations must also be considered. For example, this study did not directly assess participants' cognitive or visual abilities, nor were there any checks performed for undiagnosed motor conditions. Such variables could have influenced observed data, with autistic populations showing higher incidence rates of cognitive impairment, optometric issues (e.g., strabismus; Simmons et al., 2009) and neurodevelopmental disorders (Simonoff et al., 2008; Landry & Chouinard, 2016). Though participants were excluded if they reported co-occurring medical conditions, many of these issues can remain undetected. Levels of experience in racquet-based activities were also unclear and may generally be lower in clinical groups (see Scharoun et al., 2017). However, correlational analysis did examine relationships between sensorimotor control and levels of autistic-like traits across a large general population (i.e., the broader autism phenotype). Most participants in this analysis were neurotypical (68%), which reduces the influence of autism-related confounds (Landry & Chouinard, 2016). Notably, all but one of the between-group effects that were identified in the results section were accompanied by significant AQ correlations. These trait-based effects clearly reinforce the study's main findings, though future research could explore additional co-variables in their analyses (e.g., IQ subscale scores, clinical questionnaires, standardised motor assessments).

Additionally, impoverished depth cues and haptic feedback in VR tasks could influence action control and uncertainty expectations (Bingham et al., 2001; Harris et al., 2019),

thus limiting their generalisability to ‘real-world’ behaviour. Although this argument is, in itself, uncertain at present (Harris et al., 2019), and the use of VR affords unique methodological benefits, future studies may wish to manipulate probabilistic conditions in ‘real-world’ tasks. To do this, one may wish to select a task that is more sensitive to prior expectations. Indeed, though gaze strategies are evidently driven by prediction in the current protocol (Binaee & Diaz, 2019), time-pressed interceptive actions still rely heavily on incoming visual information (Zago et al., 2009; Diaz et al., 2013). Therefore, the addition of prior contextual cues should be considered, such as probabilistic sensory signals (e.g., predictive auditory tones: Lawson et al., 2017; kinematic cues from an opponent: Helm et al., 2020), or explicit prior information (Gray, 2015; Gredin et al., 2018). These contextual cues should not only enable research into more predictive control strategies, but they could also form the basis of future sensorimotor interventions (see ‘Moneyball Approach’ in sport: Gray, 2015).

3.1.5. Conclusions

In conclusion, autistic people tend to struggle with performing an interceptive motor skill when sensory cues are unpredictably changeable over time. These performance difficulties are underpinned by fundamental differences in predictive processing and active inference. Specifically, atypical sensory sampling behaviours and movement kinematics appear driven by aberrant precision modulation and volatility processing mechanisms. Although these results shed significant light on the potential origins of sensorimotor issues in autism, the exact source of these computational differences remains unclear. Moving forward, research should specifically examine whether impaired active inference behaviours relate to suboptimal neuromodulatory control and/or beliefs about environmental uncertainty. This would not only improve our scientific understanding of autism, but would also provide a theoretical basis for prospective interventions. Indeed, the degree to which autistic individuals benefit from targeted practical approaches will depend on how sensitive these precision-related processing atypicalities are to certain external factors (e.g., explicit contextual cues or individualised environmental modifications). By pursuing this line of enquiry in unconstrained and naturalistic daily living tasks, investigations could help develop new evidence-based interventions that help autistic people overcome sensorimotor difficulties and improve functional quality of life.

Chapter 4

This final experimental chapter begins to explore prospective approaches for reducing sensorimotor difficulties in autism. The preceding studies found that autistic people show context-sensitive differences in predictive action control, with Chapter 3 specifically highlighting a link between impaired hand-eye coordination abilities and suboptimal volatility modulation. These results implicate the role of aberrant precision weighting functions and support hypotheses that autistic people overestimate levels of uncertainty and/or instability in sensory environments (Lawson et al., 2017). However, the precise causes of these processing atypicalities remain unclear, and research must establish the practical means through which these functions can be augmented or optimised. Accordingly, this chapter examines whether explicit informational cues about environmental volatility can enhance sensorimotor control in autistic people. It is hoped that the novel study findings will assist the development of specialist evidence-based interventions that can be applied into future practice.

4.1. Study 4: Investigating the effects of explicit contextual cues on predictive sensorimotor control in autistic adults.

4.1.1. Introduction

Autistic people can face a range of daily living difficulties which impact on levels of independence, wellbeing, and quality of life (Ikeda et al., 2014; Croen et al., 2015; Van Heijst & Geurts, 2015). Some of these outcomes are linked to impaired sensorimotor control, with autistic people often experiencing clumsiness, sensory disturbances, and issues with eye-hand coordination (Fournier et al., 2010; Gowen & Hamilton, 2013; Coll et al., 2020). Indeed, motor skill abilities are predictive of personal independence (Jasmin et al., 2009), physical health (McCoy et al., 2016), and long-term socio-behavioural development (Sutera et al., 2007; MacDonald et al., 2013). However, current sensorimotor interventions show mixed results. On one hand, positive study outcomes are usually reported (e.g., DeBolt et al., 2010; Duronjić & Válková, 2010; Bremer et al., 2015; Bremer & Lloyd, 2016; Ketcheson et al., 2017), with particular benefits emerging from programmes that implement direct and individualised teaching instructions. On the other, these studies often provide minimal insight beyond the generic benefits of engaging in physical activity (Colombo-Dougovito & Block, 2019).

Consequently, there is an absence of evidence-based programmes that are proven to effectively tackle autism-related sensorimotor issues and their underlying causes.

Despite this lack of investigation, research has highlighted key mechanisms that could be targeted in future interventions. Studies suggest that sensorimotor impairments may reside in the planning or anticipatory stages of action (Hughes, 1996; Schmitz et al., 2003; Fabbri-Destro et al., 2009; Z. Wang et al., 2015; Cannon et al., 2021). More specifically, autistic individuals show clear differences in how action predictions are dynamically adjusted according to contextual uncertainty and volatility (Palmer, Paton, et al., 2015; *Study 2-3*). A recent study by Lawson *et al.* (2017) found that autistic people overestimate levels of instability in their surrounding environment when faced with unpredictably-changeable task conditions. Such findings were supported by *Study 3*, which highlighted a tendency in autism to interact with dynamic sensory cues as if they are highly uncertain or volatile. As a result, autistic individuals can be over-reactive to salient sensory cues and have difficulties forming stable representations about the world (Lawson et al., 2017, see also Palmer et al., 2017).

From a predictive processing perspective, the above findings allude to aberrant precision weighting functions (i.e., processes which modulate prior beliefs and sensory evidence according to estimates of their reliability; Palmer et al., 2017). Higher-level beliefs about environmental stability are said to regulate the weighting of top-down predictions via precision-weighted cortical gain, as facilitated by neuromodulators such as acetylcholine and phasic noradrenaline (Yu & Dayan, 2003; Friston, 2008). Under more volatile conditions, agents will increasingly rely on sensory information obtained from recent experience, in a manner that facilitates context-sensitive predictions and learning (Behrens et al., 2007). However, these computational functions appear to be suboptimal in autism (e.g., Lawson et al., 2014; Van de Cruys et al., 2014). Indeed, though autistic individuals are able to learn implicit cue-outcome relationships and adapt their behaviour according to perceived volatility (Manning et al., 2017; Sapey-Triomphe et al., 2021), such high-level representations are over-reactive to environmental change and aberrant sensory events (as shown in Lawson et al., 2017 and *Study 3*). However, the mechanisms that cause these processing atypicalities remain unclear and require further investigation.

One possibility is that autistic people have difficulties with extracting the ambiguous contextual relationships that underpin complex sensorimotor interactions (Qian & Lipkin, 2011; Van de Cruys et al., 2014). Indeed, the dynamic integration of sensory signals across the brain is shaped by higher-level beliefs about whether the world is changing (Yon & Frith, 2021). As such, precision estimates are determined by a person's ability to detect implicit statistical regularities that exist within surrounding task environments. From a practical perspective, this suggests that daily living skills could be enhanced through the provision of explicit, *statistically-accurate* information about dynamic situational probabilities. Indeed, the notion of making uncertain conditions 'more understandable' is commonly advocated in the field (Haker et al., 2016) and studies show that autistic people can be explicitly cued or primed to process context in social cognition and perceptual discrimination tasks (Plaisted et al., 1999; López et al., 2004; Balconi et al., 2012; Vermeulen, 2015; Gowen et al., 2020; Cannon et al., 2021).

An alternative possibility is that predictive sensorimotor difficulties in autism are underpinned by aberrant neuromodulatory control (Lawson et al., 2014; Quattrocki & Friston, 2014; Van de Cruys et al., 2014). Volatility processing requires error signals to be integrated across various hierarchical networks, based on implicit models of the world (Friston et al., 2013; Yon & Frith, 2021). Such processing depends on an array of factors that may be affected in autism, including: phasic noradrenergic activity (Yu & Dayan, 2003; Lawson et al., 2021), dopamine-serotonin interactions (Friston, Samothrakis, et al., 2012), and signalling in the ACC and cerebellum (Behrens et al., 2007; den Ouden et al., 2010; Palacios et al., 2021). Differences in these systems could lead to pathological neural gain and disproportionate receptiveness to sensory inputs (see Lawson et al., 2014). The provision of explicit contextual cues would be unlikely to outweigh these proposed signalling effects, with some prediction-related atypicalities appearing to persist even after individuals have been told about likely trial events (Thillay et al., 2016; Balsters et al., 2017; Greene et al., 2019; Cannon et al., 2021). However, research has also shown that autistic motor programming (Nazarali et al., 2009) and anticipatory gaze responses (Aitkin et al., 2013) are unimpaired in tasks that contain prior visual cues about upcoming movement trajectories. Consequently, it is unclear whether sensorimotor abilities are limited by difficulties in *extracting* ambiguous cue-outcome relationships from the world or differences in *modulating* actions according to these underlying environmental contingencies.

Likewise, sensorimotor differences may relate to a chronic intolerance of uncertainty that is already documented in clinical research (Boulter et al., 2014; Vasa et al., 2018). Individuals with greater intolerance of uncertainty often experience adverse emotional reactions to unpredictable stimuli (Dugas et al., 1997). Though mechanistically distinct from hierarchical precision estimates (see Bervoets et al., 2021), recent data suggest that associated increases in anxiety could impair key predictive processing functions (e.g. volatility-related learning rate modulation, Lawson et al., 2021). Furthermore, sensory issues in autism correlate with apprehension about environmental change (Wigham et al., 2015; Pickard et al., 2020). Therefore, the degree to which autistic people benefit from explicit probabilistic information could also depend on trait differences in behavioural inflexibility and/or intolerance of uncertainty.

This study examined the effects of explicit probabilistic cues on autistic sensorimotor control, using an adapted version of the virtual racquetball task from *Chapter 3*. As before, participants used a handheld controller to intercept balls that had either normal or unexpectedly-high levels of bounciness, and the likelihood of facing each outcome was varied irregularly over time. However, participants in this study were provided with advanced information about the probability of facing a normal or bouncy ball and were explicitly cued as to when these contingencies had changed. Research has shown that neurotypical individuals significantly benefit from this type of information during predictive action-based tasks (e.g., Navia et al., 2013; Gray, 2015; Gredin et al., 2018). For instance, football goalkeepers display enhanced performance when provided with advanced information about an opponent's most likely shooting direction (Navia et al., 2013). Although this type of intervention has not yet been tested in clinical populations, adaptive effects have been observed in autistic visual processing and motor imitation abilities when participants are explicitly cued to focus on goal-relevant contextual stimuli (López et al., 2004; Fulceri et al., 2018; Gowen et al., 2020; Soroor et al., 2021). As such, it was hypothesised that autistic people would show significant improvements in interceptive motor performance under cued (versus non-cued) conditions.

Importantly, when a ball is about to bounce in the current task, participants will direct their gaze away from its existing location towards its expected future position (see *Chapter 3*). Gaze then remains steady until the ball 'catches up', in what is referred to as the *predictive bounce fixation*. Importantly, these unique visuomotor behaviours are programmed according to dynamic predictions about ball bounciness (see Mann,

2019). So, when ball elasticity unexpectedly rises and fluctuates erratically over time, participants tend to increase the height and variability of their predictive bounce fixations, while reducing range of motion in their swing (Arthur & Harris, 2021). *Study 3* illustrated that such changes exist in both autistic and non-autistic people, but that autistic people show higher, more variable fixations and reduced behavioural surprise to unexpected events. These profiles signal a tendency to prepare for salient and/or recently observed ball trajectories which seems to coincide with restricted swing kinematics and impaired interception performances under volatile conditions. These effects were hypothesised to replicate within non-cued trials in this study. However, the explicit cue trials conveyed statistically-optimal prior information about dynamic environmental probabilities, in a manner that reduces contextual uncertainty. As such, these conditions were expected to facilitate relatively higher swing ROM and lower predictive bounce fixations in autistic participants, when compared to non-cued values.

4.1.2. Methods

4.1.2.1. Participants

A total of 44 participants took part in the study (30 male, 14 female, 40 right-handed, mean age: 29 ± 7 years). 22 individuals had a formal diagnosis of ASD, as provided by an expert clinician according to DSM-IV (American Psychiatric Association, 2013) or ICD-10 (World Health Organisation, 2012) criteria, while the remaining sample were age- and gender-matched neurotypical controls. Though analysis was primarily interested in assessing cue-related changes in the ASD group, these individuals could help elucidate any autism-related atypicalities shown between conditions. Power calculations indicated that this sample size would be sufficient to detect any moderate statistical effects in the regard (see *Appendix A4*), as estimated based on previous data in *Study 3* and findings presented by Lawson *et al.* (2017).

Participants did not report any history of musculoskeletal or neurological disorders and were naïve to study aims. They also had no prior experience of playing VR-based racquet sports. All individuals in the ASD group scored above the clinical ‘screening cut-off’ of 26 on the 50-item Autistic Quotient (AQ; Baron-Cohen et al., 2001), with levels of autistic-like traits proving highly consistent with previous clinical values (mean score: 35.57 ± 5.43; for normative data, see AQ; Baron-Cohen et al., 2001; Woodbury-

Smith et al., 2005). Informed consent was obtained ahead of all study procedures, in accordance with British Psychological Society guidelines. The study received approval from the School of Sport and Health Sciences Ethics Committee (University of Exeter, UK) and the Department of Psychology Ethics Committee (University of Bath, UK).

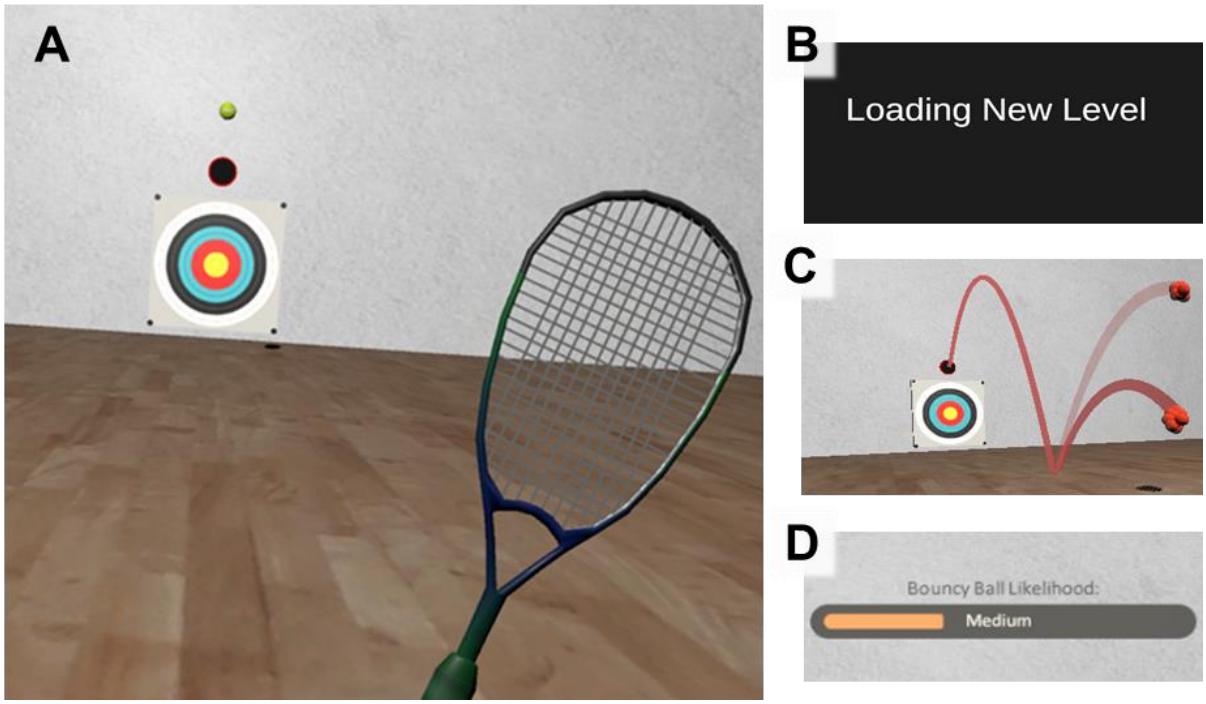

Figure 4.1. The Virtual Racquetball task in *Study 4*. Participants were required to intercept balls that bounced with either normal or unexpectedly-high levels of elasticity. Gameplay footage of the virtual racquet, ball, and target is illustrated in panel **A**. During control trials, participants received no explicit information about levels of ball bounciness and changing task conditions. However, three additional pieces of information were provided ahead of cued trials. Firstly, changes in task conditions were signalled using 'game level' transitions (**B**), which notified participants that they were about to enter a new environmental context. The proportion of normal and bouncy balls in each level were then projected in space using visual 'hawkeye' cues (**C**). A simulated 'bounceometer' on the front wall (shown in **D**) also confirmed whether a bouncy ball was 'low', 'medium', or 'high' in likelihood ahead of each trial. Together, these cues explicitly informed participants about dynamic task probabilities and environmental volatility. Supplementary Videos of the protocol can be found at: https://osf.io/5y48g/.

4.1.2.2. Apparatus and Stimuli

The virtual racquetball environment was developed on the gaming engine Unity (Unity Technologies, San Francisco, CA) and is described in Chapter 3. It was presented to participants on an HTC VivePro head-mounted display at 120 Hz (HTC Inc., Taoyuan City, Taiwan). This consumer-grade, high-precision VR system comprises two 'lighthouse' base stations, which record movements of the headset and hand controller at 90 Hz. The headset also contains an inbuilt eye-tracking system, which monitors user's gaze at 120 Hz with a spatial accuracy of 0.5-1.1. Participants were presented with a simulated 15 x 15 m racquetball court, which contained a circular target on its front wall (Figure 4.1A). They were required to position themselves 9 m behind this location before attempting to hit virtual balls towards the middle of the target using a VR hand controller. This controller was displayed as a 0.6 x 0.3 x 0.01 m virtual racquet, and the balls resembled the appearance and size of those in 'real-world' tennis (Figure 4.1A). All balls were launched from a height of 2m, following three auditory tones, and would bounce 3.5m in front of participant's prescribed starting position. Their trajectory passed through the midline of the room, which was 0.75 m to the right (for right-handers) or left (for left-handers) of this predetermined starting position.

For this study, the virtual environment was further adapted for the *cued* experimental condition. In these trials, participants would transition between six game 'levels', which provided explicit information about ball bounciness and environmental probabilities (Figure 4.1). Level changes were signalled by an auditory tone and brief 'loading screen' (see Supplementary Video at: https://osf.io/5y48g/). Following this transition, participants would be transported into a new virtual room, to signal that their surrounding environment had changed. The front wall was visually identical for all levels, as were any ball bounciness- or goal-related action cues (e.g., the ball, floor, target and racquet). However, to emphasise that the underlying contextual probabilities had changed with each level transition, participants were presented with visual 'hawkeye' cues immediately after the loading screen (Figure 4.1C). These illustrations projected the upcoming trajectory and ratio of normal and bouncy balls in each game level. Such 'hawkeye' cues were presented for 10 seconds and accurately represented the probabilistic 'ground truth' of a given level. They were accompanied by a visual indicator (referred to as the 'bounceometer'), which explicitly stated whether the likelihood of getting a bouncy ball was low, medium, or high (Figure 4.1D). Although

this probabilistic information only reflected the statistical structure of a given *level* (i.e., they were not varied on trial-by-trial basis), they were presented for 3 s ahead of each *trial* in the cued condition. Together, these explicit contextual cues directly conveyed to participants that the underlying ball bounciness probabilities had changed in the volatile task environment. Such advanced information was not available in the practice or control conditions, nor in the final nine trials (i.e., game level) of the cued block.

Participants also completed the 50-item AQ (Baron-Cohen et al., 2001) and the Intolerance of Uncertainty Scale–shortened version (IUS-S; Carleton et al., 2007; see *Appendix G*). The AQ indexed five key autistic-like traits, namely: communication, imagination, social skills, attention switching, and attention to detail. Each subscale was scored out of ten and combined into an overall total (possible range: 0-50). The IUS-S is a 12-item questionnaire measuring intolerance of uncertainty, defined as "the tendency of an individual to consider the possibility of a negative event occurring unacceptable, irrespective of the probability of occurrence" (Carleton et al., 2007). Itemised statements are rated from 1 (not at all characteristic of me) to 5 (entirely characteristic of me) and then combined into a total out of 60. Higher scores reflect greater intolerance of uncertainty, as is commonly reported in autistic populations (Boulter et al., 2014; Wigham et al., 2015; Vasa et al., 2018; Pickard et al., 2020).

4.1.2.3. Procedures

After providing written informed consent, participants were fitted with the head-mounted display and familiarised with the virtual environment. At this stage, the eye-tracker was calibrated over five gaze locations using the manufacturer's built-in routine. Calibration was repeated before each experimental condition and upon any obvious displacement of the VR headset. Once familiarised with the virtual environment, participants then completed thirty baseline racquetball trials. Throughout this initial block, all virtual balls followed the same pre- and post-bounce trajectory, which were consistent with the effects of gravity (-9.8 m/s^2). Their speed remained fixed at -9 m/s in the vertical plane (at the time of bounce), and elasticity was set at standard tennis ball levels (65%).

Participants were instructed to hit balls towards the centre of the target, but that they would not be able to see or feel where they go after hitting them. This lack of feedback was used in all experimental trials to minimise confounding effects relating to

motivation, communication skills, and task reward/error. Instead, a neutral ‘pop’ sound signalled when balls had made contact with the racquet, and any subsequent auditory and visual ball information was removed after this event.

Following the initial baseline trials, participants performed two counterbalanced experimental conditions. In both of these blocks, ball bounciness was systematically varied over time to create unstable trial order sequences (illustrated in Figure 4.2). While two-thirds of trials would contain ‘normal’ balls that were the same as those faced at baseline (and in real-world environments), a third contained ‘bouncy’ balls with unexpectedly high levels of elasticity (85%). This discernible change in post-bounce ball trajectory occurred without participant’s knowledge and would likely deviate away from any prior experiences obtained during ‘real-world’ actions (see Chapter 3). The *pre-bounce* ball speeds and trajectories were always the same as in baseline, meaning that the different type of balls were impossible to tell apart until they had made contact with the floor. Importantly, the probability of facing a normal ball changed every 6, 9 or 12 trials (between 83%, 67% and 50% likely). These unpredictably changeable post-bounce ball trajectories created a volatile environment, in which autistic people displayed impaired interceptive performances in *Study 3*.

Participants were randomly allocated one of three possible trial order sequences (available at https://osf.io/5y48g/) which would be presented to them in both experimental conditions. For the *control* block, individuals did not receive any probabilistic information about likely ball bounciness and trials were presented as one continuous sequence (Figure 4.2A). Instead, they were simply told that some balls may be more bouncy than others and that they should aim to hit as many of them as possible to the middle of the target.

Conversely, explicit information about situational probabilities were provided in the *cued* block. Here, visual cues indicated to participants both when ball bounciness probabilities were switching and how likely they were to face a ‘normal’ or ‘bouncy’ ball at any given time (see Figure 4.2B). This direct provision of contextual priors has been proven to enhance visuomotor control in various neurotypical performance domains (e.g., Navia et al., 2013; Gray, 2015; Gredin et al., 2018). Participants were told that these visual cues would help show them where the balls are going to go and how likely

they are to get a bouncy ball during each game level. They were not informed that the trial order sequences would be exactly the same in each experimental block.

The laboratory protocol generally lasted ~30 minutes in total. The two experimental conditions contained 45 trials each and were separated by a short break. The final 9 trials of each block contained identical visual information (i.e., no 'hawkeye' or 'bounceometer' cues) and thus provided a set of order-matched 'catch' trials for further examination (see Figure 4.2).

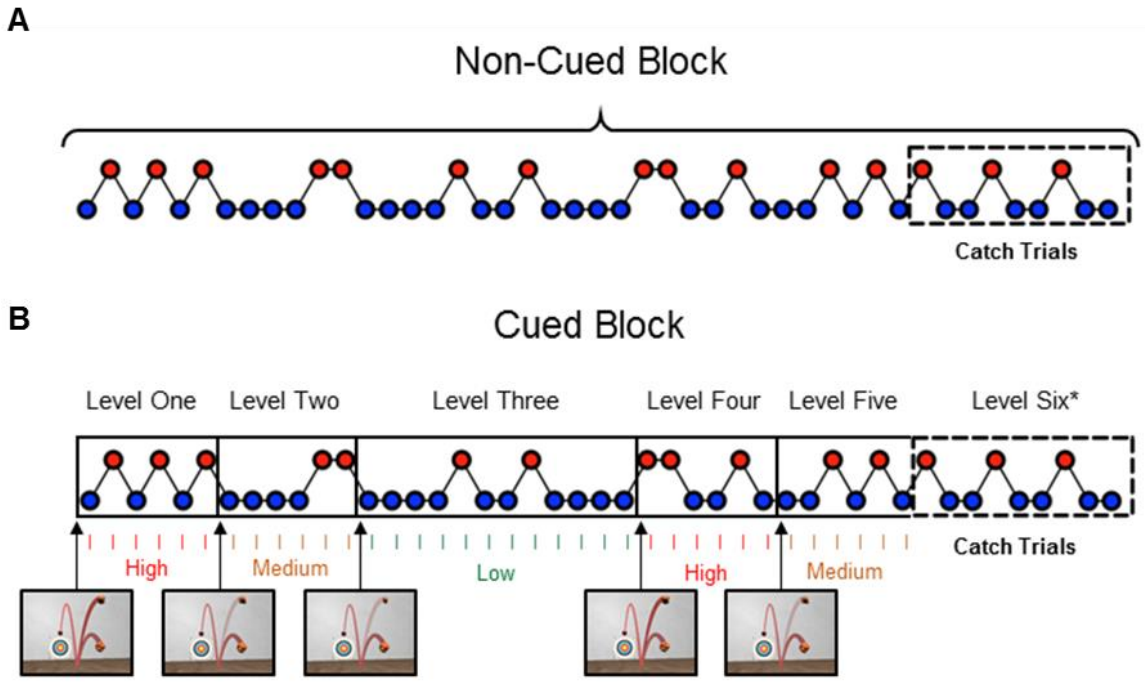

Figure 4.2. Schematic Illustration of the Experimental Protocol in *Study 4*. Participants were presented with a series of balls that bounced with either normal (blue circles) or unexpectedly-high (red circles) levels of elasticity. Though trial order sequences were the same in each condition, Cued trials were separated into six game levels. Upon entering a new game level, participants received projected 'hawkeye' cues (see arrows). Each subsequent trial was then preceded by a visual indicator, which stated whether the likelihood of facing a bouncy ball was 'low' (17%), 'medium' (33%), or 'high' (50%) for this level. Conversely, balls in the non-cued condition were presented as one continuous sequence of trials, with no additional visual information. *Note that both blocks ended with nine catch trials that contained no explicit probabilistic cues.

4.1.2.4. Data Analysis

This study focused on the context-sensitive variables relating to motor performance, swing kinematics, and gaze behaviour that proved responsive to volatility estimates in Chapter 3. Specifically, task performance was evaluated based on *interception rate*, which reflected the percentage of trials in which participants successfully hit the ball with their racquet. Kinematic variables were assessed using the positional data of the VR hand controller, which were extracted and then smoothed using a dual-pass, zero-phase Butterworth filter (frequency: 10 Hz; Franks et al., 1990). Specifically, analysis focused on the foreswing phase of interceptive actions, which started when the racquet first began to move forward and ended when it first made contact with the ball. In trials where participants failed to hit the ball, foreswing offset represents the final data point in which the ball's depth position exceeded that of the racquet.

Peak velocity of the hand controller was recorded from participants' foreswing movements, as autistic participants displayed slower, more novice-like swing actions than neurotypical individuals in *Study 3*. Additionally, ROM was assessed during this trial period to capture context-sensitive aspects of motor control. This outcome highlighted the maximum angular deviation between the VR headset and hand controller, as defined in the tranverse plane. Higher values would indicate that the hand had rotated to a greater degree around the body during the foreswing action. Conversely, decreases in ROM may signify that participants were 'fixing' movement degrees of freedom, a response which is typically prominent under volatile conditions and in autistic populations (see *Study 3*; Arthur & Harris, 2021).

Eye tracking data were converted into 'in-world' angular vectors, as defined according to head-centred egocentric coordinates. Yaw and pitch values were smoothed using a three-frame median filter and then a second-order Butterworth filter (at 15 Hz; Cesqui et al., 2015). Since autistic participants employed anticipatory saccades in a similar manner to neurotypical individuals in *Study 3*, analysis only focused on predictive fixations. To extract this information, cleaned data were entered into a spatial dispersion algorithm (Krassanakis et al., 2014), which identified periods where gaze remained steady within a 3° area for a minimum of 100 ms. Trials where eye-tracking was temporarily lost (>100 ms) or where there were >20% of missing data were excluded. Subsequent analyses focused on the median onset time, mean duration,

and average vertical position (mean pitch angle) of fixations that occur during (within 0.1s), or immediately prior to, ball bounces in each trial. This *bounce fixation* is elevated when an individual predicts that ball elasticity likely to be higher (Diaz et al., 2013; Mann et al., 2019). Furthermore, trial-to-trial variability in this bounce fixation location is typically increased under volatile conditions (see *Study 3*; Arthur & Harris, 2021).

All variables were inspected for missing data, outliers, normality, sphericity, and homogeneity of variance. They were then entered into separate mixed-model ANOVAs, which studied main effects of *condition* (cued vs control) and *group* (ASD vs neurotypical), as well as any *group-by-condition* interactions. Effect sizes were quantified using partial-eta squared and significant observations were followed up using Bonferroni-corrected *t*-tests. Prior to running the ANOVAs, manipulation checks examined whether predictive bounce fixations were sensitive to dynamic environmental probabilities. Specifically, dependent *t*-tests examined changes in bounce fixation pitch angles between baseline and control conditions, to see whether unexpected and volatile manipulations of ball bounciness led to significant adjustments in predictive gaze positions. To explore relationships with autistic-like traits and intolerance of uncertainty, Pearson's Correlation analysis examined associations between AQ, IUS-S, and all sensorimotor outcomes. These statistical tests were conducted with alpha set at $p < .05$ and are reported alongside a Bayes Factor computation (as in *Chapters 2-3*). Procedures were undertaken using JASP 0.12.2, with the full dataset available at https://osf.io/5y48g/.

4.1.3. Results

4.1.3.1. Preliminary Analysis

Poor motion tracking led to missing hand position data for one autistic participant. As such, they and their matched neurotypical counterpart were excluded from kinematic analyses only (remaining $n = 42$). A separate pair of matched participants were removed from gaze analyses, due to frequent loss of eye-tracking signal (remaining $n = 42$). Data were deemed missing completely at random (Little's MCAR test: $p > 0.05$). Two autistic participants were identified as potential outliers in the interception rate data, but their observed scores (45.56% and 54.44%) were consistent with previous values and the overall pattern of results was not affected by their inclusion. In these

instances, conventions recommend that extreme values are *not* removed (Aguinis et al., 2013), as case exclusion may disregard important information relating to clinical sensorimotor difficulties. Consequently, no data were excluded for this variable.

Notably, interception rate data were positively skewed, with 10 participants intercepting 100% of balls from experimental trials. This outcome therefore deviated from normality, along with peak swing velocity, fixation onset time, and fixation duration (all $p < .05$ for Shapiro-Wilk test). Mixed-model ANOVAs are robust to moderate deviations from statistical normality (Lix et al., 1996) and were still performed. However, Mann-Whitney *U* tests were used for follow-up comparisons and Spearman's Rho for assessing their correlations with AQ and IUS-S scores. Levene's Test highlighted significantly different levels of variance for bounce fixation pitch measures ($p < .05$). No further statistical assumptions were violated in relation to normality, sphericity, and homogeneity of variance.

Manipulation checks showed a significant change in the height of predictive bounce fixations between baseline and control conditions (average pitch angle: $t(39) = 6.73$, $p < .001$, $BF_{10} = 2.76 \times 10^5$). As expected, volatile fluctuations in ball bounciness caused both groups to cast their gaze at a higher spatial location than at baseline, despite their being no explicit informational cues in either block of trials. These results confirm assumptions that participants would elevate their predictive bounce fixations when faced with unexpectedly bouncy balls and volatile trial conditions.

4.1.3.2. Task Performance and Swing Kinematics

For task performance, analysis revealed a significant main effect of group ($F(1,42) = 8.44$, $p = .01$, $\eta_p^2 = 0.17$, $BF_{10} = 7.41$), with average interception rates significantly lower in autistic (87.75 ± 14.78%) compared to neurotypical participants (97.22 ± 3.91%; $W = 379.50$, $p = .001$, $BF_{10} = 13.23$; Figure 4.3). However, there were no significant condition effects ($F(1,42) = .08$, $p = .78$, $\eta_p^2 < 0.01$, $BF_{10} = 0.23$) or group-by-condition interactions ($F(1,42) = .06$, $p = .81$, $\eta_p^2 = 0.001$, $BF_{10} = 0.28$). AQ scores negatively correlated with interception rate in both control ($Rs = -.34$, $p = .02$, $BF_{10} = 2.69$) and cued ($Rs = -.41$, $p = .01$, $BF_{10} = 13.67$) conditions. Conversely, IUS-S values were not significantly associated with task performance in either block of trials (control: $Rs = -.16$, $p = .42$, $BF_{10} = 0.28$; cued: $Rs = -.17$, $p = .26$, $BF_{10} = 0.41$).

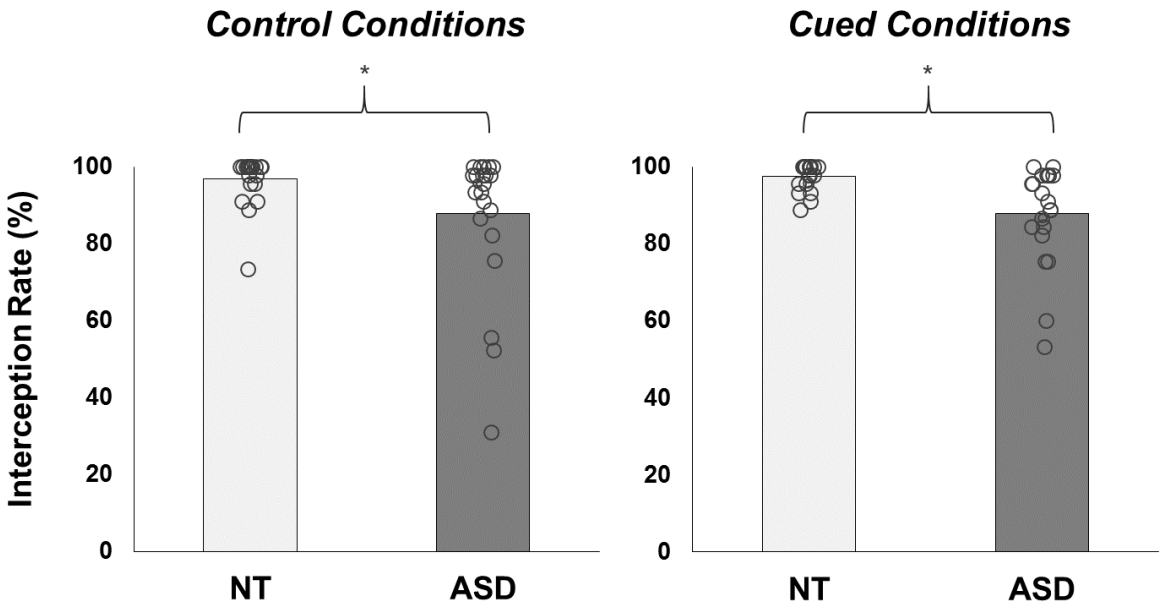

Figure 4.3. Task Performance in *Study 4*. The proportion of balls successfully intercepted in control and cued conditions for each group. NT: neurotypical; ASD: autism spectrum disorder.

There were no significant main effects of group ($F(1,40) = 1.47$, $p = .23$, $\eta_p^2 = .0.04$, $BF_{10} = 0.70$) or condition ($F(1,40) = 0.13$, $p = .73$, $\eta_p^2 < .01$, $BF_{10} = 0.23$) for peak swing velocity, nor were there any significant group-by-condition interactions for this metric ($F(1,40) = 3.82$, $p = .06$, $\eta_p^2 = .09$, $BF_{10} = 0.97$). In terms of ROM, there was a significant main effect of group ($F(1,40) = 7.58$, $p = .01$, $\eta_p^2 = 0.16$, $BF_{10} = 4.43$) and a significant group-by-condition interaction ($F(1,40) = 8.88$, $p = .01$, $\eta_p^2 = 0.18$, $BF_{10} = 7.50$). Autistic participants exhibited lower ROM values than neurotypical participants, as shown in Figure 4.4. However, while these individuals generally decreased ROM between control and cued conditions (Mean difference: -6.50 ± 12.38°; $t(20) = 2.41$, $p = .03$, $BF_{10} = 2.30$), neurotypical values remained relatively stable (Mean difference: 5.50 ± 13.68°; $t(20) = 1.84$, $p = .08$, $BF_{10} = 0.95$). ROM significantly correlated with AQ scores in the cued ($R = -.39$, $p = .01$, $BF_{10} = 4.38$) but not the control trials ($R = -.25$, $p = .11$, $BF_{10} = 0.66$). Moreover, ROM values were negatively associated with IUS-S scores in both conditions (control: $R = -.42$, $p = .01$, $BF_{10} = 8.40$; cued: $R = -.42$, $p = .01$, $BF_{10} = 7.32$). Peak swing velocities did not significantly correlate with AQ or IUS-S scores during either condition (*p's* > .06, all $BF_{10} < 2$).

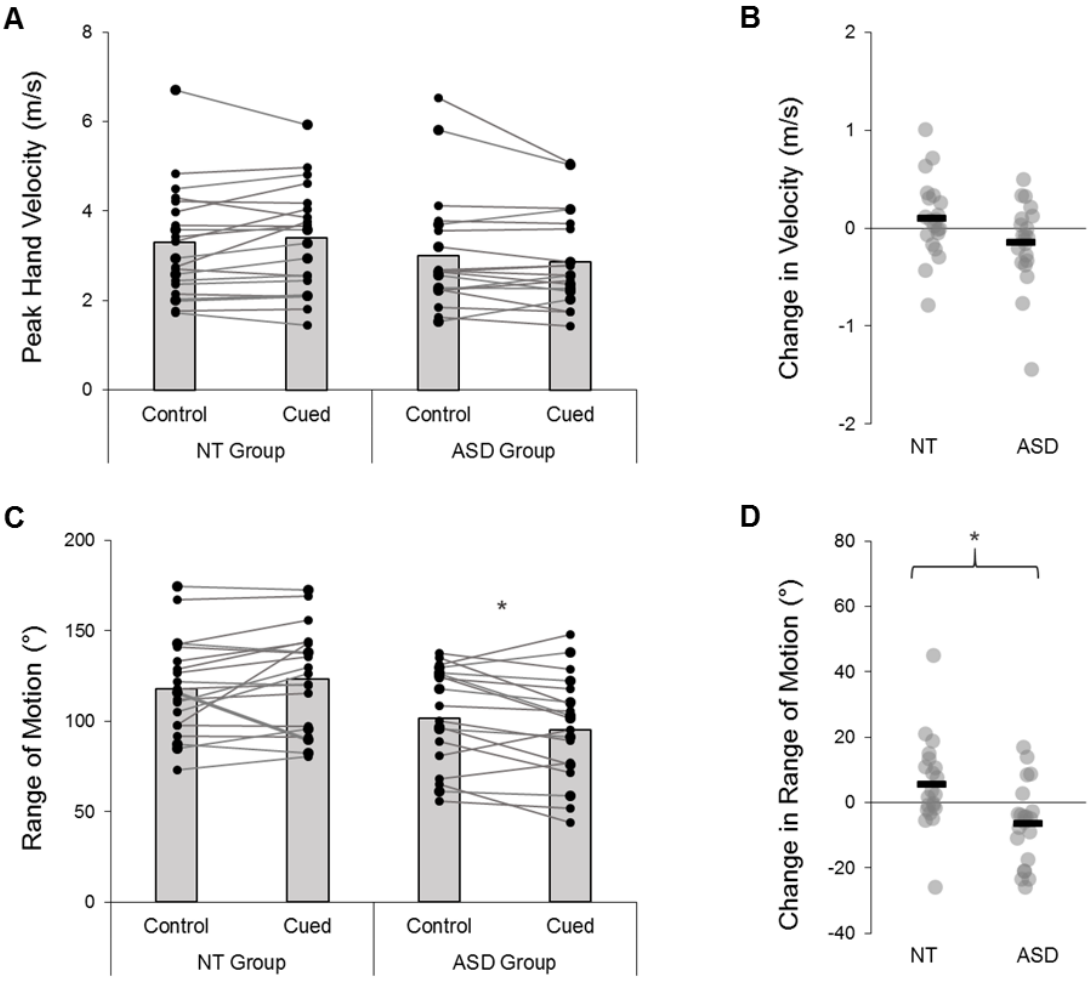

Figure 4.4. Average peak hand velocities (**A**) and range of motion (**C**) during foreswing actions in control and cued blocks. Between-condition changes are illustrated in panels **B** and **D**. NT: neurotypical; ASD: autism spectrum disorder; * denotes significant difference ($p < .05$).

4.1.3.3. Gaze Data

Groups exhibited similar gaze profiles during the task. ANOVAs revealed no significant group differences or group-by-condition interactions in relation to the onset and duration of predictive bounce fixations (p's > .30; all $BF_{10} < 0.67$). Participants maintained slightly longer fixations during the cued trials (Figure 4.5), with a significant effect of condition emerging for this metric ($F(1,40) = 6.72$, $p = .01$, $\eta_p^2 = 0.14$, $BF_{10} = 3.49$). However, this main effect did not emerge in relation to onset time ($F(1,40) = 1.56$, $p = .22$, $\eta_p^2 = 0.04$, $BF_{10} = 0.44$), and there were no significant AQ or IUS-S correlations for either fixation metric (p's > .18; all $BF_{10} < 0.67$).

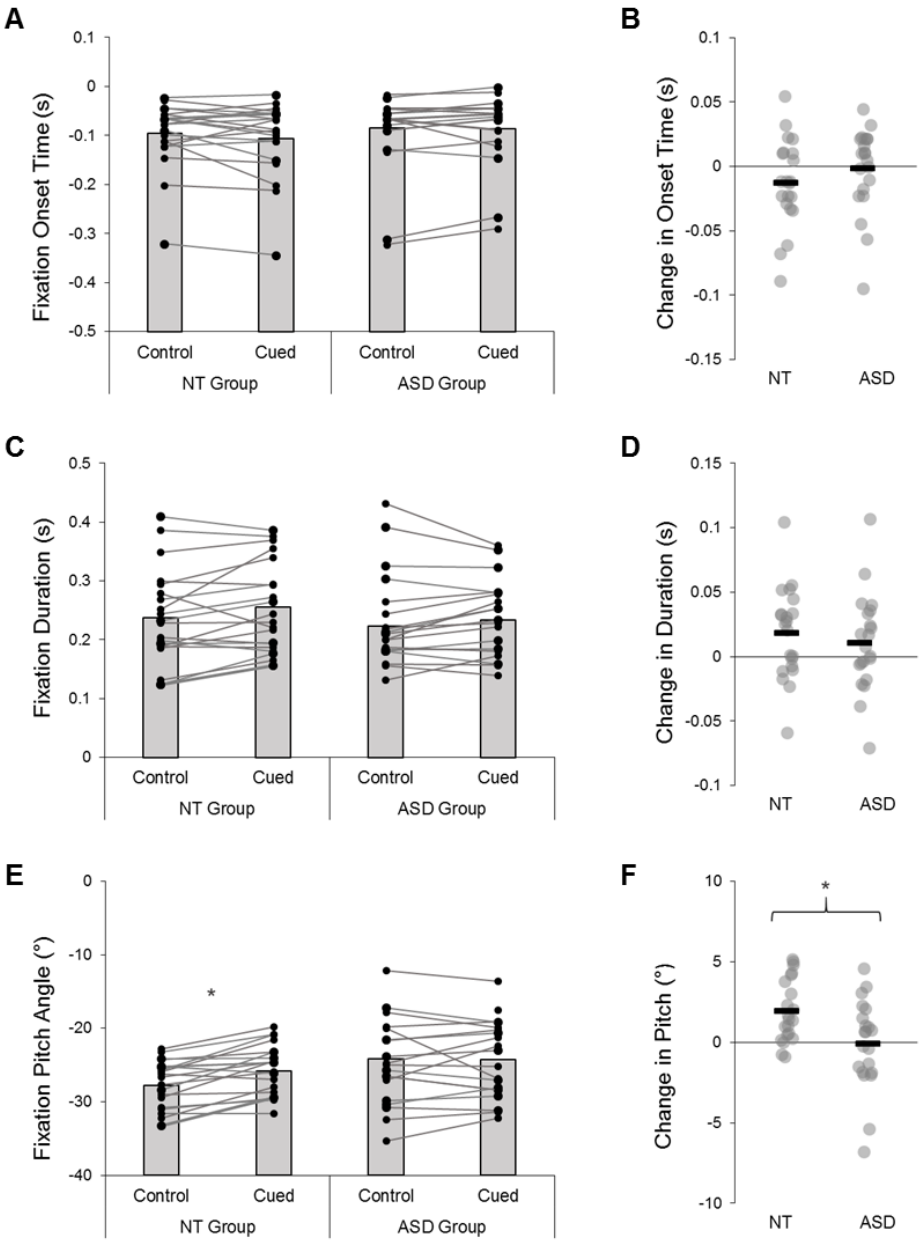

Figure 4.5. The average onset times (**A**), durations (**C**), and pitch angle locations (**E**) of predictive bounce fixations during control and cued blocks in *Study 4*. Between-condition changes are illustrated in panels **B**, **D**, and **F**. NT: neurotypical; ASD: autism spectrum disorder; * denotes statistically significant differences ($p < .05$).

Next, the average pitch angle (i.e., vertical position) of participant's predictive bounce fixation was examined. Here, both a significant main effect of condition ($F(1,40) = 6.39$, $p = .02$, $\eta_p^2 = 0.14$, $BF_{10} = 2.10$) and a significant group-by-condition interaction emerged ($F(1,40) = 7.92$, $p = .01$, $\eta_p^2 = 0.17$, $BF_{10} = 5.32$). Average pitch values generally increased from control to cued trials, however these changes were group-

dependent (see Figure 4.5). Specifically, neurotypical participants elevated the height of their bounce fixations after receiving explicit probabilistic cues (Mean difference: 1.96 ± 1.93°; $t(20) = 4.64$, $p < .001$, $BF_{10} = 184.36$), whereas autistic participants showed minimal changes between blocks (Mean difference: 0.11 ± 2.75°; $t(20) = .18$, $p = .86$, $BF_{10} = 0.23$). Surprisingly though, no statistical relationships emerged between bounce fixation pitch angles and scores on the AQ or IUS-S (p's > .19; all $BF_{10} < 0.50$).

Finally, the trial-to-trial variability in participant's predictive bounce fixation location (i.e., pitch angle) was examined. This analysis revealed a significant main effect of group ($F(1,40) = 6.99$, $p = .01$, $\eta_p^2 = 0.15$, $BF_{10} = 4.63$). Generally, autistic participants showed significantly higher pitch angle SD values than their neurotypical counterparts (Figure 4.6). However, these variability scores did not significantly differ between conditions ($F(1,40) = 1.69$, $p = .20$, $\eta_p^2 = 0.04$, $BF_{10} = 0.46$), and there were no significant group-by-condition interactions ($F(1,40) = 1.75$, $p = .19$, $\eta_p^2 = 0.04$, $BF_{10} = 0.57$). Furthermore, no statistical associations emerged between pitch angle SD, AQ totals, and IUS-S scores (p's > .12, all $BF_{10} < 0.67$).

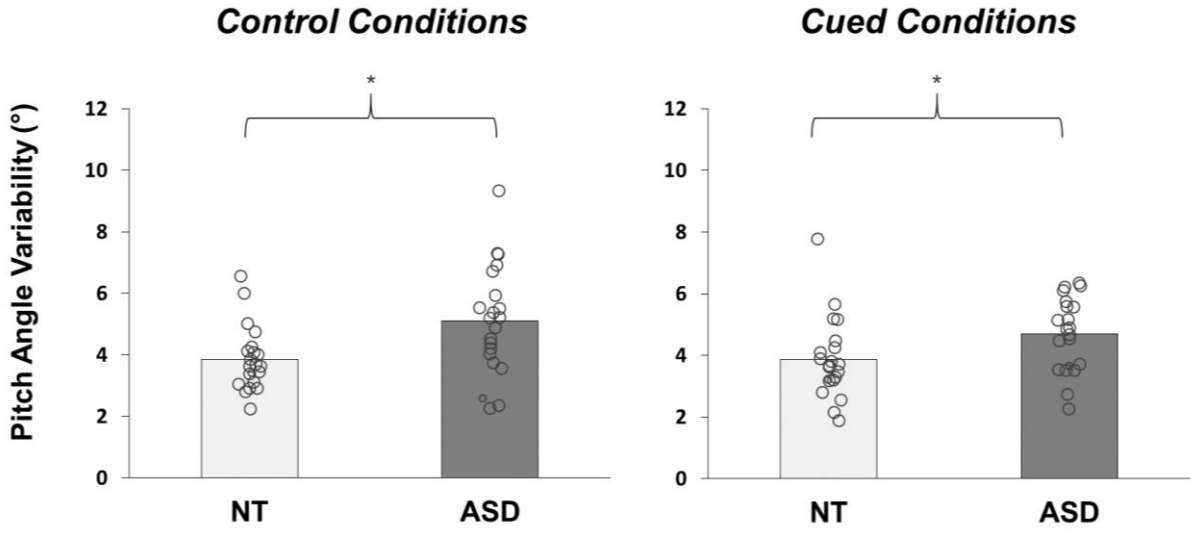

Figure 4.6. Trial-by-trial standard deviations in the pitch angle of predictive bounce fixations during control and cued blocks in *Study 4*. NT: neurotypical; ASD: autism spectrum disorder; * denotes statistically significant differences ($p < .05$).

4.1.3.3. Exploratory Analysis of Gaze Fixation Data

Follow-up tests explored whether group-dependent changes in gaze behaviours derive from altered volatility processing or whether they are simply reflecting participants' ability to use prior probabilistic information. For instance, the cued block contained periods of 6-12 trials where the likelihood of facing a bouncy ball was described as 'high' to participants. Thus, it is possible that higher pitch averages in cued versus control trials are being driven by data from these specific datapoints. Conversely, autistic participants may have difficulties interpreting these cues, leading to non-significant changes between conditions. In the analysis that follows, data from selected trials are scrutinised within each condition, with two participants and their matched counterparts excluded due to missing outcome values (remaining n = 40).

Firstly, gaze data from trials that immediately followed a 'high' probabilistic cue were extracted for each participant. Prior to these trials, participants viewed a 'hawkeye' illustration which projected an equal probability of facing a normal or bouncy ball (see Figure 4.1). This was accompanied by an indication that the current likelihood of facing a bouncy ball was relatively 'high'. If these probabilistic cues were being readily used by participants, then one would expect subsequent predictive bounce fixations to be higher than control values. Indeed, a mixed-model ANOVA found a significant effect of condition on the extracted fixation data ($F(1,38) = 50.15$, $p < .001$, $\eta_p^2 = 0.57$; $BF_{10} = 2.67\times10^5$), with both groups exhibiting increases in the height of their predictive gaze fixations (Wilcoxon Signed-Rank test: $Z = 5.51$, $p < .001$, $BF_{10} = 4.76\times10^5$). Importantly, no significant interaction effects were recorded ($F(1,38) = 2.99$, $p = .09$, $\eta_p^2 = 0.07$; $BF_{10} = 0.91$).

Next, mixed-model ANOVAs were repeated using data from catch trials only. In these trials, no probabilistic information about likely ball bounciness was provided; participants were simply cued that their surrounding environment had changed (see methods). Notably, the significant interaction effects observed in the main analyses were replicated in this data ($F(1,38) = 5.24$, $p = .03$, $\eta_p^2 = 0.12$), albeit with weaker statistical evidence against the null ($BF_{10} = 2.40$). Together, results suggest that group-dependent changes in visual sampling behaviour were not due to differences in the interpretation or understanding of prior probabilistic cues. Instead, they appear related to expectations about environmental change and/or stability.

4.1.4. Discussion

This study examined dynamic sensorimotor behaviours in autistic and neurotypical individuals following the provision of explicit veridical information about environmental volatility. Previous research has shown that contextual cues about likely task outcomes can enhance neurotypical action responses (Navia et al., 2013; Gray, 2015; Gredin et al., 2018), and it has been suggested that such an approach could help autistic individuals in uncertain task conditions (Qian & Lipkin, 2011; Haker et al., 2016). Results generally found no significant effects of these cues on interceptive motor performance and visual sampling behaviours. Lower interception rates and more restricted swing kinematics were evident in autistic sensorimotor responses, irrespective of any prior cue conditions. Overall, findings highlight fundamental differences in how prior information and environmental cues are dynamically modulated over time in autism. It is likely that sensorimotor difficulties are affected by these aberrant neural mechanisms, rather than from any broad inaccuracies or intolerances with appraising contextual uncertainty.

In line with outcomes reported in Chapters 2-3 and previous research (Palmer, Paton, et al., 2015; Robic et al., 2015; Lawson et al., 2017), autistic participants showed atypical context-sensitive adjustments in sensorimotor behaviour and volatility modulation. When compared to neurotypical individuals, they directed predictive bounce fixations towards higher spatial locations (Figures 4.4) and updated these behaviours more variably from trial to trial (Figure 4.6), in a manner that suggests they were more uncertain about upcoming ball trajectories. These atypicalities do not reflect any impairments in the ability to *detect* changing environmental probabilities (Manning et al., 2017; Sapey-Triomphe et al., 2021). Indeed, when the likelihood of facing a bouncy ball increased between baseline and control conditions, autistic people readily adjusted the height of their fixations (see *manipulation checks*). Instead, experimental data imply that autistic people show a heightened responsivity to recent, unexpectedly bouncy ball trajectories. This increased tendency to prepare for probabilistically-salient trial events replicates findings from *Study 3* and Lawson *et al.* (2017) and is consistent with proposals of impaired precision weighting in autism (e.g., Friston et al., 2013; Lawson et al., 2014; Van de Cruys et al., 2014; Palmer, Seth, et al., 2015).

Studies suggest that these predictive processing differences are linked with over-estimations of environmental volatility and inflexible surprise responses (Lawson et al., 2017; *Study 3*). Accordingly, virtual cues in this experiment were designed to provide dynamic, statistically-accurate information about contextual probabilities and stability. While neurotypical participants used these explicit cues to adjust their gaze fixation behaviours (i.e., they directed them to higher spatial locations in the cued block: Figure 4.5), autistic individuals showed minimal between-condition changes in their visual sampling and motor responses (Figure 4.3-4.6). Results indicated that there were no generic difficulties in understanding the contextual cues. Indeed, it has already been demonstrated that autistic people can use explicit situational information to guide perceptual and motor abilities (Balconi et al., 2012; Vermeulen, 2015; Thillay et al., 2016; Fulceri et al., 2018; Gowen et al., 2020; Sapey-Triomphe et al., 2021; Soroor et al., 2021), and the height of participants' predictive fixations increased following indications that a bouncy ball was highly likely (see *Section 4.1.3.3*). Instead, the null findings suggest that autistic people simply did not benefit from the explicit, probabilistic information that was afforded to them in this task. Though surprising, these results align with observations that certain prediction-related atypicalities in autism persist in the face of accurate visual cues about likely trial outcomes (Thillay et al., 2016; Balsters et al., 2017; Greene et al., 2019; Cannon et al., 2021).

According to predictive processing perspectives, precision weighting functions are enacted via alterations in synaptic neural gain, with phasic monoaminergic and cholinergic signalling said to facilitate rapid, context-sensitive adjustments in the integration of top-down expectations and bottom-up information (Yu & Dayan, 2003; Feldman & Friston, 2010). Lawson *et al.* (2014) propose that these neuromodulatory systems are aberrant in autism, leading to pathologically high levels of postsynaptic gain in the sensory cortex. As a result, autistic people show disproportionate receptiveness to sensory inputs and are over-reactive to environmental change (Lawson et al., 2017). The present data support these proposals, with autistic participants updating their bounce fixation positions more variably on a trial-to-trial basis than neurotypical controls (Figure 4.6; see also *Study 3*). Moreover, the autism group appeared to restrict swing ROM under cued conditions (Figure 4.4), a response which generally coincides with *heightened* uncertainty estimates (Arthur & Harris, 2021). Results therefore imply that autistic people were over-reactive to both implicit

and explicit cues about environmental volatility, causing them to employ visuomotor behaviours that are typically affiliated with imprecise higher-level beliefs.

Nonetheless, there was substantial inter-individual variability observed in the dataset. Figures 4.3-4.6 illustrate diverging responsivity to contextual cues and levels of task performance, with such heterogeneity proving particularly prominent in autistic individuals. These wide-ranging data patterns are consistent with clinical research (Fournier et al., 2010; Coll et al., 2020), and suggest that sensorimotor difficulties may bear varied aetiologies and neurobiological underpinnings. This notion is not at odds with computational frameworks, as aberrant precision encoding is theoretically underpinned by a myriad of interacting networks and modulatory systems (Lawson et al., 2014). Future work must consider these heterogeneous individual aetiologies when attempting to reduce sensorimotor difficulties through applied interventions.

Interestingly, relationships between sensorimotor control and intolerance of uncertainty were mostly trivial in this study. Although previous research has established links between anxiety and autism-related sensory processing issues (Wigham et al., 2015; Pickard et al., 2020), IUS-S scores did not significantly correlate with task performance or visual sampling responses in the current task. These null results are perhaps unsurprising, as associations between intolerance of uncertainty and anxiety are mechanistically distinct from those concerning hierarchical precision estimates and active inference behaviours (Bervoets et al., 2021). Indeed, the IUS-S indexes an individual's chronic disposition to appraise uncertain outcomes as aversive (Carleton et al., 2007). These durable appraisal tendencies sit in stark contrast to the highly dynamic and context-sensitive visuomotor responses that were assessed in this task. Nevertheless, intolerance of uncertainty may affect key moderators of sensorimotor development in the 'real-world', such as an individual's affective state, attention, confidence, and participation in active behaviours (e.g., Robinson & Freeston, 2015; Del Popolo Cristaldi et al., 2021). As such, one must not overlook the potential contribution that the construct plays in more applied daily living skills.

The findings above offer important practical implications. Many autism research frameworks advocate the provision of explicit contextual information about the underlying statistical properties of a task (e.g., Qian & Lipkin, 2011; Gomot & Wicker, 2012; Vermeulen, 2015; Haker et al., 2016). Though clearly beneficial in many settings,

the present data suggest that such an approach is not necessarily appropriate for developing sensorimotor skills that are inherently changeable and unpredictable in nature. Instead, results support strategies that address the implicit, heterogeneous difficulties that many autistic people have when processing dynamic and volatile sensory cues. Environmental accommodations that make the world feel more predictable for autistic people could be prioritised, like reducing external sensory 'noise', developing individualised task routines, or increasing the number of blocked learning repetitions (see Haker et al., 2016). Similarly though, practitioners should also look to help individuals deal with volatile and unpredictable elements of sensorimotor skills. Indeed, personalised task modifications may not always be possible, and so future work could focus on developing habitual behaviours that facilitate the sampling of 'optimal' sensory cues (e.g., see feedforward gaze training: Wilson & Vine, 2018; environmental scaffolding: Van de Cruys et al., 2014).

Nevertheless, there are some key limitations that should be considered when developing future practice. First, there was no direct measure of volatility beliefs in the study. Conclusions are instead based on carefully designed experimental manipulations and subsequent changes in sensorimotor behaviour. While exploratory analyses attempted to decipher volatility estimates from lower-level expectations, future work could incorporate self-rating methods that index confidence in task predictions (e.g., as in Pasturel et al., 2020). Moreover, studies could monitor changes in these functions over a higher number of trials. Evidence suggests that changes in prior contextual beliefs can occur within ten repetitions (Verstynen & Sabes, 2011), however investigations may wish to examine longer-term adaptations in sensorimotor control and volatility-related learning (as in Vossel et al., 2014; Lawson et al., 2017). Finally, despite being unconstrained and naturalistic in design, the racquetball task was performed under tightly-controlled virtual conditions. On one hand, these features permitted the examination of various implicit predictive processes. However, some potentially significant factors that contribute to sensorimotor issues may have been overlooked (e.g., access to support, social/developmental differences; Colombo-Dougovito & Block, 2019). Therefore, future research must explore how 'real-world' daily living skills can be optimally developed in autistic people, especially in activities that are deemed most important or challenging for neurodivergent populations (e.g., driving, occupational skills, healthcare operations; see Robledo et al., 2012).

4.1.5. Conclusions

In sum, autistic people display interceptive action responses that are typically associated with unstable and uncertain task conditions. Although these profiles indicate that volatility beliefs are suboptimal, they persist after an individual has received explicit and statistically-accurate information about whether an environment is changing or not. As such, sensorimotor issues are unlikely to reflect any generic difficulties in extracting likely task outcomes from this setting. Instead, results lend indirect support for proposals of aberrant neuromodulatory control in autism. It is recommended that practitioners look to help autistic people build stable action predictions through the use of individualised, evidence-based techniques.

Chapter 5

Sensorimotor issues in autism can negatively impact on personal independence and quality of life (Jasmin et al., 2009; Gowen & Hamilton, 2013); however, little is known about what causes these daily living difficulties or how they can be managed at a practical level. Accordingly, the present work aimed to identify the mechanisms that underpin sensorimotor differences in autistic people. At first, a comprehensive examination of existing research was conducted (Chapter 1), which highlighted possible associations between autism and predictive action control. This initial link was then empirically scrutinised within two object lifting experiments (Chapter 2) and a uniquely designed virtual racquetball paradigm (Chapter 3). Context-sensitive differences in active inference were identified in these investigations that are both consistent with previous evidence and directly related to sensorimotor impairments. Possible approaches for enhancing these sensorimotor functions were then explored in Chapter 4, to initiate the development of evidence-based interventions. Together, this research offers key insight into why autistic people experience sensorimotor difficulties and how these issues could be managed within applied practical settings.

5.1. Summary of Key Findings

Chapter 1 indicated that autistic sensorimotor difficulties may be linked to atypical predictive action control. Indeed, a thorough and conceptually-guided evaluation of previous research demonstrated that autism-related differences in predictive control are evident across visual, gaze, and motor systems. These results align with recent Bayesian and predictive processing frameworks by suggesting that the dynamic integration of prior expectations and sensory information may be suboptimal in autistic people. However, research findings are often inconsistent in this field and can depend on task requirements, participant characteristics, and various study design features. Therefore, questions remained about the precise mechanisms that underpin clinical sensorimotor differences.

Studies 1-4 indicated that autism-related movement differences are *not* caused by any broad impairments (or attenuations) in the use of prior expectations. Chapter 2 found that autistic people use pre-lift predictions about object heaviness to guide their perceptual, motor, and sensory sampling responses. As a result, goal-relevant visual

cues are retrieved in advance of dynamic bodily movements and heavier-looking objects are lifted with higher initial fingertip forces, in a manner that is consistent with neurotypical sensorimotor behaviour. These profiles were displayed across study populations, irrespective of an individual's clinical diagnosis status or levels of autistic-like traits. They were also apparent in participants' interception responses in *Studies 3* and *4*, with expectations about upcoming ball trajectories influencing both when and where gaze was shifted during virtual racquetball conditions. As such, the present research provides compelling evidence that autistic people do not possess any generic impairments in the ability to make and/or use goal-relevant action predictions.

Notably though, results suggest that autistic people do not *adjust* their predictions in a typical manner during dynamic sensorimotor tasks. Specifically, Chapter 2 illustrated that autistic participants show atypical context-sensitive adjustments in gaze control when sampling objects with uncertain weight properties. Chapter 3 extended these findings into interceptive visuomotor actions, with autistic people exhibiting significant performance difficulties when required to adjust to volatile fluctuations in ball bounciness. Chapter 4 showed that these difficulties persisted in spite of explicit informational cues about likely probabilistic outcomes and environmental change. Together, these results consistently indicated that autistic people may have issues with modulating action predictions in a dynamic, context-sensitive manner.

Building on these results, Chapter 3 found that autistic sensorimotor control is characterised by a tendency to interact with the world as if it is highly uncertain or volatile. Such atypicalities were reflected in both visual sampling and kinematic motor variables. Specifically, while neurotypical individuals elevated their predictive gaze fixations and reduced movement degrees of freedom in volatile trials, autistic participants showed more uncertain-like responses in both stable and volatile conditions. These participants also demonstrated reduced behavioural surprise when responding to highly bouncy ball trajectories within the virtual environment, illustrating an increased affinity to 'expect the unexpected'. Overall, the data from *Study 3* suggest that differences in volatility modulation and/or precision weighting may cause autistic individuals to sub-optimally integrate sensory information and action predictions over time.

Although autistic visual sampling responses and kinematic profiles were sensitive to underlying cue-outcome relationships across each of the presented studies, Chapter 4 found that explicit information about probabilistic uncertainty and volatility did not influence these behaviours. Specifically, autistic participants continued to interact with their surrounding sensory environment as if it was uncertain and/or unstable, even after receiving statistically-accurate information as to what task outcomes were more likely and when these contingencies were changing. These results implicate key modulatory systems in the brain, as they suggest that autistic individuals are pathologically over-reactive to environmental variability.

In summary, the present research suggests that sensorimotor difficulties in autism are underpinned by subtle differences in predictive action control that are context-sensitive in nature. Autistic people exhibit action behaviours that are typically associated with uncertain or volatile environments, indicating that the modulation of dynamic sensory information and hierarchical generative models is suboptimal in these individuals. Such atypicalities are shown across multiple experimental tasks, participant groups, and sensorimotor processing systems. The potential implications of these results and their accordance with previous research must now be considered, before any novel practical applications can be made.

5.2. Theoretical Implications

Relationships between autism and predictive sensorimotor atypicalities are relatively well-documented within research. Previous studies have found autistic individuals to have compromised movement planning abilities (Hughes, 1996; Rinehart et al., 2001; Fabbri-Destro et al., 2009; Foster et al., 2019), impaired anticipatory postural adjustments (Schmitz et al., 2003; Martineau et al., 2004), atypical feedforward grasp control (David et al., 2009; 2012; Mosconi et al., 2015; Z. Wang et al., 2015), reduced perceptual adaptation (Pellicano et al., 2007; 2013; Turi et al., 2015), and suboptimal integration of prior information and sensory feedback (e.g., Karaminis et al., 2016; Skewes & Gebauer, 2016). Such findings align with observations from *Studies 1-4,* where tendencies to predictively underestimate object lifting forces, sample uncertain visual cues, and distinguish between expected and unexpected events were all associated with autistic sensorimotor profiles. They also explain why many individuals

might experience impairments in applied movement skills, with performance expertise said to be contingent on dynamic, context-appropriate action predictions (Williams et al., 2011; Müller & Abernethy, 2012; Loffing & Cañal-Bruland, 2017; Cappuccio et al., 2020). Consequently, autism-related differences in predictive control may have deleterious effects on the performance of various sensorimotor skills and behaviours.

Recently, mechanistic links between autism and predictive control have been described using computational models of the brain. Here, daily living difficulties have been proposed to result from attenuations in the use of prior beliefs (Pellicano & Burr, 2012; Van Boxtel & Lu, 2013), overly-dominant likelihood distributions (Brock, 2012), chronically inflexible error signalling (Van de Cruys et al., 2014), aberrant precision weighting (Friston et al., 2013; Lawson et al., 2014), and general difficulties with making/learning predictions (Qian & Lipkin, 2011; Gomot & Wicker, 2012; Sinha et al., 2014). Despite these contrasting assumptions, much of these computational accounts lend themselves to the same overall hypothesis: that autistic people will be less influenced by prior expectations (relative to incoming sensory feedback) at a perceptual and behavioural level. However, findings from *Studies 1-4* offer little support for this notion, with autistic participants showing neurotypical-like anticipatory motor profiles and visual sampling behaviours across both object lifting and interceptive visuomotor tasks. These null group differences align with results from eye tracking experiments (von Hofsten et al., 2009; Aitkin et al., 2013; Ego et al., 2016), motor adaptation studies (Gidley-Larson et al., 2008; Brown et al., 2010), dynamic social cueing paradigms (Pell et al., 2016; Tewolde et al., 2018), and action–perception integration tasks (Noel et al., 2020). They also corroborate with clinical neuroimaging studies, which have shown little evidence for any *single* or *uniform* abnormality in prediction-related regions of the brain (see Qian & Lipkin, 2011). On this basis, it appears increasingly unlikely that autistic sensorimotor difficulties result from any *chronic* differences in Bayesian inference and/or prediction error signalling.

Instead, findings suggest that sensorimotor difficulties may reside from dynamic, context-sensitive aspects of action control. For instance, *Study 1* showed that associations between autistic-like traits and anticipatory grip force rates were only significant when lifting objects that were unexpectedly-heavy and not unexpectedly-light. Moreover, *Study 3* revealed that autism-related difficulties with hand-eye coordination depend on levels of environmental uncertainty and/or stability. Here,

between-group differences in interceptive task performance were consigned to volatile conditions, with autistic participants increasingly struggling when goal-relevant sensory cues were probabilistically unstable over time. Indeed, autism-related processing atypicalities are usually more pronounced in complex and/or ambiguous task environments (see Bertone et al., 2003; Tewolde et al., 2018; Cannon et al., 2021). So, while the ability to make and use predictions does not appear to be chronically affected in autistic people, individuals may have difficulties adjusting sensorimotor actions to uncertain and dynamic task conditions (e.g., during social interactions or complex movement skills; Palmer, Paton, et al., 2015; 2017; Cannon et al., 2021).

Active Inference frameworks outline a number of mechanisms that are involved in the context-sensitive control of sensorimotor behaviours. According to these perspectives, bodily movements continuously seek to resolve future prediction errors (or Bayesian surprise; Friston et al., 2010; Adams et al., 2013; Shipp et al., 2013; Friston et al., 2017; Parr & Friston, 2019). This minimisation of 'free energy' is achieved by selecting action models that either directly fulfil context-sensitive predictions (i.e., pragmatic actions) or reduce their associated uncertainty (i.e., epistemic actions; see Friston et al., 2015). So, in relatively predictable environments, an agent might select familiar movement strategies that are heavily driven by prior beliefs about future outcomes (Parr & Friston, 2019). Conversely, under more uncertain conditions, agents may implement more exploratory actions and sensory sampling behaviours (e.g., see Friston, Adams, et al., 2012; Beesley et al., 2015; Walker et al., 2019). Such 'exploitation vs exploration' trade-offs were shown in *Study 2*, where neurotypical participants increased the number of disambiguatory, object-driven fixations before lifting items with unfamiliar weight properties. Here, agents are controlling their actions according to the reliability of prior beliefs and sensory cues – the more uncertain objects elicited imprecise predictive models about required lifting forces, leading to greater epistemic visual sampling responses. These context-sensitive gaze adjustments illustrated dynamic precision weighting functions, which regulate both how sensory information is passed between hierarchical networks and how it is retained over time (see Yon & Frith, 2021).

By examining these dynamic aspects of active inference, the present work provides clear insight into which predictive processes might be atypical in autistic sensorimotor operations. For example, *Study 2* found that autistic participants demonstrated significantly diminished changes in visual sampling behaviour between stable and

uncertain trials. So, in contrast to the context-sensitive gaze adjustments shown by their neurotypical counterparts (described above), autistic individuals appeared to sample familiar and unfamiliar objects in a non-discriminant way. These effects are consistent with recent proposals that precision weighting is aberrant in autistic people (e.g., Friston et al., 2013; Lawson et al., 2014). Specifically, Lawson *et al.* (2014) posit that suboptimal hierarchical encoding of precision could represent a single underlying neuropathology of autism, which can account for a diverse array of perceptual and action-based characteristics. These claims have received wide-ranging support from behavioural and neurological experiments (e.g., Palmer, Paton, et al., 2015; Robic et al., 2015; Thillay et al., 2016; Lawson et al., 2017; Goris et al., 2018; Noel et al., 2020). They also explain the context-dependent effects observed in *Studies 1* and *3*, as precision-related differences in prediction error minimisation are argued to be more pronounced in uncertain environments (Lawson et al., 2014; Palmer et al., 2017). Therefore, atypical responses to unexpected object lifting outcomes and ball bounciness trajectories may reflect subtle differences in precision weighting functions, as opposed to chronically impaired predictive action modelling.

According to Lawson *et al.* (2014), aberrant precision control may underlie some of the key traits that are used to characterise and/or diagnose autism. Social and communicative difficulties, for example, are hypothesised to result from imbalances in the weighting ascribed to certain sensory evidence, which impairs the mapping of ambiguous contextual cues (see also Palmer, Seth, et al., 2015). Moreover, restrictive and repetitive patterns of behaviour are viewed as coping strategies for reducing sensory prediction errors (through the self-generation of highly predictable action cues). In support of these proposals, *Studies 1-4* identified frequent correlations between autistic-like traits and sensorimotor prediction. As in the main group comparisons, associations rarely converged on any chronic attenuations in the use of prior knowledge; instead, significant effects were consigned to context-sensitive measures of behaviour (e.g., pGFR underestimation in *Study 1*, visual search rate in *Study 2*, and swing ROM in *Study 3*). Indeed, relationships between autistic-like traits and predictive abilities have been reported in multiple empirical observations (e.g., Palmer et al., 2013; Palmer, Paton, et al., 2015; Buckingham et al., 2016; Karvelis et al., 2018; Arthur et al., 2019), but are likely to depend on task-specific factors (e.g., complexity and uncertainty: see Palmer et al., 2017). Therefore, it appears that

context-sensitive atypicalities in active inference and precision weighting are a common covariate of autistic behavioural traits and daily living abilities.

Hierarchical precision estimates will also determine how internal action models are updated over time (Friston et al., 2009; Yon, 2021). Individuals will dynamically revise their predictions according to perceived stability and reliability in their environment, with sensory evidence assigned larger weightings when estimates of uncertainty or volatility are high (Yu & Dayan, 2003; Behrens et al., 2007; Mathys et al., 2011; 2014). These learning rate adjustments ensure that agents build optimal expectations about the world that are impervious to probabilistically salient outcomes. They also enable agents to respond to unstable conditions, as demonstrated in *Study 3*. Here, neuro-typical gaze fixations were directed to higher, more variable predictive locations during volatile trial periods (when ball bounciness changed irregularly over time). As a result, participants tracked unexpectedly-bouncy balls in a similar manner to those with standard tennis-like elasticity profiles in these trials, despite their being clear distinctions in visual sampling during the stable baseline block. These findings show that individuals were less surprised by probabilistically salient events when they predicted that their environment is unstable (see also Vossel et al., 2014). Autistic participants exhibited little distinction between expected and unexpected ball outcomes in *either* block of trials (i.e., dampened surprise responses; Nazarali et al., 2009; Lawson et al., 2017; Goris et al., 2018). As with gaze findings in *Study 2*, these results indicated that precision weighting functions may be suboptimal in autistic individuals.

Although results point towards a common, autism-related atypicality in precision control, this computational function likely encompasses a variety of neural processing systems. Mechanistically speaking, prediction error signals that are encoded in superficial pyramidal cells are said to be passed between connecting layers of the cortical hierarchy (Feldman & Friston, 2010; Bastos et al., 2012; Adams et al., 2013; Shipp et al., 2013). The post-synaptic gain that is ascribed to these signals is determined by their precision, in a process facilitated by dynamic monoaminergic and cholinergic activity (Yu & Dayan, 2003; Friston, 2010). Crucially, these precision estimates are influenced by a complex array of interacting operations, ranging from subjective meta-cognitive beliefs about the world to subcortical brain pathways and implicit error feedback (Palacios et al., 2021; Yon & Frith, 2021). From an anatomical perspective, neuroimaging studies implicate the ACC and dorsolateral prefrontal cortex

in the processing of environmental uncertainty (Behrens et al., 2007; den Ouden et al., 2010; Bland & Schaefer, 2012), while the frontal lobes and cerebellum appear involved in the building of internal action models (Mori et al., 2001; Ding et al., 2009).

Given the notable variability observed between individuals in the present work, it seems unlikely that autism-related sensorimotor issues derive from any singular abnormality in these aforementioned neural networks (see related discussions in: Fournier et al., 2010; Mosconi & Sweeney, 2015). Indeed, *Studies 2-4* showed that autistic people display heterogeneous performance abilities and diverse patterns of predictive action control. That said, the absence of a single neurobiological origin aligns with consensus in clinical research (see *Section 1.2*). In fact, by unifying multiple possible causes under one 'functional umbrella' (Lawson et al., 2014), computational explanations accommodate a wide range of phenotypes and underlying aetiologies (Brock, 2014). As a consequence, novel targeted interventions and individualised practical approaches can be developed (Haker et al., 2016; see *Section 5.3*).

Nevertheless, it can be assumed that these prediction-related sensorimotor atypicalities are unlikely to result from any global deficits in working memory or top-down attentional processing. A mechanistic independence between cognitive and sensorimotor abilities has been proposed in previous research (e.g., van Swieten et al., 2010; Wunsch et al., 2016; Ansuini et al., 2018; Chouinard et al., 2018) and findings from *Studies 1-4* indirectly support these claims. During both object lifting and interceptive racquetball experiments, autistic and non-autistic individuals fixated on overwhelmingly similar sensory cues that were goal-directed and future-orientated in nature. In fact, when attempting to track dynamic virtual ball trajectories in *Studies 3* and *4*, autistic participants utilised a top-down attentional strategy which has been widely associated with visuomotor *expertise* (e.g., Land & McLeod, 2000; Hayhoe et al., 2012; Mann et al., 2013; Mann, 2019). Despite this, they still exhibited poorer overall interception abilities, a finding which has been consistently observed in clinical studies (Green et al., 2002; Vanvuchelen et al., 2007; Whyatt & Craig, 2013a; Ament et al., 2015). So, in contrast with traditional cognitive perspectives (e.g., Ciesielski et al., 1990; Ozonoff et al., 1991; Happé & Frith, 2006; Rajendran & Mitchell, 2007), autistic visuomotor behaviours did not appear to be accompanied by any discernible executive dysfunctions or global attentional biases.

Moreover, *Study 4* implies that sensorimotor issues are unlikely to reflect any broad deficits in extracting hidden environmental probabilities from the world. Here, explicit information about likely task outcomes were provided to participants prior to each trial, in a manner that should alleviate any difficulties with understanding implicit contextual relationships (see Qian & Lipkin, 2011; Gomot & Wicker, 2012; Sinha et al., 2014). However, autistic people showed no significant changes in interceptive visuomotor control following the provision of these statistically-veridical cues. So, impaired action performance levels persisted in the absence of any broad deficits in meta-learning or cognition (as in Manning et al., 2017; Sapey-Triomphe et al., 2021).

Instead, *Studies 3-4* were suggestive of autism-related differences in neuromodulatory gain control. Autistic participants tended to predictively position their gaze in a manner that facilitates the sampling of recent, probabilistically-salient trial outcomes (i.e., bouncy ball trajectories). This increased tendency to 'expect the unexpected' typically occurs when a context is perceived to be uncertain or unstable (i.e., when higher-level precision estimates are low; Yon & Frith, 2021). In keeping with this idea, Lawson *et al.* (2017) found that autistic people overestimate environmental volatility and are disproportionately receptive to sensory inputs during associative learning. *Study 4* demonstrates that these processing features remain even after participants have been explicitly cued about dynamic task probabilities and occurrences of contextual change. Null data findings are perhaps unsurprising here, as precision estimates regulate behaviour implicitly, via hierarchical adjustments in postsynaptic gain (Feldman & Friston, 2010; Adams et al., 2013; Shipp et al., 2013). Such dynamic error signalling is coordinated by classic neuromodulators like noradrenaline, acetylcholine, dopamine, and serotonin (Yu & Dayan, 2003; Friston, 2008; Bland & Schaefer, 2012; Lawson et al., 2021). Many of these systems have been reported to be atypical in autistic populations (e.g., Lake et al., 1977; Perry et al., 2001; Lam et al., 2006; Harrington et al., 2013; Wiggins et al., 2014; Lawson et al., 2017). In fact, Lawson *et al.* (2017) showed that aberrant precision weighting functions correlate with heightened phasic noradrenergic responsivity. Therefore, atypical active inference behaviours in autism could emerge from neuromodulatory differences in the brain, which impair abilities to form stable, statistically-optimal predictions about dynamic sensory environments.

Overall, the present work offers unique theoretical insight into the mechanistic underpinnings of autistic sensorimotor difficulties. In contrast to various cognitive

theories and simple Bayesian frameworks, the ability to make predictions and use top-down information does not appear to be chronically impaired in autism. Instead, movement-related difficulties correspond with subtle, context-sensitive differences in predictive action control. From a computational perspective, findings highlights the role of aberrant precision weighting functions in autistic people. Although these processing atypicalities do not necessarily reflect any single biological or environmental mechanism, they do implicate key neuromodulatory circuits that regulate synaptic activity across the brain. It is hoped that these novel results will influence future practice and be used to enhance clinical sensorimotor interventions for the autism community. As such, various potential applications of this work must now be explored.

5.3. Applications and Future Research

Sensorimotor impairments in autism can bring about various daily living issues, by constraining levels of personal independence, wellness, and overall quality of life (Jasmin et al., 2009; Robledo et al., 2012; Gowen & Hamilton, 2013; Coll et al., 2020). However, current motor skill interventions are lacking in scientific rationale and rarely produce any functional benefits beyond those already associated with gross physical activity (Colombo-Dougovito & Block, 2019). Significant questions remain as to how sensorimotor difficulties can be reduced or managed at a practical level, and the paucity of research in this topic has done little to actually improve the lives of autistic people. As such, there is a serious need for evidence-based research that focuses on *why* autistic people experience sensorimotor impairments and *how* these underlying processes can be enhanced through targeted practical interventions.

A key finding for future practice is the observation that movement-related issues are associated with *context-sensitive* processing differences and not any *chronic* predictive impairments. Indeed, despite being underpinned by subconscious generative beliefs and hierarchical neural networks, active inference in the sensorimotor system proves to be highly responsive to situational factors (e.g., task preferences, estimations of uncertainty, expected risk; Friston et al., 2017). Applied specialists should therefore aim to provide the optimal conditions for helping autistic people perform daily living skills and behaviours. Since the broad ability to make and use predictions does not appear to be impaired in autism, practitioners should specifically be looking to facilitate

the formation of stable, contextually-accurate internal models. Such an approach would align with self-advocacy perspectives of autism, as it puts the emphasis on transforming non-inclusive environments to better accommodate neurodivergent individuals and populations (for recent discussion, see Leadbitter et al., 2021).

To combat difficulties associated with processing environmental uncertainty, it has been suggested that practitioners could teach individuals about the hidden probabilistic regularities that underlie complex daily living tasks (Qian & Lipkin, 2011; Haker et al., 2016). Prior situational information can enhance various neurotypical performances (McRobert et al., 2011; Navia et al., 2013; Gray, 2015; Gray & Cañal-Bruland, 2018; Gredin et al., 2018; Wang et al., 2019) and autistic people have been shown to benefit from explicit contextual cues or priming during social and perceptual tasks (Plaisted et al., 1999; López et al., 2004; Balconi et al., 2012; Vermeulen, 2015; Gowen et al., 2020; Soroor et al., 2021). Although supporting evidence exists in some applied settings (e.g., Hallett et al., 2021), the present work indicates that such an approach may have limited efficacy in dynamic sensorimotor domains. Indeed, autism-related performance impairments in *Study 4* were not alleviated by veridical prior information about current task likelihoods and environmental stability. In fact, swing kinematics appeared *less* efficient under cued trials than during non-cued conditions. In line with these observations, previous research has found that autism-related differences in anticipatory gaze behaviours, neural activity, and perspective-taking remain when individuals are informed about probable trial events (Thillay et al., 2016; Balsters et al., 2017; Greene et al., 2019; Cannon et al., 2021). As such, approaches that attempt to explicitly make uncertain environments 'more understandable' for autistic people have received limited empirical support in the context of dynamic sensorimotor skills.

Nonetheless, there are various alternative methods through which everyday environments could be made more predictable and/or less uncertain for autistic people. For example, Haker and colleagues (2016) advocate the use of step-by-step learning, high-repetition teaching methods, and proactive efforts to minimise surrounding noise. When viewed through the lens active inference, these strategies could help individuals build stable, statistically-optimal action models, while limiting exposure to salient sensory information. In line with this approach, researchers have previously supported the use of structured task environments that change in highly lawful or unsurprising ways (e.g., Rapin, 1997; Qian & Lipkin, 2011; Robic et al., 2015; Lieder et al., 2019).

Indeed, *Study 3* showed that autism-related difficulties in hand-eye coordination are less prominent under stable, as opposed to volatile, task conditions. Moreover, adaptive sensorimotor outcomes have been displayed in interventions that utilise direct and progressive teaching instructions (Colombo-Dougovito & Block, 2019) or blocked practice schedules (Foster et al., 2020). Therefore, the concept of making the world more predictable and stable for autistic people holds significant promise in the context of sensorimotor control.

Furthermore, evidence from high-performance industries present new and alternative techniques through which dynamic sensorimotor control could be improved. Sporting professionals, for example, will frequently implement strategies that reduce future uncertainty, through overlearning key skills and executing familiar pre-performance routines (Boutcher, 1990; Hardy et al., 1996; Cotterill, 2010; see Cappuccio et al., 2020 for active inference perspective). Similarly, aviation pilots regularly undertake prescribed 'flow' procedures that ensure the regular sampling of safety-critical information, while closely simulating a range of possible events in training to reduce future surprise (Landman et al., 2017). Though some of these exact approaches may not readily translate onto more rudimentary daily living activities, the general principles of nurturing goal-relevant action models and preparing for potentially-unexpected sensory events could be incorporated within applied autism practice. For instance, when teaching movement skills like throwing and catching, professionals may wish to use instructions that aim to facilitate the sampling of optimal contextual cues. An example of this could be feedforward gaze training, where individuals are taught where to direct their gaze during key phases of their action responses (see Wood et al., 2017; Wilson & Vine, 2018). Alternatively, service providers could implement familiar routine procedures or simulations that help autistic people prepare for computationally 'noisy' sensory environments (e.g., in healthcare settings: Nicolaidis et al., 2015; Boada & Parellada, 2017; Bradshaw et al., 2019; or when learning to drive: Cox et al., 2020). It must be stressed here that skilled practitioners and members from within the autism community will often be best placed to design targeted and effective sensorimotor interventions. However, it is hoped that these specialists will look beyond traditional clinical conventions and consider novel methodological approaches.

What is clear is that prospective sensorimotor interventions should be individualised and modified according to contextual factors. Aberrant precision weighting functions

could stem from a myriad of mechanisms that differ from person to person (Lawson et al., 2014). As such, the present work exercises caution against the use of pre-packaged, 'one size fits all' practical approaches. Indeed, previous studies suggest that personalised teaching methods can be particularly beneficial for developing autistic movement skills (Bremer et al., 2015; Bremer & Lloyd, 2016) and computational analyses tools could help shape this adaptive learning process (Rosenberg et al., 2015; Haker et al., 2016). Though primarily used for experimental purposes in the present work, technological aids like VR offer notable promise for applied interventions due to their unique ability to customise user experience and simulate immersive 'real-world' interactions (Farley et al., 2019). These methods can serve as a means for making sensory environments more predictable for autistic people, while ensuring that training is conducted in a safe and engaging way (Bradley & Newbutt, 2018). VR also presents a novel means through which training methods can be adapted according to personal preferences or levels of progress in a task (see Zahabi et al., 2020). Whether such sophisticated technological tools are incorporated or not, practitioners should ultimately be looking to foster conditions that are tailored to specific individual needs and adjusted with ongoing skill development (Colombo-Dougovito & Block, 2019).

Moving forward, future research should investigate how context-sensitive predictive control can be enhanced in autistic people to improve their day-to-day lives. The present work offers initial foresight in this line of enquiry, and the focus must now shift onto examining novel approaches for combatting sensorimotor difficulties. Specifically, studies should explore how active inference mechanisms like precision weighting and volatility modulation can be optimised at a practical level, and whether adaptive daily living abilities can be improved through targeted skill interventions. Importantly, evidence has shown that many autistic people struggle in terms of employment opportunities (Knapp et al., 2009; Lounds-Taylor et al., 2015), functional independence (Jasmin et al., 2009), health status (Croen et al., 2015), and general wellbeing (Ikeda et al., 2014; Van Heijst & Geurts, 2015). These practical issues are considered a key priority of research by individuals and policymakers within the autism community (Pellicano et al., 2014; Cusack & Sterry, 2016).

The present work incorporated this practical focus into the design of each study, by centring analyses on naturalistic and unconstrained action behaviours. Indeed, precisely regulated object interactions underpin various daily living skills, like writing,

dressing, or making a cup of tea (Land et al., 1999; Hayhoe & Ballard, 2005; Land, 2009). Similarly, impaired hand-eye coordination abilities can limit participation in physical activity (Must et al., 2015; Scharoun et al., 2017) and contribute to autism-related health and social issues (Sutera et al., 2007; MacDonald et al., 2013; McCoy et al., 2016). It is hoped that future work will continue to pursue these practically-focused outcomes, through developing new evidence-based methodologies that relate to functional quality of life. In particular, research may need to study tasks that are not conventionally assessed in the laboratory but are limited by sensorimotor difficulties (e.g., driving; healthcare experiences; occupational skills; Robledo et al., 2012). By linking such 'real-world' outcomes with data-driven empirical scrutiny, one can both improve the scientific understanding of autism and the daily lives of autistic people.

When conducting this future work, there are some key theoretical issues that require consideration. First, studies should establish the degree to which subtle enhancements in active inference translate onto meaningful 'real-world' effects. Indeed, while sensorimotor expertise is frequently bracketed with optimal predictive control (e.g., Williams et al., 2011; Loffing & Cañal-Bruland, 2017; Fiehler et al., 2019), no studies have formally documented how computational functions are refined during motor learning and applied skill interventions. Researchers are hopeful that autism-related difficulties can be reduced through targeting these underlying mechanisms (Qian & Lipkin, 2011; Sinha et al., 2014; Haker et al., 2016), but future investigations must empirically scrutinise these claims. When doing so, researchers should pay attention to unique inter-individual variability that exists within their datasets. Such enquiry does not necessitate any new 'types' or 'subtypes' of autism to be identified (note: this could be ethically harmful: Marchant & Robert, 2008). Instead, it could simply be recognised that the efficacy of interventions might differ between individuals, and that it is their responsibility to avoid 'averaging out' any potentially-significant responses in their analyses. Autism-related processing differences likely result from a myriad of neuro-biological and situational factors (Lawson et al., 2014), and the development of effective and personalised clinical programmes may thus depend on a study's ability to accommodate for diverse sensorimotor responses and individual phenotypes.

Secondly, research needs to further examine links between anxiety and sensorimotor issues in autism. Previous clinical work has shown that self-reported levels of trait anxiety correlate with sensory sensitivities (Wigham et al., 2015; Neil et al., 2016) and

predictive action responses (Amoruso et al., 2019). These associations are said to be mediated by intolerance of uncertainty (Boulter et al., 2014; Pickard et al., 2020), however *Study 4* found no significant relationships between this key personality construct and measures of visuomotor control. Such results reinforce proposals that intolerance of uncertainty is distinct from hierarchical precision estimates in the brain (Bervoets et al., 2021). From an active inference perspective, it could even be argued that all individuals are 'intolerant' of uncertainty, since we are constantly attempting to minimise it from our surrounding sensory environment (Clark, 2015b; Bervoets et al., 2021). In fact, data from Lawson et al. (2017) and *Studies 3-4* imply that aberrant prediction error responses are likely to create a *greater* sense of uncertainty in autism. Together, it seems that it is these context-sensitive representations of uncertainty (or precision) that affect autistic sensorimotor operations, and not the stable, psycho-behavioural traits reported in intolerance of uncertainty frameworks (e.g., Dugas et al., 1997; Boulter et al., 2014; South & Rodgers, 2017).

Nevertheless, the potential influence of anxiety on autism-related daily living difficulties must not be overlooked. Indeed, many autistic people experience adverse reactions to uncertain environments (e.g., social settings, unfamiliar events; Rutter, 1978) and there are overlapping neuromodulatory systems involved in the regulation of predictive processing and autonomic stress responses (Paulus & Stein, 2006; Blier & El Mansari, 2007; Lawson et al., 2021). The negative effects of anxiety on goal-directed sensorimotor control have been well documented in sport psychology research (Baumeister, 1984; Beilock & Gray, 2007; Wilson, 2008; Gray, 2011; Vine et al., 2016) and have recently been linked with mechanisms of active inference (see Cappuccio et al., 2020). It is also possible that anxiety is a potential *outcome* of aberrant precision weighting operations (Bervoets et al., 2021; Stark et al., 2021), with predictive learning functions seen to shape whether aversive environmental outcomes are perceived to be likely and/or avoidable in the future (Browning et al., 2015). Therefore, anxiety may still contribute to (or interact with) sensorimotor differences in autism, and future work should aim to improve our mechanistic understanding of these relationships (e.g., through the use of pupillometry and cardiovascular analysis: Lawson et al., 2021).

5.4. Limitations of the Thesis

It must first be acknowledged that the current work provides only indirect evidence for the role of aberrant precision weighting in autistic sensorimotor functions. Although *Studies 1-4* show a consistent pattern of context-sensitive results, no formal estimations of model parameters were computed. Furthermore, a number of the observed effects were small in magnitude and should be generalised with caution. Nevertheless, computational studies are often criticised for post-hoc model fitting exercises and a lack of 'real-world' data observations (Maloney & Zhang, 2010; Palmer et al., 2017). In contrast to this, the unconstrained and hypothesis-driven methods from *Studies 1-4* provide unique experimental insight into predictive processing atypicalities during natural movement tasks. Both object lifting and interceptive motor actions were selected for this reason, having previously been shown to follow Bayes-optimal principles in neurotypical populations (Körding & Wolpert, 2004; Battaglia & Schrater, 2007; Arthur & Harris, 2021). Consequently, the present work ties together an array of clinical, sensorimotor, and computational investigatory approaches. Future research should integrate these perspectives further, by examining how clinically-significant action behaviours can be optimised through innovative, evidence-based practical interventions.

When conducting this applied research, it is imperative that investigations are sufficiently powered to detect complex, potentially subtle differences in individual behaviour. Previous studies are often based on limited sample sizes and display a lack of population generalisability (see Gowen & Hamilton, 2013; Whyatt & Craig, 2013a; Coll et al., 2020). To circumvent these issues, the present experiments were designed using *a-priori* sample size calculations (*Appendix A*). Specifically, *Studies 1*-4 were powered to identify any moderate or large statistical effects that existed within the data, in accordance with previous empirical reports (e.g., Z. Wang et al., 2015; Buckingham et al., 2016; Lawson et al., 2017; Arthur et al., 2019) and meta-analyses (e.g., Fournier et al., 2010; see also Coll et al., 2020). These studies may have therefore been unable to detect sensorimotor differences that were small in magnitude. However, such weak statistical effects would be unlikely to highlight any mechanisms that *meaningfully* contribute to autistic daily living difficulties. While such an argument is also true for intervention-based research, this line of enquiry is unlikely to benefit from the high levels of experimental control that were afforded in the lab-based protocols of *Studies*

1-4. As such, practically meaningful differences in sensorimotor behaviour could be moderated by additional factors that are pertinent in 'real-world' clinical programmes (e.g., levels of communication, attention, and required motivation; Haker et al., 2016).

Linked to the point above, a final limitation of the present research is the possible role of extraneous variables. Evidence suggests that autism-related sensorimotor difficulties may be influenced by cognitive abilities, socio-communicative preferences, and co-occurring clinical conditions (e.g., DCD, ADHD: Piek & Dyck, 2004; Fournier et al., 2010; Whyatt & Craig, 2013b). *Studies 1-4* did not employ any IQ subscales, clinical observation techniques, standardised diagnostic checks or motor assessment batteries, and so the effects of these potentially confounding variables remain unclear. Nevertheless, the procedures of *Studies 1-4* were specifically designed to minimise high-level cognitive demands and communicative requirements (as recommended in Haker et al., 2016). Moreover, it has been suggested that these issues can be reduced using non-clinical methodological approaches, which examine associations between autistic-like traits and hypothesis-driven data outcomes across the broader autism phenotype (see Landry & Chouinard, 2016). Indeed, much of the context-sensitive differences that were displayed by autistic participants in this work were also accompanied by complementary trait-based correlations. The fact that these effects replicated in large, *mostly neurotypical* samples is important, as it implies that clinically-related confounds were not driving the key between-group study results. However, as researchers begin to translate these findings into applied practice, they should consider the role of cognitive abilities, communication skills, and co-occurring conditions on any intervention-based sensorimotor outcomes.

5.4. Conclusions

This thesis aimed to investigate the aetiology of sensorimotor differences in autism. Empirical assessment of object lifting and interceptive visuomotor behaviours indicated that autistic movement control is underpinned by context-sensitive differences in predictive action modelling. Specifically, the hierarchical integration of prior information and dynamic sensory cues appears to be atypical in autistic people, which causes difficulties in the processing of uncertain and volatile task conditions. Though likely to vary from person to person, results support proposals of aberrant neuromodulatory

functions in autism. Moving forward, applied specialists should account for these context-sensitive processing differences when developing novel, evidence-based practical interventions. At the same time, researchers must evaluate the most effective methods for developing predictive action models that are both stable and contextually appropriate. Together, this approach could help autistic people improve sensorimotor skills, in a manner that fosters independence and enhances overall quality of life.

References

Adams, R. A., Shipp, S., & Friston, K. J. (2013). Predictions not commands: active inference in the motor system. *Brain Structure and Function, 218*(3), 611-643.

Adams, W. J., Graf, E. W., & Ernst, M. O. (2004). Experience can change the'light-from-above'prior. *Nature Neuroscience, 7*(10), 1057-1058.

Aguinis, H., Gottfredson, R. K., & Joo, H. (2013). Best-practice recommendations for defining, identifying, and handling outliers. *Organizational Research Methods, 16*(2), 270-301.

Aitkin, C. D., Santos, E. M., & Kowler, E. (2013). Anticipatory smooth eye movements in autism spectrum disorder. *PloS one, 8*(12), e83230.

Allen, G., & Courchesne, E. (2003). Differential effects of developmental cerebellar abnormality on cognitive and motor functions in the cerebellum: an fMRI study of autism. *American Journal of Psychiatry, 160*(2), 262-273.

Almeida, R. A., Dickinson, J. E., Maybery, M. T., Badcock, J. C., & Badcock, D. R. (2013). Visual search targeting either local or global perceptual processes differs as a function of autistic-like traits in the typically developing population. *Journal of Autism and Developmental Disorders, 43*(6), 1272-1286.

Amaral, D. G., Schumann, C. M., & Nordahl, C. W. (2008). Neuroanatomy of autism. *Trends in Neurosciences, 31*(3), 137-145.

Ament, K., Mejia, A., Buhlman, R., Erklin, S., Caffo, B., Mostofsky, S., & Wodka, E. (2015). Evidence for specificity of motor impairments in catching and balance in children with autism. *Journal of Autism and Developmental Disorders, 45*(3), 742-751.

Amoruso, L., Narzisi, A., Pinzino, M., Finisguerra, A., Billeci, L., Calderoni, S., . . . Urgesi, C. (2019). Contextual priors do not modulate action prediction in children with autism. *Proceedings of the Royal Society B, 286*(1908), 20191319.

Ansuini, C., Podda, J., Battaglia, F. M., Veneselli, E., & Becchio, C. (2018). One hand, two hands, two people: Prospective sensorimotor control in children with autism. *Developmental Cognitive Neuroscience, 29*, 86-96.

Anzulewicz, A., Sobota, K., & Delafield-Butt, J. T. (2016). Toward the autism motor signature: Gesture patterns during smart tablet gameplay identify children with autism. *Scientific Reports, 6*, 31107.

Arthur, T., & Harris, D. (2021). Predictive eye movements are adjusted in a Bayes-optimal fashion in response to unexpectedly changing environmental probabilities. *Cortex, 145*, 212-225.

Arthur, T., Vine, S., Brosnan, M., & Buckingham, G. (2019). Exploring how material cues drive sensorimotor prediction across different levels of autistic-like traits. *Experimental Brain Research, 237*(9), 2255–2267.

Asperger, H. (1944). Die "Autistischen psychopathen" im kindesalter. *Archiv Für Psychiatrie und Nervenkrankheiten, 117*(1), 76-136.

American Psychiatric Association (2013). *Diagnostic and statistical manual of mental disorders (DSM-V)*. Washington DC: American Psychiatric Association.

Auksztulewicz, R., & Friston, K. (2016). Repetition suppression and its contextual determinants in predictive coding. *Cortex, 80*, 125-140.

Austin, E. J. (2005). Personality correlates of the broader autism phenotype as assessed by the Autism Spectrum Quotient (AQ). *Personality and Individual Differences, 38*(2), 451-460.

Baio, J., Wiggins, L., Christensen, D. L., Maenner, M. J., Daniels, J., Warren, Z., . . . White, T. (2018). Prevalence of autism spectrum disorder among children aged 8 years—autism and developmental disabilities monitoring network, 11 sites, United States, 2014. *MMWR Surveillance Summaries, 67*(6).

Balconi, M., Amenta, S., & Ferrari, C. (2012). Emotional decoding in facial expression, scripts and videos: A comparison between normal, autistic and Asperger children. *Research in Autism Spectrum Disorders, 6*(1), 193-203.

Baldi, P., & Itti, L. (2010). Of bits and wows: A Bayesian theory of surprise with applications to attention. *Neural Networks, 23*(5), 649-666.

Balsters, J. H., Apps, M. A., Bolis, D., Lehner, R., Gallagher, L., & Wenderoth, N. (2017). Disrupted prediction errors index social deficits in autism spectrum disorder. *Brain, 140*(1), 235-246.

Barkley, R. A. (2012). *Executive functions: What they are, how they work, and why they evolved*. New York: Guilford Press.

Barnard-Brak, L., Brewer, A., Chesnut, S., Richman, D., & Schaeffer, A. M. (2016). The sensitivity and specificity of the social communication questionnaire for autism spectrum with respect to age. *Autism Research, 9*(8), 838-845.

Barnes, K. A., Howard Jr, J. H., Howard, D. V., Gilotty, L., Kenworthy, L., Gaillard, W. D., & Vaidya, C. J. (2008). Intact implicit learning of spatial context and temporal sequences in childhood autism spectrum disorder. *Neuropsychology, 22*(5), 563-570.

Baron-Cohen, S., Wheelwright, S., Skinner, R., Martin, J., & Clubley, E. (2001). The autism-spectrum quotient (AQ): Evidence from asperger syndrome/high-functioning autism, malesand females, scientists and mathematicians. *Journal of Autism and Developmental Disorders, 31*(1), 5-17.

Bastos, A. M., Usrey, W. M., Adams, R. A., Mangun, G. R., Fries, P., & Friston, K. J. (2012). Canonical microcircuits for predictive coding. *Neuron, 76*(4), 695-711.

Battaglia, P. W., & Schrater, P. R. (2007). Humans trade off viewing time and movement duration to improve visuomotor accuracy in a fast reaching task. *Journal of Neuroscience, 27*(26), 6984-6994.

Baumeister, R. F. (1984). Choking under pressure: self-consciousness and paradoxical effects of incentives on skillful performance. *Journal of Personality and Social Psychology, 46*(3), 610-620.

Bayes, T. (1763). An essay towards solving a problem in the doctrine of chances. *Philosophical Transactions 53*, 370-418.

Beck, J. M., Latham, P. E., & Pouget, A. (2011). Marginalization in neural circuits with divisive normalization. *Journal of Neuroscience, 31*(43), 15310-15319.

Bedford, R., Pickles, A., & Lord, C. (2016). Early gross motor skills predict the subsequent development of language in children with autism spectrum disorder. *Autism Research, 9*(9), 993-1001.

Beesley, T., Nguyen, K. P., Pearson, D., & Le Pelley, M. E. (2015). Uncertainty and predictiveness determine attention to cues during human associative learning. *Quarterly Journal of Experimental Psychology, 68*(11), 2175-2199.

Behrens, T. E., Woolrich, M. W., Walton, M. E., & Rushworth, M. F. (2007). Learning the value of information in an uncertain world. *Nature Neuroscience, 10*(9), 1214-1221.

Beilock, S. L., & Gray, R. (2007). Why do athletes choke under pressure? In G. Tenenbaum & R. Eklund (Eds.), *Handbook of Sport Psychology* (pp. 425-444). Hoboken, NJ, US: John Wiley & Sons, Inc.

Bejjanki, V. R., Knill, D. C., & Aslin, R. N. (2016). Learning and inference using complex generative models in a spatial localization task. *Journal of Vision, 16*(5), 9-22.

Ben-Sasson, A., Hen, L., Fluss, R., Cermak, S. A., Engel-Yeger, B., & Gal, E. (2009). A meta-analysis of sensory modulation symptoms in individuals with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 39*(1), 1-11.

Berkeley, S. L., Zittel, L. L., Pitney, L. V., & Nichols, S. E. (2001). Locomotor and object control skills of children diagnosed with autism. *Adapted Physical Activity Quarterly, 18*(4), 405-416.

Bernstein, N. (1967). *The co-ordination and regulation of movements*. London: Pergamon.

Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2003). Motion perception in autism: a “complex” issue. *Journal of Cognitive Neuroscience, 15*(2), 218-225.

Bertone, A., Mottron, L., Jelenic, P., & Faubert, J. (2005). Enhanced and diminished visuo-spatial information processing in autism depends on stimulus complexity. *Brain, 128*(10), 2430-2441.

Berument, S. K., Rutter, M., Lord, C., Pickles, A., & Bailey, A. (1999). Autism screening questionnaire: diagnostic validity. *The British Journal of Psychiatry, 175*(5), 444-451.

Bervoets, J., Milton, D., & Van de Cruys, S. (2021). Autism and intolerance of uncertainty: an ill-fitting pair. *Trends in Cognitive Sciences, 25*(12), 1009-1010.

Bhat, A. N., Landa, R. J., & Galloway, J. C. (2011). Current perspectives on motor functioning in infants, children, and adults with autism spectrum disorders. *Physical Therapy, 91*(7), 1116-1129.

Binaee, K., & Diaz, G. (2019). Movements of the eyes and hands are coordinated by a common predictive strategy. *Journal of Vision, 19*(12), 3-19.

Bingham, G. P., Bradley, A., Bailey, M., & Vinner, R. (2001). Accommodation, occlusion, and disparity matching are used to guide reaching: A comparison of actual versus virtual environments. *Journal of Experimental Psychology: Human Perception and Performance, 27*(6), 1314-1334.

Blakemore, S.-J., Tavassoli, T., Calò, S., Thomas, R. M., Catmur, C., Frith, U., & Haggard, P. (2006). Tactile sensitivity in Asperger syndrome. *Brain and Cognition, 61*(1), 5-13.

Blanche, E. I., Reinoso, G., Chang, M. C., & Bodison, S. (2012). Proprioceptive processing difficulties among children with autism spectrum disorders and developmental disabilities. *American Journal of Occupational Therapy, 66*(5), 621-624.

Bland, A., & Schaefer, A. (2012). Unexpected uncertainty, volatility and decision-making. *Frontiers in Neuroscience, 6*, 00085.

Blier, P., & El Mansari, M. (2007). The importance of serotonin and noradrenaline in anxiety. *International Journal of Psychiatry in Clinical Practice, 11*(2), 16-23.

Bo, J., Lee, C.-M., Colbert, A., & Shen, B. (2016). Do children with autism spectrum disorders have motor learning difficulties? *Research in Autism Spectrum Disorders, 23*, 50-62.

Boada, L., & Parellada, M. (2017). Seeing the doctor without fear: www.doctortea.org for the desensitization for medical visits in autism spectrum disorders. *Revista de Psiquiatría y Salud Mental, 10*(1), 28-32.

Bogdashina, O. (2003). *Sensory perceptual issues in autism and asperger syndrome: different sensory experiences-different perceptual worlds*. London, UK: Jessica Kingsley Publishers.

Boulter, C., Freeston, M., South, M., & Rodgers, J. (2014). Intolerance of uncertainty as a framework for understanding anxiety in children and adolescents with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 44*(6), 1391-1402.

Boutcher, S. H. (1990). The role of performance routines in sport. In G. Jones & L. Hardy (Eds.), *Stress and performance in sport* (pp. 231–246). Chichester, UK: Wiley.

Boyd, B. A., Baranek, G. T., Sideris, J., Poe, M. D., Watson, L. R., Patten, E., & Miller, H. (2010). Sensory features and repetitive behaviors in children with autism and developmental delays. *Autism Research, 3*(2), 78-87.

Bradley, R., & Newbutt, N. (2018). Autism and virtual reality head-mounted displays: A state of the art systematic review. *Journal of Enabling Technologies, 12*(3), 101-113.

Bradshaw, P., Pellicano, E., van Driel, M., & Urbanowicz, A. (2019). How can we support the healthcare needs of autistic adults without intellectual disability? *Current Developmental Disorders Reports, 6*(2), 45-56.

Brandwein, A. B., Foxe, J. J., Butler, J. S., Frey, H.-P., Bates, J. C., Shulman, L. H., & Molholm, S. (2015). Neurophysiological indices of atypical auditory processing and multisensory integration are associated with symptom severity in autism. *Journal of Autism and Developmental Disorders, 45*(1), 230-244.

Brayanov, J. B., & Smith, M. A. (2010). Bayesian and "anti-Bayesian" biases in sensory integration for action and perception in the size–weight illusion. *Journal of Neurophysiology, 103*(3), 1518-1531.

Bremer, E., Balogh, R., & Lloyd, M. (2015). Effectiveness of a fundamental motor skill intervention for 4-year-old children with autism spectrum disorder: A pilot study. *Autism, 19*(8), 980-991.

Bremer, E., & Lloyd, M. (2016). School-based fundamental-motor-skill intervention for children with autism-like characteristics: an exploratory study. *Adapted Physical Activity Quarterly, 33*(1), 66-88.

Brenner, L. A., Turner, K. C., & Müller, R.-A. (2007). Eye movement and visual search: are there elementary abnormalities in autism? *Journal of Autism and Developmental Disorders, 37*(7), 1289-1309.

Brock, J. (2012). Alternative Bayesian accounts of autistic perception: comment on Pellicano and Burr. *Trends in Cognitive Sciences, 16*(12), 573-574.

Brock, J. (2014). Combining the old and the new. *The Psychologist, 27*(10), 750-753.

Brosnan, M. J., Scott, F. J., Fox, S., & Pye, J. (2004). Gestalt processing in autism: Failure to process perceptual relationships and the implications for contextual understanding. *Journal of Child Psychology and Psychiatry, 45*(3), 459-469.

Brown, H., Adams, R. A., Parees, I., Edwards, M., & Friston, K. (2013). Active inference, sensory attenuation and illusions. *Cognitive Processing, 14*(4), 411-427.

Brown, H. R., & Friston, K. J. (2012). Dynamic causal modelling of precision and synaptic gain in visual perception—an EEG study. *Neuroimage, 63*(1), 223-231.

Brown, J., Aczel, B., Jiménez, L., Kaufman, S. B., & Grant, K. P. (2010). Intact implicit learning in autism spectrum conditions. *Quarterly Journal of Experimental Psychology, 63*(9), 1789-1812.

Browning, M., Behrens, T. E., Jocham, G., O'reilly, J. X., & Bishop, S. J. (2015). Anxious individuals have difficulty learning the causal statistics of aversive environments. *Nature Neuroscience, 18*(4), 590-596.

Buckingham, G. (2014). Getting a grip on heaviness perception: a review of weight illusions and their probable causes. *Experimental Brain Research, 232*(6), 1623-1629.

Buckingham, G., & Goodale, M. A. (2013). Size matters: a single representation underlies our perceptions of heaviness in the size-weight illusion. *PLoS One, 8*(1), e54709.

Buckingham, G., Michelakakis, E. E., & Rajendran, G. (2016). The influence of prior knowledge on perception and action: relationships to autistic traits. *Journal of Autism and Developmental Disorders, 46*(5), 1716-1724.

Burack, J. A. (1994). Selective attention deficits in persons with autism: preliminary evidence of an inefficient attentional lens. *Journal of Abnormal Psychology, 103*(3), 535-543.

Burdet, E., Osu, R., Franklin, D. W., Milner, T. E., & Kawato, M. (2001). The central nervous system stabilizes unstable dynamics by learning optimal impedance. *Nature, 414*(6862), 446-449.

Burge, J., Ernst, M. O., & Banks, M. S. (2008). The statistical determinants of adaptation rate in human reaching. *Journal of Vision, 8*(4), 20-40.

Buswell, G. T. (1920). *An experimental study of the eye-voice span in reading*: University of Chicago.

Campione, G. C., Piazza, C., Villa, L., & Molteni, M. (2016). Three-dimensional kinematic analysis of prehension movements in young children with autism spectrum disorder: new insights on motor impairment. *Journal of Autism and Developmental Disorders, 46*(6), 1985-1999.

Cañal-Bruland, R., Filius, M., & Oudejans, R. (2015). Sitting on a fastball. *Journal of Motor Behavior, 47*(4), 267-270.

Cannon, J., O'Brien, A. M., Bungert, L., & Sinha, P. (2021). Prediction in Autism Spectrum Disorder: A Systematic Review of Empirical Evidence. *Autism Research, 14*(4), 604-630.

Cappuccio, M. L., Kirchhoff, M. D., Alnajjar, F., & Tani, J. (2020). Unfulfilled prophecies in sport performance: Active inference and the choking effect. *Journal of Consciousness Studies, 27*(3-4), 152-184.

Carleton, R. N., Norton, M. P. J., & Asmundson, G. J. (2007). Fearing the unknown: A short version of the Intolerance of Uncertainty Scale. *Journal of Anxiety Disorders, 21*(1), 105-117.

Casanova, M. F., Buxhoeveden, D. P., Switala, A. E., & Roy, E. (2002). Minicolumnar pathology in autism. *Neurology, 58*(3), 428-432.

Casartelli, L., Molteni, M., & Ronconi, L. (2016). So close yet so far: Motor anomalies impacting on social functioning in autism spectrum disorder. *Neuroscience & Biobehavioral Reviews, 63*, 98-105.

Cascio, C., McGlone, F., Folger, S., Tannan, V., Baranek, G., Pelphrey, K. A., & Essick, G. (2008). Tactile perception in adults with autism: a multidimensional psychophysical study. *Journal of Autism and Developmental Disorders, 38*(1), 127-137.

Cashaback, J. G., McGregor, H. R., Pun, H. C., Buckingham, G., & Gribble, P. L. (2017). Does the sensorimotor system minimize prediction error or select the most likely prediction during object lifting? *Journal of Neurophysiology, 117*(1), 260-274.

Cashin, A., & Barker, P. (2009). The triad of impairment in autism revisited. *Journal of Child and Adolescent Psychiatric Nursing, 22*(4), 189-193.

Cavallo, A., Romeo, L., Ansuini, C., Battaglia, F., Nobili, L., Pontil, M., . . . Becchio, C. (2021). Identifying the signature of prospective motor control in children with autism. *Scientific Reports, 11*, 3165.

Cerminara, N. L., Apps, R., & Marple-Horvat, D. E. (2009). An internal model of a moving visual target in the lateral cerebellum. *The Journal of Physiology, 587*(2), 429-442.

Cesqui, B., Mezzetti, M., Lacquaniti, F., & d'Avella, A. (2015). Gaze behavior in one-handed catching and its relation with interceptive performance: What the eyes can't tell. *PLoS One, 10*(3), e0119445.

Cesqui, B., van De Langenberg, R., Lacquaniti, F., & d'Avella, A. (2013). A novel method for measuring gaze orientation in space in unrestrained head conditions. *Journal of Vision, 13*(8), 28-49.

Chaidez, V., Hansen, R. L., & Hertz-Picciotto, I. (2014). Gastrointestinal problems in children with autism, developmental delays or typical development. *Journal of Autism and Developmental Disorders, 44*(5), 1117-1127.

Chang, C.-H., Wade, M. G., Stoffregen, T. A., Hsu, C.-Y., & Pan, C.-Y. (2010). Visual tasks and postural sway in children with and without autism spectrum disorders. *Research in Developmental Disabilities, 31*(6), 1536-1542.

Charpentier, A. (1891). Analyse experimentale de quelques elements de la sensation de poids. *Archive de Physiologie Normale et Pathologiques, 3*, 122-135.

Chattington, M., Wilson, M., Ashford, D., & Marple-Horvat, D. (2007). Eye–steering coordination in natural driving. *Experimental Brain Research, 180*(1), 1-14.

Chen, L.-C., Su, W.-C., Ho, T.-L., Lu, L., Tsai, W.-C., Chiu, Y.-N., & Jeng, S.-F. (2019). Postural Control and Interceptive Skills in Children With Autism Spectrum Disorder. *Physical Therapy, 99*(9), 1231-1241.

Chouinard, P. A., Leonard, G., & Paus, T. (2005). Role of the primary motor and dorsal premotor cortices in the anticipation of forces during object lifting. *Journal of Neuroscience, 25*(9), 2277-2284.

Chouinard, P. A., Royals, K. A., Landry, O., & Sperandio, I. (2018). The Shepard illusion is reduced in children with an autism spectrum disorder because of perceptual rather than attentional mechanisms. *Frontiers in Psychology, 9*, 2452-2481.

Ciesielski, K. T., Courchesne, E., & Elmasian, R. (1990). Effects of focused selective attention tasks on event-related potentials in autistic and normal individuals. *Electroencephalography and Clinical Neurophysiology, 75*(3), 207-220.

Clark, A. (2015a). Radical predictive processing. *The Southern Journal of Philosophy, 53*, 3-27.

Clark, A. (2015b). *Surfing uncertainty: Prediction, action, and the embodied mind*: Oxford University Press.

Coll, S.-M., Foster, N. E., Meilleur, A., Brambati, S. M., & Hyde, K. L. (2020). Sensorimotor skills in autism spectrum disorder: A meta-analysis. *Research in Autism Spectrum Disorders, 76*, 101570.

Colombo-Dougovito, A. M., & Block, M. E. (2019). Fundamental motor skill interventions for children and adolescents on the autism spectrum: a literature review. *Review Journal of Autism and Developmental Disorders, 6*(2), 159-171.

Cook, E., & Leventhal, B. L. (1996). The serotonin system in autism. *Current Opinion in Pediatrics, 8*, 348-354.

Cook, J. L., Blakemore, S.-J., & Press, C. (2013). Atypical basic movement kinematics in autism spectrum conditions. *Brain, 136*(9), 2816-2824.

Cooper, N. R., Simpson, A., Till, A., Simmons, K., & Puzzo, I. (2013). Beta event-related desynchronization as an index of individual differences in processing human facial expression: further investigations of autistic traits in typically developing adults. *Frontiers in Human Neuroscience, 7*(159), 1-8.

Corbetta, M., Akbudak, E., Conturo, T. E., Snyder, A. Z., Ollinger, J. M., Drury, H. A., . . . Van Essen, D. C. (1998). A common network of functional areas for attention and eye movements. *Neuron, 21*(4), 761-773.

Corbetta, M., Patel, G., & Shulman, G. L. (2008). The reorienting system of the human brain: from environment to theory of mind. *Neuron, 58*(3), 306-324.

Costa, V. D., & Rudebeck, P. H. (2016). More than meets the eye: the relationship between pupil size and locus coeruleus activity. *Neuron, 89*(1), 8-10.

Cotterill, S. (2010). Pre-performance routines in sport: Current understanding and future directions. *International Review of Sport and Exercise Psychology, 3*(2), 132-153.

Courchesne, E. (1997). Brainstem, cerebellar and limbic neuroanatomical abnormalities in autism. *Current Opinion in Neurobiology, 7*(2), 269-278.

Courchesne, E., Kilman, B. A., Galambos, R., & Lincoln, A. J. (1984). Autism: processing of novel auditory information assessed by event-related brain potentials. *Electroencephalography and Clinical Neurophysiology/Evoked Potentials Section, 59*(3), 238-248.

Courchesne, E., Press, G., & Yeung-Courchesne, R. (1993). Parietal lobe abnormalities detected with MR in patients with infantile autism. *American Journal of Roentgenology, 160*(2), 387-393.

Cox, D. J., Brown, T., Ross, V., Moncrief, M., Schmitt, R., Gaffney, G., & Reeve, R. (2017). Can youth with autism spectrum disorder use virtual reality driving

simulation training to evaluate and improve driving performance? An exploratory study. *Journal of Autism and Developmental Disorders, 47*(8), 2544-2555.

Cox, D. J., Owens, J. M., Barnes, L., Moncrief, M., Boukhechba, M., Buckman, S., . . . Wotring, B. (2020). A pilot study comparing newly licensed drivers with and without autism and experienced drivers in simulated and on-road driving. *Journal of Autism and Developmental Disorders, 50*(4), 1258-1268.

Crippa, A., Forti, S., Perego, P., & Molteni, M. (2013). Eye-hand coordination in children with high functioning autism and Asperger's disorder using a gap-overlap paradigm. *Journal of Autism and Developmental Disorders, 43*(4), 841-850.

Crippa, A., Salvatore, C., Perego, P., Forti, S., Nobile, M., Molteni, M., & Castiglioni, I. (2015). Use of machine learning to identify children with autism and their motor abnormalities. *Journal of Autism and Developmental Disorders, 45*(7), 2146-2156.

Croen, L. A., Zerbo, O., Qian, Y., Massolo, M. L., Rich, S., Sidney, S., & Kripke, C. (2015). The health status of adults on the autism spectrum. *Autism, 19*(7), 814-823.

Cross, R. (2010). Bounce of an oval shaped football. *Sports Technology, 3*(3), 168-180.

Croydon, A., Karaminis, T., Neil, L., Burr, D., & Pellicano, E. (2017). The light-from-above prior is intact in autistic children. *Journal of Experimental Child Psychology, 161*, 113-125.

Currie, J., & MacLeod, W. B. (2017). Diagnosing expertise: Human capital, decision making, and performance among physicians. *Journal of Labor Economics, 35*(1), 1-43.

Cusack, J., & Sterry, R. (2016). *Your questions: Shaping future autism research*. In. Retrieved from https://www.autistica.org.uk/downloads/files/Autism-Top-10-Your-Priorities-for-Autism-Research.pdf

D'Cruz, A.-M., Mosconi, M. W., Steele, S., Rubin, L. H., Luna, B., Minshew, N., & Sweeney, J. A. (2009). Lateralized response timing deficits in autism. *Biological Psychiatry, 66*(4), 393-397.

Dakin, S., & Frith, U. (2005). Vagaries of visual perception in autism. *Neuron, 48*(3), 497-507.

Dalton, K. M., Nacewicz, B. M., Johnstone, T., Schaefer, H. S., Gernsbacher, M. A., Goldsmith, H. H., . . . Davidson, R. J. (2005). Gaze fixation and the neural circuitry of face processing in autism. *Nature Neuroscience, 8*(4), 519-526.

David, F. J., Baranek, G. T., Giuliani, C. A., Mercer, V. S., Poe, M. D., & Thorpe, D. E. (2009). A pilot study: coordination of precision grip in children and adolescents with high functioning autism. *Pediatric Physical Therapy, 21*(2), 205.

David, F. J., Baranek, G. T., Wiesen, C., Miao, A. F., & Thorpe, D. E. (2012). Coordination of precision grip in 2–6 years-old children with autism spectrum disorders compared to children developing typically and children with developmental disabilities. *Frontiers in Integrative Neuroscience, 6*, 122.

DeBolt, L., Clinton, E., & Ball, A. (2010). The effects of an adapted physical education program on children with autism: A case study. *Kentucky Newsletter for Health, Physical Education, Recreation & Dance, 47*, 24-27.

Del Popolo Cristaldi, F., Mento, G., Sarlo, M., & Buodo, G. (2021). Dealing with uncertainty: A high-density EEG investigation on how intolerance of uncertainty affects emotional predictions. *PloS one, 16*(7), e0254045.

den Ouden, H. E., Daunizeau, J., Roiser, J., Friston, K. J., & Stephan, K. E. (2010). Striatal prediction error modulates cortical coupling. *Journal of Neuroscience, 30*(9), 3210-3219.

Denckla, M. B. (1985). Revised neurological examination and subtle signs. *Psychopharmacol Bulletin, 21*, 773-779.

Deravet, N., Blohm, G., de Xivry, J.-J. O., & Lefèvre, P. (2018). Weighted integration of short-term memory and sensory signals in the oculomotor system. *Journal of Vision, 18*(5), 16-35.

Di Martino, A., Ross, K., Uddin, L. Q., Sklar, A. B., Castellanos, F. X., & Milham, M. P. (2009). Functional brain correlates of social and nonsocial processes in autism spectrum disorders: an activation likelihood estimation meta-analysis. *Biological Psychiatry, 65*(1), 63-74.

Diamond, A. (2000). Close interrelation of motor development and cognitive development and of the cerebellum and prefrontal cortex. *Child Development, 71*(1), 44-56.

Diaz, G., Cooper, J., & Hayhoe, M. (2013). Memory and prediction in natural gaze control. *Philosophical Transactions of the Royal Society B: Biological Sciences, 368*(1628), 20130064.

Dichter, G. S., Felder, J. N., & Bodfish, J. W. (2009). Autism is characterized by dorsal anterior cingulate hyperactivation during social target detection. *Social Cognitive and Affective Neuroscience, 4*(3), 215-226.

Ding, J., Powell, D., & Jiang, Y. (2009). Dissociable frontal controls during visible and memory-guided eye-tracking of moving targets. *Human Brain Mapping, 30*(11), 3541-3552.

Domínguez-Zamora, F. J., Gunn, S. M., & Marigold, D. S. (2018). Adaptive gaze strategies to reduce environmental uncertainty during a sequential visuomotor behaviour. *Scientific Reports, 8*(1), 14112.

Donnellan, A., Hill, D., & Leary, M. (2013). Rethinking autism: implications of sensory and movement differences for understanding and support. *Frontiers in Integrative Neuroscience, 6*(124), 124-134. doi:10.3389/fnint.2012.00124

Dugas, M. J., Freeston, M. H., & Ladouceur, R. (1997). Intolerance of uncertainty and problem orientation in worry. *Cognitive Therapy and Research, 21*(6), 593-606.

Duronjić, M., & Válková, H. (2010). The influence of early intervention movement programs on motor skills development in preschoolers with autism spectrum disorder (case studies). *Acta Gymnica, 40*(2), 37-45.

Dyck, M. J., Piek, J. P., Hay, D., Smith, L., & Hallmayer, J. (2006). Are abilities abnormally interdependent in children with autism? *Journal of Clinical Child and Adolescent Psychology, 35*(1), 20-33.

Dziuk, M., Larson, J. G., Apostu, A., Mahone, E., Denckla, M., & Mostofsky, S. (2007). Dyspraxia in autism: association with motor, social, and communicative deficits. *Developmental Medicine & Child Neurology, 49*(10), 734-739.

Eastough, D., & Edwards, M. G. (2007). Movement kinematics in prehension are affected by grasping objects of different mass. *Experimental Brain Research, 176*(1), 193-198.

Ecker, C., Bookheimer, S. Y., & Murphy, D. G. (2015). Neuroimaging in autism spectrum disorder: brain structure and function across the lifespan. *The Lancet Neurology, 14*(11), 1121-1134.

Ego, C., Bonhomme, L., de Xivry, J.-J. O., Da Fonseca, D., Lefèvre, P., Masson, G. S., & Deruelle, C. (2016). Behavioral characterization of prediction and internal models in adolescents with autistic spectrum disorders. *Neuropsychologia, 91*, 335-345.

Ernst, M. O. (2009). Perceptual learning: inverting the size–weight illusion. *Current Biology, 19*(1), R23-R25.

Estes, A., Zwaigenbaum, L., Gu, H., John, T. S., Paterson, S., Elison, J. T., . . . Schultz, R. T. (2015). Behavioral, cognitive, and adaptive development in infants with autism spectrum disorder in the first 2 years of life. *Journal of Neurodevelopmental Disorders, 7*(1), 24-34.

Ewbank, M. P., Pell, P. J., Powell, T. E., Von dem Hagen, E. A., Baron-Cohen, S., & Calder, A. J. (2017). Repetition suppression and memory for faces is reduced in adults with autism spectrum conditions. *Cerebral Cortex, 27*(1), 92-103.

Ewbank, M. P., Rhodes, G., von dem Hagen, E. A., Powell, T. E., Bright, N., Stoyanova, R. S., . . . Calder, A. J. (2014). Repetition suppression in ventral visual cortex is diminished as a function of increasing autistic traits. *Cerebral Cortex, 25*(10), 3381-3393.

Ewing, L., Leach, K., Pellicano, E., Jeffery, L., & Rhodes, G. (2013). Reduced face aftereffects in autism are not due to poor attention. *PloS One, 8*(11), e81353.

Fabbri-Destro, M., Cattaneo, L., Boria, S., & Rizzolatti, G. (2009). Planning actions in autism. *Experimental Brain Research, 192*(3), 521-525.

Faisal, A. A., Selen, L. P., & Wolpert, D. M. (2008). Noise in the nervous system. *Nature Reviews Neuroscience, 9*(4), 292-303.

Farley, O. R., Spencer, K., & Baudinet, L. (2019). Virtual Reality in Sports Coaching, Skill Acquisition and Application to Surfing: A Review. *Journal of Human Sport and Exercise, 15*(3), 535-548.

Fatemi, S. H., Aldinger, K. A., Ashwood, P., Bauman, M. L., Blaha, C. D., Blatt, G. J., . . . Dickson, P. E. (2012). Consensus paper: pathological role of the cerebellum in autism. *The Cerebellum, 11*(3), 777-807.

Fatemi, S. H., Halt, A. R., Realmuto, G., Earle, J., Kist, D. A., Thuras, P., & Merz, A. (2002). Purkinje cell size is reduced in cerebellum of patients with autism. *Cellular and Molecular Neurobiology, 22*(2), 171-175.

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G* Power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods, 39*(2), 175-191.

Feldman, H., & Friston, K. (2010). Attention, uncertainty, and free-energy. *Frontiers in Human Neuroscience, 4*(215), 1-23.

Fiehler, K., Brenner, E., & Spering, M. (2019). Prediction in goal-directed action. *Journal of Vision, 19*(9), 10-30.

Flash, T., & Hogan, N. (1985). The coordination of arm movements: an experimentally confirmed mathematical model. *Journal of Neuroscience, 5*(7), 1688-1703.

Fooken, J., & Spering, M. (2019). Eye movements as a readout of sensorimotor decision processes. *Journal of Neurophysiology, 123(4),* 1439-1447.

Foster, N. C., Bennett, S. J., Causer, J., Elliott, D., Bird, G., & Hayes, S. J. (2019). Getting off to a shaky start: specificity in planning and feedforward control during sensorimotor learning in autism spectrum disorder. *Autism Research, 13(3),* 423-435.

Foster, N. C., Bennett, S. J., Causer, J., Elliott, D., Bird, G., & Hayes, S. J. (2020). Facilitating sensorimotor integration via blocked practice underpins imitation learning of atypical biological kinematics in autism spectrum disorder. *Autism, 24*(6), 1494-1505.

Fournier, K. A., Hass, C. J., Naik, S. K., Lodha, N., & Cauraugh, J. H. (2010). Motor coordination in autism spectrum disorders: a synthesis and meta-analysis. *Journal of Autism and Developmental Disorders, 40*(10), 1227-1240.

Franklin, D. W., & Wolpert, D. M. (2011). Computational mechanisms of sensorimotor control. *Neuron, 72*(3), 425-442.

Franks, I. M., Sanderson, D. J., & Van Donkelaar, P. (1990). A comparison of directly recorded and derived acceleration data in movement control research. *Human Movement Science, 9*(6), 573-582.

Freeth, M., Chapman, P., Ropar, D., & Mitchell, P. (2010). Do gaze cues in complex scenes capture and direct the attention of high functioning adolescents with ASD? Evidence from eye-tracking. *Journal of Autism and Developmental Disorders, 40*(5), 534-547.

Friston, K. (2005). A theory of cortical responses. *Philosophical transactions of the Royal Society B: Biological sciences, 360*(1456), 815-836.

Friston, K. (2008). Hierarchical models in the brain. *PLoS Comput Biol, 4*(11), e1000211.

Friston, K. (2010). The free-energy principle: a unified brain theory? *Nature Reviews Neuroscience, 11*(2), 127-138.

Friston, K. (2011). What is optimal about motor control? *Neuron, 72*(3), 488-498.

Friston, K., Adams, R., Perrinet, L., & Breakspear, M. (2012). Perceptions as hypotheses: saccades as experiments. *Frontiers in Psychology, 3*, 151-171.

Friston, K., Daunizeau, J., Kilner, J., & Kiebel, S. (2010). Action and behavior: a free-energy formulation. *Biological Cybernetics, 102*(3), 227-260.

Friston, K., FitzGerald, T., Rigoli, F., Schwartenbeck, P., & Pezzulo, G. (2017). Active inference: a process theory. *Neural Computation, 29*(1), 1-49.

Friston, K., & Kiebel, S. (2009). Predictive coding under the free-energy principle. *Philosophical Transactions of the Royal Society B: Biological Sciences, 364*(1521), 1211-1221.

Friston, K., Kilner, J., & Harrison, L. (2006). A free energy principle for the brain. *Journal of Physiology, 100*(1-3), 70-87.

Friston, K., Lawson, R., & Frith, C. (2013). On hyperpriors and hypopriors: comment on Pellicano and Burr. *Trends in Cognitive Sciences, 17*(1), 1.

Friston, K., Rigoli, F., Ognibene, D., Mathys, C., Fitzgerald, T., & Pezzulo, G. (2015). Active inference and epistemic value. *Cognitive Neuroscience, 6*(4), 187-214.

Friston, K., Samothrakis, S., & Montague, R. (2012). Active inference and agency: optimal control without cost functions. *Biological Cybernetics, 106*(8-9), 523-541.

Friston, K., Stephan, K., Montague, R., & Dolan, R. (2014). Computational psychiatry: the brain as a phantastic organ. *The Lancet Psychiatry, 1*(2), 148-158.

Friston, K. J., Daunizeau, J., & Kiebel, S. J. (2009). Reinforcement learning or active inference? *PloS One, 4*(7), e6421.

Froese, T., & Ikegami, T. (2013). The brain is not an isolated “black box,” nor is its goal to become one. *Behavioral and Brain Sciences, 36*(3), 213-214.

Fuentes, C. T., Mostofsky, S. H., & Bastian, A. J. (2009). Children with autism show specific handwriting impairments. *Neurology, 73*(19), 1532-1537.

Fulceri, F., Tonacci, A., Lucaferro, A., Apicella, F., Narzisi, A., Vincenti, G., . . . Contaldo, A. (2018). Interpersonal motor coordination during joint actions in children with and without autism spectrum disorder: The role of motor information. *Research in Developmental Disabilities, 80*, 13-23.

Furneaux, S., & Land, M. F. (1999). The effects of skill on the eye–hand span during musical sight–reading. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 266*(1436), 2435-2440.

Garrido, M. I., Kilner, J. M., Kiebel, S. J., & Friston, K. J. (2009). Dynamic causal modeling of the response to frequency deviants. *Journal of Neurophysiology, 101*(5), 2620-2631.

Gaymard, B., Lynch, J., Ploner, C., Condy, C., & Rivaud-Pechoux, S. (2003). The parieto-collicular pathway: anatomical location and contribution to saccade generation. *European Journal of Neuroscience, 17*(7), 1518-1526.

Gepner, B., & Mestre, D. R. (2002). Brief report: postural reactivity to fast visual motion differentiates autistic from children with Asperger syndrome. *Journal of Autism and Developmental Disorders, 32*(3), 231-238.

Gernsbacher, M. A., Sauer, E. A., Geye, H. M., Schweigert, E. K., & Hill Goldsmith, H. (2008). Infant and toddler oral-and manual-motor skills predict later speech fluency in autism. *Journal of Child Psychology and Psychiatry, 49*(1), 43-50.

Gernsbacher, M. A., Stevenson, J. L., & Dern, S. (2017). Specificity, contexts, and reference groups matter when assessing autistic traits. *PloS one, 12*(2), e0171931.

Ghaziuddin, M., & Butler, E. (1998). Clumsiness in autism and Asperger syndrome: A further report. *Journal of Intellectual Disability Research, 42*(1), 43-48.

Ghaziuddin, M., Butler, E., Tsai, L., & Ghaziuddin, N. (1994). Is clumsiness a marker for Asperger syndrome? *Journal of Intellectual Disability Research, 38*(5), 519-527.

Gidley-Larson, J., & Mostofsky, S. (2006). Motor deficits in autism. In *Autism: A neurological disorder of early brain development* (pp. 231-247). London: Mac Keith Press.

Gidley-Larson, J. C., Bastian, A. J., Donchin, O., Shadmehr, R., & Mostofsky, S. H. (2008). Acquisition of internal models of motor tasks in children with autism. *Brain, 131*(11), 2894-2903.

Gillberg, C., & Coleman, M. (1992). *The biology of the autistic syndromes*. Oxford: MacKeith.

Glazebrook, C., Gonzalez, D., Hansen, S., & Elliott, D. (2009). The role of vision for online control of manual aiming movements in persons with autism spectrum disorders. *Autism, 13*(4), 411-433.

Glazebrook, C. M., Elliott, D., & Lyons, J. (2006). A kinematic analysis of how young adults with and without autism plan and control goal-directed movements. *Motor Control, 10*(3), 244-264.

Goldberg, M. C., Lasker, A., Zee, D. S., Garth, E., Tien, A., & Landa, R. (2002). Deficits in the initiation of eye movements in the absence of a visual target in adolescents with high functioning autism. *Neuropsychologia, 40*(12), 2039-2049.

Gomot, M., Blanc, R., Clery, H., Roux, S., Barthelemy, C., & Bruneau, N. (2011). Candidate electrophysiological endophenotypes of hyper-reactivity to change in autism. *Journal of Autism and Developmental Disorders, 41*(6), 705-714.

Gomot, M., & Wicker, B. (2012). A challenging, unpredictable world for people with autism spectrum disorder. *International Journal of Psychophysiology, 83*(2), 240-247.

Gordon, A. M., Forssberg, H., Johansson, R. S., & Westling, G. (1991). Visual size cues in the programming of manipulative forces during precision grip. *Experimental Brain Research, 83*(3), 477-482.

Gordon, B., & Stark, S. (2007). Procedural learning of a visual sequence in individuals with autism. *Focus on Autism and Other Developmental Disabilities, 22*(1), 14-22.

Goris, J., Braem, S., Nijhof, A. D., Rigoni, D., Deschrijver, E., Van de Cruys, S., . . . Brass, M. (2018). Sensory prediction errors are less modulated by global context in autism spectrum disorder. *Biological Psychiatry: Cognitive Neuroscience and Neuroimaging, 3*(8), 667-674.

Gowen, E., & Hamilton, A. F. d. C. (2013). Motor abilities in autism: a review using a computational context. *Journal of Autism and Developmental Disorders, 43*(2), 323-344.

Gowen, E., & Miall, R. C. (2005). Behavioural aspects of cerebellar function in adults with Asperger syndrome. *The Cerebellum, 4*(4), 279-289.

Gowen, E., Vabalas, A., Casson, A. J., & Poliakoff, E. (2020). Instructions to attend to an observed action increase imitation in autistic adults. *Autism, 24*(3), 730-743.

Gray, R. (2011). Links between attention, performance pressure, and movement in skilled motor action. *Current Directions in Psychological Science, 20*(5), 301-306.

Gray, R. (2015). *The moneyball problem: What is the best way to present situational statistics to an athlete?* Paper presented at the 59th International Annual Meeting of the Human Factors and Ergonomics Society, HFES 2014.

Gray, R., & Cañal-Bruland, R. (2018). Integrating visual trajectory and probabilistic information in baseball batting. *Psychology of Sport and Exercise, 36*, 123-131.

Gredin, N. V., Bishop, D. T., Broadbent, D. P., Tucker, A., & Williams, A. M. (2018). Experts integrate explicit contextual priors and environmental information to improve anticipation efficiency. *Journal of Experimental Psychology: Applied, 24*(4), 16-24.

Green, D., Baird, G., Barnett, A. L., Henderson, L., Huber, J., & Henderson, S. E. (2002). The severity and nature of motor impairment in Asperger's syndrome: a comparison with specific developmental disorder of motor function. *Journal of Child Psychology and Psychiatry, 43*(5), 655-668.

Green, D., Charman, T., Pickles, A., Chandler, S., Loucas, T., Simonoff, E., & Baird, G. (2009). Impairment in movement skills of children with autistic spectrum disorders. *Developmental Medicine & Child Neurology, 51*(4), 311-316.

Greene, R. K., Zheng, S., Kinard, J. L., Mosner, M. G., Wiesen, C. A., Kennedy, D. P., & Dichter, G. S. (2019). Social and nonsocial visual prediction errors in autism spectrum disorder. *Autism Research, 12*(6), 878-883.

Gregory, R. L. (1980). Perceptions as hypotheses. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences, 290*(1038), 181-197.

Guha, T., Yang, Z., Grossman, R. B., & Narayanan, S. S. (2016). A computational study of expressive facial dynamics in children with autism. *IEEE Transactions on Affective Computing, 9*(1), 14-20.

Hadjikhani, N., Chabris, C. F., Joseph, R. M., Clark, J., McGrath, L., Aharon, I., . . . Harris, G. J. (2004). Early visual cortex organization in autism: an fMRI study. *Neuroreport, 15*(2), 267-270.

Hadjiosif, A. M., & Smith, M. A. (2015). Flexible control of safety margins for action based on environmental variability. *Journal of Neuroscience, 35*(24), 9106-9121.

Haker, H., Schneebeli, M., & Stephan, K. E. (2016). Can Bayesian theories of autism spectrum disorder help improve clinical practice? *Frontiers in Psychiatry, 7*(107), **1-17**.

Hallett, V., Mueller, J., Breese, L., Hollett, M., Beresford, B., Irvine, A., . . . Charman, T. (2021). Introducing 'Predictive Parenting': A feasibility study of a new group parenting intervention targeting emotional and behavioral difficulties in children with autism spectrum disorder. *Journal of Autism and Developmental Disorders, 51*(1), 323-333.

Hamilton, A. F. d. C., Joyce, D. W., Flanagan, J. R., Frith, C. D., & Wolpert, D. M. (2007). Kinematic cues in perceptual weight judgement and their origins in box lifting. *Psychological Research, 71*(1), 13-21.

Hamner, T., & Vivanti, G. (2019). Eye-Tracking Research in Autism Spectrum Disorder: What Are We Measuring and for What Purposes? *Current Developmental Disorders Reports, 6*(2), 37-44.

Hannant, P., Tavassoli, T., & Cassidy, S. (2016). The role of sensorimotor difficulties in autism spectrum conditions. *Frontiers in Neurology, 7*(124).

Happé, F., & Frith, U. (2006). The weak coherence account: detail-focused cognitive style in autism spectrum disorders. *Journal of Autism and Developmental Disorders, 36*(1), 5-25.

Happé, F., Ronald, A., & Plomin, R. (2006). Time to give up on a single explanation for autism. *Nature Neuroscience, 9*(10), 1218-1220.

Hardy, L., Jones, G., & Gould, D. (1996). *Understanding psychological preparation for sport: Theory and practice of elite performers*. Chichester, UK: Wiley.

Harrington, R. A., Lee, L. C., Crum, R. M., Zimmerman, A. W., & Hertz-Picciotto, I. (2013). Serotonin hypothesis of autism: implications for selective serotonin reuptake inhibitor use during pregnancy. *Autism Research, 6*(3), 149-168.

Harris, D. J., Buckingham, G., Wilson, M. R., & Vine, S. J. (2019). Virtually the same? How impaired sensory information in virtual reality may disrupt vision for action. *Experimental Brain Research, 237*(11), 2761-2766.

Haswell, C. C., Izawa, J., Dowell, L. R., Mostofsky, S. H., & Shadmehr, R. (2009). Representation of internal models of action in the autistic brain. *Nature Neuroscience, 12*(8), 970-972.

Hayes, S. J., Andrew, M., Foster, N. C., Elliott, D., Gowen, E., & Bennett, S. J. (2018). Sensorimotor learning and associated visual perception are intact but unrelated in autism spectrum disorder. *Autism Research, 11*(2), 296-304.

Hayhoe, M., & Ballard, D. (2005). Eye movements in natural behavior. *Trends in Cognitive Sciences, 9*(4), 188-194.

Hayhoe, M., Mennie, N., Sullivan, B., & Gorgos, K. (2002). *The role of internal models and prediction in catching balls.* Paper presented at the Proceedings of AAAI fall symposium series.

Hayhoe, M. M., & Matthis, J. S. (2018). Control of gaze in natural environments: effects of rewards and costs, uncertainty and memory in target selection. *Interface focus, 8*(4), e20180009.

Hayhoe, M. M., McKinney, T., Chajka, K., & Pelz, J. B. (2012). Predictive eye movements in natural vision. *Experimental Brain Research, 217*(1), 125-136.

Haznedar, M. M., Buchsbaum, M. S., Metzger, M., Solimando, A., Spiegel-Cohen, J., & Hollander, E. (1997). Anterior cingulate gyrus volume and glucose metabolism in autistic disorder. *American Journal of Psychiatry, 154*(8), 1047-1050.

Hebert, E. P., Landin, D., & Solmon, M. A. (1996). Practice schedule effects on the performance and learning of low-and high-skilled students: An applied study. *Research Quarterly for Exercise and Sport, 67*(1), 52-58.

Heinen, S. J., Badler, J. B., & Ting, W. (2005). Timing and velocity randomization similarly affect anticipatory pursuit. *Journal of Vision, 5*(6), 493-503.

Helm, F., Cañal-Bruland, R., Mann, D. L., Troje, N. F., & Munzert, J. (2020). Integrating situational probability and kinematic information when anticipating disguised movements. *Psychology of Sport and Exercise, 46*, 101607.

Helmholtz, H. V. (1867). “Handbuch der physiologischen Optik” In G. Karsten (Ed.), *Allgemeine Encyklopädie der Physik* (Vol. 9). Leipzig: Voss.

Henderson, J. M. (2003). Human gaze control during real-world scene perception. *Trends in Cognitive Sciences, 7*(11), 498-504.

Henderson, S. E., & Sugden, D. A. (1992). *Movement Assessment Battery for Children*. London: The Psychological Corporation.

Herbert, M. R., Ziegler, D. A., Makris, N., Filipek, P. A., Kemper, T. L., Normandin, J. J., . . . Caviness Jr, V. S. (2004). Localization of white matter volume increase in autism and developmental language disorder. *Annals of Neurology, 55*(4), 530-540.

Hippler, K., & Klicpera, C. (2003). A retrospective analysis of the clinical case records of ‘autistic psychopaths’ diagnosed by Hans Asperger and his team at the University Children's Hospital, Vienna. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 358*(1430), 291-301.

Hohwy, J. (2013). *The predictive mind*: Oxford University Press.

Hollander, E., Anagnostou, E., Chaplin, W., Esposito, K., Haznedar, M. M., Licalzi, E., . . . Buchsbaum, M. (2005). Striatal volume on magnetic resonance imaging and repetitive behaviors in autism. *Biological Psychiatry, 58*(3), 226-232.

Holm, S. (1979). A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics*, 65-70.

Hudson, T. E., Maloney, L. T., & Landy, M. S. (2007). Movement planning with probabilistic target information. *Journal of Neurophysiology, 98*(5), 3034-3046.

Hughes, C. (1996). Brief report: Planning problems in autism at the level of motor control. *Journal of Autism and Developmental Disorders, 26*(1), 99-107.

Hughes, C., Russell, J., & Robbins, T. W. (1994). Evidence for executive dysfunction in autism. *Neuropsychologia, 32*(4), 477-492.

Ikeda, E., Hinckson, E., & Krägeloh, C. (2014). Assessment of quality of life in children and youth with autism spectrum disorder: A critical review. *Quality of Life Research, 23*(4), 1069-1085.

Izawa, J., Pekny, S. E., Marko, M. K., Haswell, C. C., Shadmehr, R., & Mostofsky, S. H. (2012). Motor learning relies on integrated sensory inputs in ADHD, but over-selectively on proprioception in autism spectrum conditions. *Autism Research, 5*(2), 124-136.

Jaber, M. (2016). The cerebellum as a major player in motor disturbances related to autistic syndrome disorders. *L'encephale, 43*(2), 170-175.

Jacobs, R. A. (1999). Optimal integration of texture and motion cues to depth. *Vision Research, 39*(21), 3621-3629.

Jarrold, C., & Brock, J. (2004). To match or not to match? Methodological issues in autism-related research. *Journal of Autism and Developmental Disorders, 34*(1), 81-86.

Jasmin, E., Couture, M., McKinley, P., Reid, G., Fombonne, E., & Gisel, E. (2009). Sensori-motor and daily living skills of preschool children with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 39*(2), 231-241.

Jazayeri, M., & Shadlen, M. N. (2010). Temporal context calibrates interval timing. *Nature Neuroscience, 13*(8), 1020-1028.

Jenmalm, P., Schmitz, C., Forssberg, H., & Ehrsson, H. H. (2006). Lighter or heavier than predicted: neural correlates of corrective mechanisms during erroneously programmed lifts. *Journal of Neuroscience, 26*(35), 9015-9021.

Jeste, S. S., Kirkham, N., Senturk, D., Hasenstab, K., Sugar, C., Kupelian, C., . . . Norona, A. (2015). Electrophysiological evidence of heterogeneity in visual statistical learning in young children with ASD. *Developmental Science, 18*(1), 90-105.

Johansson, R. S., & Westling, G. (1988). Coordinated isometric muscle commands adequately and erroneously programmed for the weight during lifting task with precision grip. *Experimental Brain Research, 71*(1), 59-71.

Johansson, R. S., Westling, G., Bäckström, A., & Flanagan, J. R. (2001). Eye–hand coordination in object manipulation. *Journal of Neuroscience, 21*(17), 6917-6932.

Johnson, B., Rinehart, N., Papadopoulos, N., Tonge, B., Millist, L., White, O., & Fielding, J. (2012). A closer look at visually guided saccades in autism and Asperger's disorder. *Frontiers in integrative neuroscience, 6*, 99-106.

Johnson, B. P., Lum, J. A., Rinehart, N. J., & Fielding, J. (2016). Ocular motor disturbances in autism spectrum disorders: Systematic review and comprehensive meta-analysis. *Neuroscience & Biobehavioral Reviews, 69*, 260-279.

Johnson, B. P., Rinehart, N. J., White, O., Millist, L., & Fielding, J. (2013). Saccade adaptation in autism and Asperger's disorder. *Neuroscience, 243*, 76-87.

Jones, V., & Prior, M. (1985). Motor imitation abilities and neurological signs in autistic children. *Journal of Autism and Developmental Disorders, 15*(1), 37-46.

Jones, W., Carr, K., & Klin, A. (2008). Absence of preferential looking to the eyes of approaching adults predicts level of social disability in 2-year-old toddlers with autism spectrum disorder. *Archives of General Psychiatry, 65*(8), 946-954.

Joseph, R. M., Keehn, B., Connolly, C., Wolfe, J. M., & Horowitz, T. S. (2009). Why is visual search superior in autism spectrum disorder? *Developmental Science, 12*(6), 1083-1096.

Kanner, L. (1943). Autistic disturbances of affective contact. *Nervous Child, 2*(3), 217-250.

Karaminis, T., Cicchini, G. M., Neil, L., Cappagli, G., Aagten-Murphy, D., Burr, D., & Pellicano, E. (2016). Central tendency effects in time interval reproduction in autism. *Scientific Reports, 6*(1), 28570.

Karmel, B. Z., Gardner, J. M., Meade, L. S., Cohen, I. L., London, E., Flory, M. J., . . . Parab, S. (2010). Early medical and behavioral characteristics of NICU infants later classified with ASD. *Pediatrics, 126*(3), 457-467.

Karvelis, P., Seitz, A. R., Lawrie, S. M., & Seriès, P. (2018). Autistic traits, but not schizotypy, predict increased weighting of sensory information in Bayesian visual integration. *ELife, 7*, e34115.

Kassner, M., Patera, W., & Bulling, A. (2014). *Pupil: an open source platform for pervasive eye tracking and mobile gaze-based interaction.* Paper presented at the Adjunct Proceedings of the 2014 ACM International Joint Conference on Pervasive and Ubiquitous Computing (UbiComp).

Kenny, L., Hattersley, C., Molins, B., Buckley, C., Povey, C., & Pellicano, E. (2016). Which terms should be used to describe autism? Perspectives from the UK autism community. *Autism, 20*(4), 442-462.

Ketcheson, L., Hauck, J., & Ulrich, D. (2017). The effects of an early motor skill intervention on motor skills, levels of physical activity, and socialization in young children with autism spectrum disorder: A pilot study. *Autism, 21*(4), 481-492.

Kiebel, S. J., Von Kriegstein, K., Daunizeau, J., & Friston, K. J. (2009). Recognizing sequences of sequences. *PLoS Computational Biology, 5*(8), e1000464.

Kleinhans, N. M., Johnson, L. C., Richards, T., Mahurin, R., Greenson, J., Dawson, G., & Aylward, E. (2009). Reduced neural habituation in the amygdala and social impairments in autism spectrum disorders. *American Journal of Psychiatry, 166*(4), 467-475.

Klin, A., Jones, W., Schultz, R., Volkmar, F., & Cohen, D. (2002). Visual fixation patterns during viewing of naturalistic social situations as predictors of social competence in individuals with autism. *Archives of General Psychiatry, 59*(9), 809-816.

Knapp, M., Romeo, R., & Beecham, J. (2009). Economic cost of autism in the UK. *Autism, 13*(3), 317-336.

Knill, D. C., & Pouget, A. (2004). The Bayesian brain: the role of uncertainty in neural coding and computation. *Trends in Neurosciences, 27*(12), 712-719.

Knill, D. C., & Saunders, J. A. (2003). Do humans optimally integrate stereo and texture information for judgments of surface slant? *Vision Research, 43*(24), 2539-2558.

Koh, H. C., Milne, E., & Dobkins, K. (2010). Spatial contrast sensitivity in adolescents with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 40*(8), 978-987.

Kohen-Raz, R., Volkman, F. R., & Cohen, D. J. (1992). Postural control in children with autism. *Journal of Autism and Developmental Disorders, 22*(3), 419-432.

Kok, P., & de Lange, F. P. (2015). Predictive coding in sensory cortex. In B. U. Forstmann & W. E-J (Eds.), *An Introduction to Model-based Cognitive Neuroscience* (pp. 221-244). New York, NY: Springer.

Körding, K. (2007). Decision theory: what" should" the nervous system do? *Science, 318*(5850), 606-610.

Körding, K. P., Beierholm, U., Ma, W. J., Quartz, S., Tenenbaum, J. B., & Shams, L. (2007). Causal inference in multisensory perception. *PLoS one, 2*(9), e943.

Körding, K. P., & Wolpert, D. M. (2004). Bayesian integration in sensorimotor learning. *Nature, 427*(6971), 244-247.

Krassanakis, V., Filippakopoulou, V., & Nakos, B. (2014). EyeMMV toolbox: An eye movement post-analysis tool based on a two-step spatial dispersion threshold for fixation identification. *Journal of Eye Movement Research, 7*(1).

Kwon, O.-S., & Knill, D. C. (2013). The brain uses adaptive internal models of scene statistics for sensorimotor estimation and planning. *Proceedings of the National Academy of Sciences, 110*(11), E1064-E1073.

Lai, M. C., Lombardo, M. V., & Baron-Cohen, S. (2014). Autism. *The Lancet, 383*, 896-910.

Lake, C. R., Ziegler, M. G., & Murphy, D. L. (1977). Increased norepinephrine levels and decreased dopamine-β-hydroxylase activity in primary autism. *Archives of General Psychiatry, 34*(5), 553-556.

Lam, K. S., Aman, M. G., & Arnold, L. E. (2006). Neurochemical correlates of autistic disorder: a review of the literature. *Research in Developmental Disabilities, 27*(3), 254-289.

Land, M. F. (2009). Vision, eye movements, and natural behavior. *Visual Neuroscience, 26*(1), 51-62.

Land, M. F., & Furneaux, S. (1997). The knowledge base of the oculomotor system. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences, 352*(1358), 1231-1239.

Land, M. F., & Lee, D. N. (1994). Where we look when we steer. *Nature, 369*(6483), 742-744.

Land, M. F., & McLeod, P. (2000). From eye movements to actions: how batsmen hit the ball. *Nature Neuroscience, 3*(12), 1340-1345.

Land, M. F., Mennie, N., & Rusted, J. (1999). Eye movements and the roles of vision in activities of daily living: making a cup of tea. *Perception, 28*(4), 1311-1328.

Land, M. F., & Tatler, B. W. (2001). Steering with the head: The visual strategy of a racing driver. *Current Biology, 11*(15), 1215-1220.

Landman, A., Groen, E. L., Van Paassen, M., Bronkhorst, A. W., & Mulder, M. (2017). Dealing with unexpected events on the flight deck: a conceptual model of startle and surprise. *Human Factors, 59*(8), 1161-1172.

Landry, O., & Chouinard, P. A. (2016). Why we should study the broader autism phenotype in typically developing populations. *Journal of Cognition and Development, 17*(4), 584-595.

Larson, J., & Mostofsky, S. H. (2008). Evidence that the pattern of visuomotor sequence learning is altered in children with autism. *Autism Research, 1*(6), 341-353.

Lawson, R. P., Bisby, J., Nord, C. L., Burgess, N., & Rees, G. (2021). The Computational, Pharmacological, and Physiological Determinants of Sensory Learning under Uncertainty. *Current Biology, 31*(1), 163-172.

Lawson, R. P., Mathys, C., & Rees, G. (2017). Adults with autism overestimate the volatility of the sensory environment. *Nature Neuroscience, 20*(9), 1293-1299.

Lawson, R. P., Rees, G., & Friston, K. J. (2014). An aberrant precision account of autism. *Frontiers in Human Neuroscience, 8*, 302.

Leadbitter, K., Buckle, K. L., Ellis, C., & Dekker, M. (2021). Autistic Self-Advocacy and the Neurodiversity Movement: Implications for Autism Early Intervention Research and Practice. *Frontiers in Psychology, 12*, 782.

Leary, M. R., & Hill, D. A. (1996). Moving on: autism and movement disturbance. *Mental Retardation, 34*(1), 39-53.

Lee, T. S., Yang, C. F., Romero, R. D., & Mumford, D. (2002). Neural activity in early visual cortex reflects behavioral experience and higher-order perceptual saliency. *Nature Neuroscience, 5*(6), 589-597.

Leigh, R. J., & Zee, D. S. (2006). *The Neurology of Eye Movements* (Fourth Edition ed.): Oxford University Press.

Lephart, S. M., Riemann, B. L., & Fu, F. H. (2000). Introduction to the Sensorimotor System. In L. S. M & F. F. H (Eds.), *Proprioception and Neuromuscular Control in Joint Stability* (pp. 37-51). Champaign, IL: Human Kinetics.

Li, C.-L., Aivar, M. P., Tong, M. H., & Hayhoe, M. M. (2018). Memory shapes visual search strategies in large-scale environments. *Scientific Reports, 8*(1), 4324-4335.

Licari, M. K., Reynolds, J. E., Tidman, S., Ndiaye, S., Sekaran, S. N., Reid, S. L., & Lay, B. S. (2018). Visual tracking behaviour of two-handed catching in boys with developmental coordination disorder. *Research in Developmental Disabilities, 83*, 280-286.

Lieder, I., Adam, V., Frenkel, O., Jaffe-Dax, S., Sahani, M., & Ahissar, M. (2019). Perceptual bias reveals slow-updating in autism and fast-forgetting in dyslexia. *Nature Neuroscience, 22*(2), 256-264.

Lix, L. M., Keselman, J. C., & Keselman, H. J. (1996). Consequences of assumption violations revisited: A quantitative review of alternatives to the one-way analysis of variance F test. *Review of Educational Research, 66*(4), 579-619.

Loffing, F., & Cañal-Bruland, R. (2017). Anticipation in sport. *Current Opinion in Psychology, 16*, 6-11.

López, B., Donnelly, N., Hadwin, J., & Leekam, S. (2004). Face processing in high-functioning adolescents with autism: Evidence for weak central coherence. *Visual Cognition, 11*(6), 673-688.

Lord, C., Elsabbagh, M., Baird, G., & Veenstra-Vanderweele, J. (2018). Autism spectrum disorder. *The Lancet, 392*(10146), 508-520.

Lord, C., Risi, S., Lambrecht, L., Cook, E. H., Leventhal, B. L., DiLavore, P. C., . . . Rutter, M. (2000). The Autism Diagnostic Observation Schedule—Generic: A standard measure of social and communication deficits associated with the spectrum of autism. *Journal of Autism and Developmental Disorders, 30*(3), 205-223.

Lounds-Taylor, J., Henninger, N. A., & Mailick, M. R. (2015). Longitudinal patterns of employment and postsecondary education for adults with autism and average-range IQ. *Autism, 19*(7), 785-793.

Luna, B., Doll, S. K., Hegedus, S. J., Minshew, N. J., & Sweeney, J. A. (2007). Maturation of executive function in autism. *Biological Psychiatry, 61*(4), 474-481.

MacDonald, M., Lord, C., & Ulrich, D. (2013). The relationship of motor skills and adaptive behavior skills in young children with autism spectrum disorders. *Research in Autism Spectrum Disorders, 7*(11), 1383-1390.

Maiello, G., Paulun, V. C., Klein, L. K., & Fleming, R. W. (2018). The sequential-weight illusion. *i-Perception, 9*(4), 93-99.

Maloney, L. T., & Zhang, H. (2010). Decision-theoretic models of visual perception and action. *Vision Research, 50*(23), 2362-2374.

Manjiviona, J., & Prior, M. (1995). Comparison of Asperger syndrome and high-functioning autistic children on a test of motor impairment. *Journal of Autism and Developmental Disorders, 25*(1), 23-39.

Mann, D. L. (2019). Predictive processing in the control of interceptive motor actions. In M. L. Cappuccio (Ed.), *Handbook of Embodied Cognition and Sport Psychology* (pp. 651–668). Cambridge, Massachusetts The MIT Press.

Mann, D. L., Nakamoto, H., Logt, N., Sikkink, L., & Brenner, E. (2019). Predictive eye movements when hitting a bouncing ball. *Journal of Vision, 19*(14), 28-49.

Mann, D. L., Spratford, W., & Abernethy, B. (2013). The head tracks and gaze predicts: how the world's best batters hit a ball. *PloS one, 8*(3), e58289.

Mann, D. T., Williams, A. M., Ward, P., & Janelle, C. M. (2007). Perceptual-cognitive expertise in sport: A meta-analysis. *Journal of Sport and Exercise Psychology, 29*(4), 457-478.

Manning, C., Kilner, J., Neil, L., Karaminis, T., & Pellicano, E. (2017). Children on the autism spectrum update their behaviour in response to a volatile environment. *Developmental Science, 20*(5), e12435.

Manoach, D., Lindgren, K., & Barton, J. (2004). Deficient saccadic inhibition in Asperger's disorder and the social-emotional processing disorder. *Journal of Neurology, Neurosurgery & Psychiatry, 75*(12), 1719-1726.

Marchant, G. E., & Robert, J. S. (2008). Genetic testing for autism predisposition: Ethical, legal and social challenges. *Houston Journal of Health Law & Policy, 9*, 203-235.

Martin, K. B., Hammal, Z., Ren, G., Cohn, J. F., Cassell, J., Ogihara, M., . . . Messinger, D. S. (2018). Objective measurement of head movement differences in children with and without autism spectrum disorder. *Molecular Autism, 9*(1), 14-24.

Martineau, J., Schmitz, C., Assaiante, C., Blanc, R., & Barthélémy, C. (2004). Impairment of a cortical event-related desynchronisation during a bimanual load-lifting task in children with autistic disorder. *Neuroscience Letters, 367*(3), 298-303.

Masterton, B. A., & Biederman, G. B. (1983). Proprioceptive versus visual control in autistic children. *Journal of Autism and Developmental Disorders, 13*(2), 141-152.

Mathys, C., Daunizeau, J., Friston, K. J., & Stephan, K. E. (2011). A Bayesian foundation for individual learning under uncertainty. *Frontiers in Human Neuroscience, 5*, 39-59.

Mathys, C. D., Lomakina, E. I., Daunizeau, J., Iglesias, S., Brodersen, K. H., Friston, K. J., & Stephan, K. E. (2014). Uncertainty in perception and the Hierarchical Gaussian Filter. *Frontiers in Human Neuroscience, 8*, 825-849.

Matthis, J. S., Yates, J. L., & Hayhoe, M. M. (2018). Gaze and the control of foot placement when walking in natural terrain. *Current Biology, 28*(8), 1224-1233.

Maurer, R. G., & Damasio, A. R. (1982). Childhood autism from the point of view of behavioral neurology. *Journal of Autism and Developmental Disorders, 12*(2), 195-205.

McCoy, S. M., Jakicic, J. M., & Gibbs, B. B. (2016). Comparison of obesity, physical activity, and sedentary behaviors between adolescents with autism spectrum disorders and without. *Journal of Autism and Developmental Disorders, 46*(7), 2317-2326.

McLaughlin, S. C. (1967). Parametric adjustment in saccadic eye movements. *Perception & Psychophysics, 2*(8), 359-362.

McRobert, A. P., Ward, P., Eccles, D. W., & Williams, A. M. (2011). The effect of manipulating context-specific information on perceptual–cognitive processes during a simulated anticipation task. *British Journal of Psychology, 102*(3), 519-534.

Miall, R. C., Christensen, L. O., Cain, O., & Stanley, J. (2007). Disruption of state estimation in the human lateral cerebellum. *PLoS Biol, 5*(11), e316.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience, 24*(1), 167-202.

Minshew, N. J., Luna, B., & Sweeney, J. A. (1999). Oculomotor evidence for neocortical systems but not cerebellar dysfunction in autism. *Neurology, 52*(5), 917-917.

Mitchell, M. L., & Jolley, J. M. (2013). *Research Design Explained* (8th ed.). Belmont, CA: Wadsworth.

Miyahara, M., Tsujii, M., Hori, M., Nakanishi, K., Kageyama, H., & Sugiyama, T. (1997). Brief report: motor incoordination in children with Asperger syndrome and learning disabilities. *Journal of Autism and Developmental Disorders, 27*(5), 595-603.

Miyazaki, M., Nozaki, D., & Nakajima, Y. (2005). Testing Bayesian models of human coincidence timing. *Journal of Neurophysiology, 94*(1), 395-399.

Molloy, C. A., Dietrich, K. N., & Bhattacharya, A. (2003). Postural stability in children with autism spectrum disorder. *Journal of Autism and Developmental Disorders, 33*(6), 643-652.

Moraes, R., Lewis, M. A., & Patla, A. E. (2004). Strategies and determinants for selection of alternate foot placement during human locomotion: influence of spatial and temporal constraints. *Experimental Brain Research, 159*(1), 1-13.

Mori, S., Matsuyama, K., Mori, F., & Nakajima, K. (2001). Supraspinal sites that induce locomotion in the vertebrate central nervous system. In E. Ruzicka, M. Hallett, & J. Jankovic (Eds.), *Advances in Neurology: Gait Disorders* (Vol. 87). Philadelphia: Lippincott Williams & Wilkins.

Mosconi, M., Kay, M., D'cruz, A.-M., Seidenfeld, A., Guter, S., Stanford, L., & Sweeney, J. (2009). Impaired inhibitory control is associated with higher-order repetitive behaviors in autism spectrum disorders. *Psychological Medicine, 39*(9), 1559 -1566.

Mosconi, M. W., Luna, B., Kay-Stacey, M., Nowinski, C. V., Rubin, L. H., Scudder, C., . . . Sweeney, J. A. (2013). Saccade adaptation abnormalities implicate dysfunction of cerebellar-dependent learning mechanisms in autism spectrum disorders (ASD). *PLoS One, 8*(5), e63709.

Mosconi, M. W., Mohanty, S., Greene, R. K., Cook, E. H., Vaillancourt, D. E., & Sweeney, J. A. (2015). Feedforward and feedback motor control abnormalities implicate cerebellar dysfunctions in autism spectrum disorder. *Journal of Neuroscience, 35*(5), 2015-2025.

Mosconi, M. W., & Sweeney, J. A. (2015). Sensorimotor dysfunctions as primary features of autism spectrum disorders. *Science China Life Sciences, 58*(10), 1016-1023.

Mostofsky, S. H., Bunoski, R., Morton, S. M., Goldberg, M. C., & Bastian, A. J. (2004). Children with autism adapt normally during a catching task requiring the cerebellum. *Neurocase, 10*(1), 60-64.

Mostofsky, S. H., Goldberg, M. C., Landa, R. J., & Denckla, M. B. (2000). Evidence for a deficit in procedural learning in children and adolescents with autism: implications for cerebellar contribution. *Journal of the International Neuropsychological Society, 6*(7), 752-759.

Mostofsky, S. H., Powell, S. K., Simmonds, D. J., Goldberg, M. C., Caffo, B., & Pekar, J. J. (2009). Decreased connectivity and cerebellar activity in autism during motor task performance. *Brain, 132*(9), 2413-2425.

Mottron, L., Dawson, M., Soulieres, I., Hubert, B., & Burack, J. (2006). Enhanced perceptual functioning in autism: An update, and eight principles of autistic perception. *Journal of Autism and Developmental Disorders, 36*(1), 27-43.

Mottron, L., Mineau, S., Martel, G., Bernier, C. S.-C., Berthiaume, C., Dawson, M., . . . Faubert, J. (2007). Lateral glances toward moving stimuli among young children with autism: Early regulation of locally oriented perception? *Development and Psychopathology, 19*(1), 23-36.

Müller, R.-A., Cauich, C., Rubio, M. A., Mizuno, A., & Courchesne, E. (2004). Abnormal activity patterns in premotor cortex during sequence learning in autistic patients. *Biological psychiatry, 56*(5), 323-332.

Müller, S., & Abernethy, B. (2012). Expert anticipatory skill in striking sports: A review and a model. *Research Quarterly for Exercise and Sport, 83*(2), 175-187.

Mumford, D. (1992). On the computational architecture of the neocortex. *Biological Cybernetics, 66*(3), 241-251.

Murphy, C. P., Jackson, R. C., Cooke, K., Roca, A., Benguigui, N., & Williams, A. M. (2016). Contextual information and perceptual-cognitive expertise in a dynamic, temporally-constrained task. *Journal of Experimental Psychology: Applied, 22*(4), 455-470.

Murray, N. P., & Janelle, C. M. (2003). Anxiety and performance: A visual search examination of the processing efficiency theory. *Journal of Sport and Exercise Psychology, 25*(2), 171-187.

Murray, S. O., Kersten, D., Olshausen, B. A., Schrater, P., & Woods, D. L. (2002). Shape perception reduces activity in human primary visual cortex. *Proceedings of the National Academy of Sciences, 99*(23), 15164-15169.

Must, A., Phillips, S., Curtin, C., & Bandini, L. G. (2015). Barriers to physical activity in children with autism spectrum disorders: relationship to physical activity and screen time. *Journal of Physical Activity and Health, 12*(4), 529-534.

Nassar, M. R., Wilson, R. C., Heasly, B., & Gold, J. I. (2010). An approximately Bayesian delta-rule model explains the dynamics of belief updating in a changing environment. *Journal of Neuroscience, 30*(37), 12366-12378.

Navia, J. A., van der Kamp, J., & Ruiz, L. M. (2013). On the use of situation and body information in goalkeeper actions during a soccer penalty kick. *International Journal of Sport Psychology, 44*(3), 234-251.

Nayate, A., Bradshaw, J. L., & Rinehart, N. J. (2005). Autism and Asperger's disorder: are they movement disorders involving the cerebellum and/or basal ganglia? *Brain Research Bulletin, 67*(4), 327-334.

Nazarali, N., Glazebrook, C. M., & Elliott, D. (2009). Movement planning and reprogramming in individuals with autism. *Journal of Autism and Developmental Disorders, 39*(10), 1401-1411.

Nebel, M. B., Joel, S. E., Muschelli, J., Barber, A. D., Caffo, B. S., Pekar, J. J., & Mostofsky, S. H. (2014). Disruption of functional organization within the primary motor cortex in children with autism. *Human Brain Mapping, 35*(2), 567-580.

Neil, L., Olsson, N. C., & Pellicano, E. (2016). The relationship between intolerance of uncertainty, sensory sensitivities, and anxiety in autistic and typically developing children. *Journal of Autism and Developmental Disorders, 46*(6), 1962-1973.

Neumann, D., Spezio, M. L., Piven, J., & Adolphs, R. (2006). Looking you in the mouth: abnormal gaze in autism resulting from impaired top-down modulation of visual attention. *Social Cognitive and Affective Neuroscience, 1*(3), 194-202.

NICE, N. I. f. H. a. C. E. (2013). Autism: management of autism in children and young people: guideline consultation. Retrieved from: http://guidance.nice.org.uk/CG/Wave25/4/Consultation/Latest

Nicolaidis, C., Raymaker, D. M., Ashkenazy, E., McDonald, K. E., Dern, S., Baggs, A. E., . . . Boisclair, W. C. (2015). “Respect the way I need to communicate with you”: Healthcare experiences of adults on the autism spectrum. *Autism, 19*(7), 824-831.

Niehorster, D. C., Li, L., & Lappe, M. (2017). The accuracy and precision of position and orientation tracking in the HTC vive virtual reality system for scientific research. *i-Perception, 8*(3), 1-23.

Noel, J.-P., Lakshminarasimhan, K. J., Park, H., & Angelaki, D. E. (2020). Increased variability but intact integration during visual navigation in Autism Spectrum Disorder. *Proceedings of the National Academy of Sciences, 117*(20), 11158-11166.

Norman, D. A., & Shallice, T. (1986). Attention to action. In *Consciousness and Self-Regulation* (pp. 1-18). Boston, MA: Springer.

O'Reilly, J. X., Jbabdi, S., Rushworth, M. F., & Behrens, T. E. (2013). Brain systems for probabilistic and dynamic prediction: computational specificity and integration. *PLoS Biol, 11*(9), e1001662.

O'Riordan, M. A., Plaisted, K. C., Driver, J., & Baron-Cohen, S. (2001). Superior visual search in autism. *Journal of Experimental Psychology: Human Perception and Performance, 27*(3), 719-730.

O'Sullivan, I., Burdet, E., & Diedrichsen, J. (2009). Dissociating variability and effort as determinants of coordination. *PLoS Computational Biology, 5*(4), e1000345.

O’Riordan, M., & Passetti, F. (2006). Discrimination in autism within different sensory modalities. *Journal of Autism and Developmental Disorders, 36*(5), 665-675.

Organisation, W. H. (2012). *The ICD-10 Classification of Mental and Behavioural Disoders - Clinical Descriptions and Diagnostic Guidelines.* . Geneva: WHO.

Organisation, W. H. (2018). *ICD-11 Clinical Descriptions and Diagnostic Guidelines for Mental and Behavioural Disorders.* Geneva: WHO.

Osborne, J. W. (2013). *Best practices in data cleaning: A complete guide to everything you need to do before and after collecting your data*. Thousand Oaks: Sage.

Ozonoff, S., & McEvoy, R. E. (1994). A longitudinal study of executive function and theory of mind development in autism. *Development and Psychopathology, 6*(3), 415-431.

Ozonoff, S., Pennington, B. F., & Rogers, S. J. (1991). Executive function deficits in high-functioning autistic individuals: relationship to theory of mind. *Journal of child Psychology and Psychiatry, 32*(7), 1081-1105.

Palacios, E. R., Houghton, C., & Chadderton, P. (2021). Accounting for uncertainty: inhibition for neural inference in the cerebellum. *Proceedings of the Royal Society B, 288*(1947), 20210276.

Palmer, C. J., Lawson, R. P., & Hohwy, J. (2017). Bayesian approaches to autism: Towards volatility, action, and behavior. *Psychological Bulletin, 143*(5), 521-542.

Palmer, C. J., Lawson, R. P., Shankar, S., Clifford, C. W., & Rees, G. (2018). Autistic adults show preserved normalisation of sensory responses in gaze processing. *Cortex, 103*, 13-23.

Palmer, C. J., Paton, B., Hohwy, J., & Enticott, P. G. (2013). Movement under uncertainty: the effects of the rubber-hand illusion vary along the nonclinical autism spectrum. *Neuropsychologia, 51*(10), 1942-1951.

Palmer, C. J., Paton, B., Kirkovski, M., Enticott, P. G., & Hohwy, J. (2015). Context sensitivity in action decreases along the autism spectrum: a predictive processing perspective. *Proceedings of the Royal Society B: Biological sciences, 282*(1802), 1-9.

Palmer, C. J., Seth, A. K., & Hohwy, J. (2015). The felt presence of other minds: Predictive processing, counterfactual predictions, and mentalising in autism. *Consciousness and Cognition, 36*, 376-389.

Palmer, H. A., Newell, K. M., Gordon, D., Smith, L., & Williams, G. K. (2018). Qualitative and quantitative change in the kinematics of learning a non-dominant overarm throw. *Human Movement Science, 62*, 134-142.

Pan, C.-Y., Tsai, C.-L., & Chu, C.-H. (2009). Fundamental movement skills in children diagnosed with autism spectrum disorders and attention deficit hyperactivity disorder. *Journal of Autism and Developmental Disorders, 39*(12), 1694-1705.

Parr, T., & Friston, K. J. (2019). Generalised free energy and active inference. *Biological Cybernetics, 113*(5), 495-513.

Pasturel, C., Montagnini, A., & Perrinet, L. U. (2020). Humans adapt their anticipatory eye movements to the volatility of visual motion properties. *PLoS Computational Biology, 16*(4), e1007438.

Patla, A. E. (1998). How is human gait controlled by vision. *Ecological Psychology, 10*(3-4), 287-302.

Patla, A. E., & Vickers, J. N. (2003). How far ahead do we look when required to step on specific locations in the travel path during locomotion? *Experimental Brain Research, 148*(1), 133-138.

Patriquin, M. A., Hartwig, E. M., Friedman, B. H., Porges, S. W., & Scarpa, A. (2019). Autonomic response in autism spectrum disorder: Relationship to social and cognitive functioning. *Biological Psychology, 145*, 185-197.

Paulus, M. P., & Stein, M. B. (2006). An insular view of anxiety. *Biological Psychiatry, 60*(4), 383-387.

Pell, P. J., Mareschal, I., Calder, A. J., von dem Hagen, E. A., Clifford, C. W., Baron-Cohen, S., & Ewbank, M. P. (2016). Intact priors for gaze direction in adults with high-functioning autism spectrum conditions. *Molecular Autism, 7*(1), 25-35.

Pellicano, E., & Burr, D. (2012). When the world becomes 'too real': a Bayesian explanation of autistic perception. *Trends in Cognitive Sciences, 16*(10), 504-510.

Pellicano, E., Dinsmore, A., & Charman, T. (2014). What should autism research focus upon? Community views and priorities from the United Kingdom. *Autism, 18*(7), 756-770.

Pellicano, E., Jeffery, L., Burr, D., & Rhodes, G. (2007). Abnormal adaptive face-coding mechanisms in children with autism spectrum disorder. *Current Biology, 17*(17), 1508-1512.

Pellicano, E., Rhodes, G., & Calder, A. J. (2013). Reduced gaze aftereffects are related to difficulties categorising gaze direction in children with autism. *Neuropsychologia, 51*(8), 1504-1509.

Pelphrey, K. A., Sasson, N. J., Reznick, J. S., Paul, G., Goldman, B. D., & Piven, J. (2002). Visual scanning of faces in autism. *Journal of Autism and Developmental Disorders, 32*(4), 249-261.

Pennington, B. F., & Ozonoff, S. (1996). Executive functions and developmental psychopathology. *Journal of Child Psychology and Psychiatry, 37*(1), 51-87.

Pensiero, S., Fabbro, F., Michieletto, P., Accardo, A., & Brambilla, P. (2009). Saccadic characteristics in autistic children. *Functional Neurology; New Trends in Interventional Neurosciences, 24*(3), 153-158.

Perry, E. K., Lee, M. L., Martin-Ruiz, C. M., Court, J. A., Volsen, S. G., Merrit, J., . . . Perry, R. H. (2001). Cholinergic activity in autism: abnormalities in the cerebral cortex and basal forebrain. *American Journal of Psychiatry, 158*(7), 1058-1066.

Pickard, H., Hirsch, C., Simonoff, E., & Happé, F. (2020). Exploring the cognitive, emotional and sensory correlates of social anxiety in autistic and neurotypical adolescents. *Journal of Child Psychology and Psychiatry, 61*(12), 1317-1327.

Piek, J. P., & Dyck, M. J. (2004). Sensory-motor deficits in children with developmental coordination disorder, attention deficit hyperactivity disorder and autistic disorder. *Human Movement Science, 23*(3), 475-488.

Plaisted, K., Swettenham, J., & Rees, L. (1999). Children with autism show local precedence in a divided attention task and global precedence in a selective attention task. *The Journal of Child Psychology and Psychiatry and Allied Disciplines, 40*(5), 733-742.

Poljac, E., Poljac, E., & Wagemans, J. (2013). Reduced accuracy and sensitivity in the perception of emotional facial expressions in individuals with high autism spectrum traits. *Autism, 17*(6), 668-680.

Prior, M., & Hoffmann, W. (1990). Brief report: neuropsychological testing of autistic children through an exploration with frontal lobe tests. *Journal of Autism and Developmental Disorders, 20*(4), 581-590.

Qian, N., & Lipkin, R. M. (2011). A learning-style theory for understanding autistic behaviors. *Frontiers in Human Neuroscience, 5*, 77.

Qiu, A., Adler, M., Crocetti, D., Miller, M. I., & Mostofsky, S. H. (2010). Basal ganglia shapes predict social, communication, and motor dysfunctions in boys with autism spectrum disorder. *Journal of the American Academy of Child & Adolescent Psychiatry, 49*(6), 539-551.

Quattrocki, E., & Friston, K. (2014). Autism, oxytocin and interoception. *Neuroscience & Biobehavioral Reviews, 47*, 410-430.

Rajendran, G., & Mitchell, P. (2007). Cognitive theories of autism. *Developmental Review, 27*(2), 224-260.

Ramaswami, M. (2014). Network plasticity in adaptive filtering and behavioral habituation. *Neuron, 82*(6), 1216-1229.

Rane, P., Cochran, D., Hodge, S. M., Haselgrove, C., Kennedy, D., & Frazier, J. A. (2015). Connectivity in autism: a review of MRI connectivity studies. *Harvard Review of Psychiatry, 23*(4), 223-244.

Rao, R. P., & Ballard, D. H. (1999). Predictive coding in the visual cortex: a functional interpretation of some extra-classical receptive-field effects. *Nature Neuroscience, 2*(1), 79-87.

Rapin, I. (1997). Autism. *New England Journal of Medicine, 337*(2), 97-104.

Reid, M., Elliott, B., & Crespo, M. (2013). Mechanics and learning practices associated with the tennis forehand: a review. *Journal of Sports Science & Medicine, 12*(2), 23-29.

Rigoli, D., Piek, J. P., Kane, R., & Oosterlaan, J. (2012). An examination of the relationship between motor coordination and executive functions in adolescents. *Developmental Medicine & Child Neurology, 54*(11), 1025-1031.

Rincover, A., & Ducharme, J. M. (1987). Variables influencing stimulus overselectivity and" tunnel vision" in developmentally delayed children. *American Journal of Mental Deficiency, 91*(4), 422-430.

Rinehart, N. J., Bradshaw, J. L., Brereton, A. V., & Tonge, B. J. (2001). Movement preparation in high-functioning autism and Asperger disorder: a serial choice reaction time task involving motor reprogramming. *Journal of Autism and Developmental Disorders, 31*(1), 79-88.

Rizzolatti, G., & Luppino, G. (2001). The cortical motor system. *Neuron, 31*(6), 889-901.

Robertson, A. E., & Simmons, D. R. (2013). The relationship between sensory sensitivity and autistic traits in the general population. *Journal of Autism and Developmental Disorders, 43*(4), 775-784.

Robertson, C. E., & Baron-Cohen, S. (2017). Sensory perception in autism. *Nature Reviews Neuroscience*.

Robertson, C. E., Kravitz, D. J., Freyberg, J., Baron-Cohen, S., & Baker, C. I. (2013). Slower rate of binocular rivalry in autism. *Journal of Neuroscience, 33*(43), 16983-16991.

Robic, S., Sonié, S., Fonlupt, P., Henaff, M.-A., Touil, N., Coricelli, G., . . . Schmitz, C. (2015). Decision-making in a changing world: a study in autism spectrum disorders. *Journal of Autism and Developmental Disorders, 45*(6), 1603-1613.

Robinson, E. B., Koenen, K. C., McCormick, M. C., Munir, K., Hallett, V., Happé, F., . . . Ronald, A. (2011). Evidence that autistic traits show the same etiology in the general population and at the quantitative extremes (5%, 2.5%, and 1%). *Archives of General Psychiatry, 68*(11), 1113-1121.

Robinson, G., & Freeston, M. (2015). Intolerance of uncertainty as a predictor of performance anxiety and robustness of sport confidence in university student-athletes. *Journal of Clinical Sport Psychology, 9*(4), 335-344.

Robledo, J., Donnellan, A. M., & Strandt-Conroy, K. (2012). An exploration of sensory and movement differences from the perspective of individuals with autism. *Frontiers in Integrative Neuroscience, 6*(107), 1-13.

Rodrigues, S. T., Vickers, J. N., & Williams, A. M. (2002). Head, eye and arm coordination in table tennis. *Journal of Sports Sciences, 20*(3), 187-200.

Rogers, T. D., McKimm, E., Dickson, P. E., Goldowitz, D., Blaha, C. D., & Mittleman, G. (2013). Is autism a disease of the cerebellum? An integration of clinical and pre-clinical research. *Frontiers in Systems Neuroscience, 7*, 15.

Ropar, D., & Mitchell, P. (1999). Are individuals with autism and Asperger's syndrome susceptible to visual illusions? *Journal of Child Psychology and Psychiatry, 40*(8), 1283-1293.

Rosenberg, A., Patterson, J. S., & Angelaki, D. E. (2015). A computational perspective on autism. *Proceedings of the National Academy of Sciences, 112*(30), 9158-9165.

Rubenstein, J., & Merzenich, M. M. (2003). Model of autism: increased ratio of excitation/inhibition in key neural systems. *Genes, Brain and Behavior, 2*(5), 255-267.

Runswick, O. R., Green, R., & North, J. S. (2020). The effects of skill-level and playing-position on the anticipation of ball-bounce in rugby union. *Human Movement Science, 69*, 102544.

Russell, J. (1997). *Autism as an executive disorder*. Oxford, UK: Oxford University Press.

Rutter, M. (1978). Diagnosis and definition of childhood autism. *Journal of Autism and Childhood Schizophrenia, 8*(2), 139-161.

Ruzich, E., Allison, C., Smith, P., Watson, P., Auyeung, B., Ring, H., & Baron-Cohen, S. (2015). Measuring autistic traits in the general population: a systematic review of the Autism-Spectrum Quotient (AQ) in a nonclinical population sample of 6,900 typical adult males and females. *Molecular autism, 6*(2), 1-12.

Saccone, E. J., & Chouinard, P. A. (2019). The influence of size in weight illusions is unique relative to other object features. *Psychonomic Bulletin & Review, 26*(1), 77-89.

Sacrey, L.-A. R., Germani, T., Bryson, S. E., & Zwaigenbaum, L. (2014). Reaching and grasping in autism spectrum disorder: a review of recent literature. *Frontiers in Neurology, 5*(6).

Salvucci, D. D., & Goldberg, J. H. (2000). *Identifying fixations and saccades in eye-tracking protocols.* Paper presented at the Proceedings of the symposium on Eye tracking research & applications- ETRA '00, Palm Beach Gardens, Florida, United States.

Sapey-Triomphe, L.-A., Weilnhammer, V. A., & Wagemans, J. (2021). Associative learning under uncertainty in adults with autism: Intact learning of the cue-outcome contingency, but slower updating of priors. *Autism, 17*, e13623613211045026.

Sasson, N. J., Elison, J. T., Turner-Brown, L. M., Dichter, G. S., & Bodfish, J. W. (2011). Brief report: Circumscribed attention in young children with autism. *Journal of Autism and Developmental Disorders, 41*(2), 242-247.

Sasson, N. J., Turner-Brown, L. M., Holtzclaw, T. N., Lam, K. S., & Bodfish, J. W. (2008). Children with autism demonstrate circumscribed attention during passive viewing of complex social and nonsocial picture arrays. *Autism Research, 1*(1), 31-42.

Sato, Y., & Kording, K. P. (2014). How much to trust the senses: Likelihood learning. *Journal of Vision, 14*(13), 1-13.

Sawyer, A. C., Williamson, P., & Young, R. L. (2012). Can gaze avoidance explain why individuals with Asperger's syndrome can't recognise emotions from facial expressions? *Journal of Autism and Developmental Disorders, 42*(4), 606-618.

Schanding, G. T., Nowell, K. P., & Goin-Kochel, R. P. (2012). Utility of the social communication questionnaire-current and social responsiveness scale as teacher-report screening tools for autism spectrum disorders. *Journal of Autism and Developmental Disorders, 42*(8), 1705-1716.

Scharoun, S. M., Wright, K. T., Robertson-Wilson, J. E., Fletcher, P. C., & Bryden, P. J. (2017). Physical Activity in Individuals with Autism Spectrum Disorders (ASD): A Review. In *Autism-Paradigms, Recent Research and Clinical Applications*: InTech.

Schmitt, L. M., Cook, E. H., Sweeney, J. A., & Mosconi, M. W. (2014). Saccadic eye movement abnormalities in autism spectrum disorder indicate dysfunctions in cerebellum and brainstem. *Molecular Autism, 5*(1), 47-60.

Schmitz, C., Martineau, J., Barthélémy, C., & Assaiante, C. (2003). Motor control and children with autism: deficit of anticipatory function? *Neuroscience letters, 348*(1), 17-20.

Schuwerk, T., Sodian, B., & Paulus, M. (2016). Cognitive mechanisms underlying action prediction in children and adults with autism spectrum condition. *Journal of Autism and Developmental Disorders, 46*(12), 3623-3639.

Schwartz, O., Hsu, A., & Dayan, P. (2007). Space and time in visual context. *Nature Reviews Neuroscience, 8*(7), 522-535.

Sears, L. L., Vest, C., Mohamed, S., Bailey, J., Ranson, B. J., & Piven, J. (1999). An MRI study of the basal ganglia in autism. *Progress in Neuro-Psychopharmacology & Biological Psychiatry, 23*(4), 613-624.

Senju, A., & Johnson, M. H. (2009). Atypical eye contact in autism: models, mechanisms and development. *Neuroscience & Biobehavioral Reviews, 33*(8), 1204-1214.

Shah, A., & Frith, U. (1993). Why do autistic individuals show superior performance on the block design task? *Journal of Child Psychology and Psychiatry, 34*(8), 1351-1364.

Shipp, S., Adams, R. A., & Friston, K. J. (2013). Reflections on agranular architecture: predictive coding in the motor cortex. *Trends in Neurosciences, 36*(12), 706-716.

Siaperas, P., Ring, H. A., McAllister, C. J., Henderson, S., Barnett, A., Watson, P., & Holland, A. J. (2012). Atypical movement performance and sensory integration in Asperger's syndrome. *Journal of Autism and Developmental Disorders, 42*(5), 718-725.

Simmons, D. R., Robertson, A. E., McKay, L. S., Toal, E., McAleer, P., & Pollick, F. E. (2009). Vision in autism spectrum disorders. *Vision Research, 49*(22), 2705-2739.

Simonoff, E., Pickles, A., Charman, T., Chandler, S., Loucas, T., & Baird, G. (2008). Psychiatric disorders in children with autism spectrum disorders: prevalence, comorbidity, and associated factors in a population-derived sample. *Journal of the American Academy of Child & Adolescent Psychiatry, 47*(8), 921-929.

Sinha, P., Kjelgaard, M. M., Gandhi, T. K., Tsourides, K., Cardinaux, A. L., Pantazis, D., . . . Held, R. M. (2014). Autism as a disorder of prediction. *Proceedings of the National Academy of Sciences, 111*(42), 15220-15225.

Skewes, J. C., & Gebauer, L. (2016). Brief report: suboptimal auditory localization in autism spectrum disorder: support for the bayesian account of sensory symptoms. *Journal of Autism and Developmental Disorders, 46*(7), 2539-2547.

Song, R., Liu, J., & Kong, X. (2016). Autonomic dysfunction and autism: subtypes and clinical perspectives. *North American Journal of Medicine and Science, 9*(4).

Soroor, G., Mokhtari, S., & Pouretemad, H. (2021). Priming Global Processing Strategy Improves the Perceptual Performance of Children with Autism Spectrum Disorders. *Journal of Autism and Developmental Disorders*, https://doi.org/10.1007/s10803-10021-05007-10807.

South, M., & Rodgers, J. (2017). Sensory, emotional and cognitive contributions to anxiety in autism spectrum disorders. *Frontiers in Human Neuroscience, 11*(20).

Sparaci, L., Formica, D., Lasorsa, F. R., Mazzone, L., Valeri, G., & Vicari, S. (2015). Untrivial pursuit: measuring motor procedures learning in children with autism. *Autism Research, 8*(4), 398-411.

Stanley-Cary, C., Rinehart, N., Tonge, B., White, O., & Fielding, J. (2011). Greater disruption to control of voluntary saccades in autistic disorder than Asperger's disorder: evidence for greater cerebellar involvement in autism? *The Cerebellum, 10*(1), 70-80.

Stark, E., Stacey, J., Mandy, W., Kringelbach, M. L., & Happé, F. (2021). Autistic Cognition: Charting Routes to Anxiety. *Trends in Cognitive Sciences, 25*(7), 571-581.

Stevenson, I. H., Fernandes, H. L., Vilares, I., Wei, K., & Körding, K. P. (2009). Bayesian integration and non-linear feedback control in a full-body motor task. *PLoS Computational Biology, 5*(12), e1000629.

Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience, 9*(4), 578-585.

Stoit, A. M., van Schie, H. T., Slaats-Willemse, D. I., & Buitelaar, J. K. (2013). Grasping motor impairments in autism: not action planning but movement execution is deficient. *Journal of Autism and Developmental Disorders, 43*(12), 2793-2806.

Sturm, A., Kuhfeld, M., Kasari, C., & McCracken, J. T. (2017). Development and validation of an item response theory-based Social Responsiveness Scale short form. *Journal of Child Psychology and Psychiatry, 58*(9), 1053-1061.

Sutera, S., Pandey, J., Esser, E. L., Rosenthal, M. A., Wilson, L. B., Barton, M., . . . Dumont-Mathieu, T. (2007). Predictors of optimal outcome in toddlers diagnosed with autism spectrum disorders. *Journal of Autism and Developmental Disorders, 37*(1), 98-107.

Takamuku, S., Ohta, H., Kanai, C., Hamilton, A. F. d. C., & Gomi, H. (2021). Seeing motion of controlled object improves grip timing in adults with autism spectrum condition: evidence for use of inverse dynamics in motor control. *Experimental Brain Research, 239*(4), 1047-1059.

Takarae, Y., Minshew, N. J., Luna, B., Krisky, C. M., & Sweeney, J. A. (2004). Pursuit eye movement deficits in autism. *Brain, 127*(12), 2584-2594.

Takarae, Y., Minshew, N. J., Luna, B., & Sweeney, J. A. (2004). Oculomotor abnormalities parallel cerebellar histopathology in autism. *Journal of Neurology, Neurosurgery & Psychiatry, 75*(9), 1359-1361.

Talsma, D., Senkowski, D., Soto-Faraco, S., & Woldorff, M. G. (2010). The multifaceted interplay between attention and multisensory integration. *Trends in Cognitive Sciences, 14*(9), 400-410.

Tam, F. I., King, J. A., Geisler, D., Korb, F. M., Sareng, J., Ritschel, F., . . . Ehrlich, S. (2017). Altered behavioral and amygdala habituation in high-functioning adults with autism spectrum disorder: an fMRI study. *Scientific Reports, 7*, 13611.

Tassinari, H., Hudson, T. E., & Landy, M. S. (2006). Combining priors and noisy visual cues in a rapid pointing task. *Journal of Neuroscience, 26*(40), 10154-10163.

Tavassoli, T., Latham, K., Bach, M., Dakin, S. C., & Baron-Cohen, S. (2011). Psychophysical measures of visual acuity in autism spectrum conditions. *Vision Research, 51*(15), 1778-1780.

Teitelbaum, P., Teitelbaum, O., Nye, J., Fryman, J., & Maurer, R. G. (1998). Movement analysis in infancy may be useful for early diagnosis of autism. *Proceedings of the National Academy of Sciences, 95*(23), 13982-13987.

Teufel, C., & Fletcher, P. C. (2016). The promises and pitfalls of applying computational models to neurological and psychiatric disorders. *Brain, 139*(10), 2600-2608.

Teufel, C., & Fletcher, P. C. (2020). Forms of prediction in the nervous system. *Nature Reviews Neuroscience, 21*(4), 231-242.

Tewolde, F. G., Bishop, D. V., & Manning, C. (2018). Visual motion prediction and verbal false memory performance in autistic children. *Autism Research, 11*(3), 509-518.

Thakkar, K. N., Polli, F. E., Joseph, R. M., Tuch, D. S., Hadjikhani, N., Barton, J. J., & Manoach, D. S. (2008). Response monitoring, repetitive behaviour and anterior cingulate abnormalities in autism spectrum disorders (ASD). *Brain, 131*(9), 2464-2478.

Thillay, A., Lemaire, M., Roux, S., Houy-Durand, E., Barthélémy, C., Knight, R. T., . . . Bonnet-Brilhault, F. (2016). Atypical brain mechanisms of prediction according to uncertainty in autism. *Frontiers in Neuroscience, 10*, 317.

Todorov, E., & Jordan, M. I. (1998). Smoothness maximization along a predefined path accurately predicts the speed profiles of complex arm movements. *Journal of Neurophysiology, 80*(2), 696-714.

Tomchek, S. D., & Dunn, W. (2007). Sensory processing in children with and without autism: a comparative study using the short sensory profile. *American Journal of Occupational Therapy, 61*(2), 190-200.

Tommerdahl, M., Tannan, V., Cascio, C., Baranek, G., & Whitsel, B. (2007). Vibrotactile adaptation fails to enhance spatial localization in adults with autism. *Brain Research, 1154*, 116-123.

Tong, M. H., Zohar, O., & Hayhoe, M. M. (2017). Control of gaze while walking: task structure, reward, and uncertainty. *Journal of Vision, 17*(1), 28-47.

Toni, I., Krams, M., Turner, R., & Passingham, R. E. (1998). The time course of changes during motor sequence learning: a whole-brain fMRI study. *Neuroimage, 8*(1), 50-61.

Torres, E. B., Brincker, M., Isenhower III, R. W., Yanovich, P., Stigler, K. A., Nurnberger Jr, J. I., . . . José, J. V. (2013). Autism: the micro-movement perspective. *Frontiers in Integrative Neuroscience, 7*, 32.

Torres, E. B., & Denisova, K. (2016). Motor noise is rich signal in autism research and pharmacological treatments. *Scientific Reports, 6*(1), 37422.

Trevarthen, C., & Delafield-Butt, J. T. (2013). Autism as a developmental disorder in intentional movement and affective engagement. *Frontiers in Integrative Neuroscience, 7*(49).

Turi, M., Burr, D. C., Igliozzi, R., Aagten-Murphy, D., Muratori, F., & Pellicano, E. (2015). Children with autism spectrum disorder show reduced adaptation to number. *Proceedings of the National Academy of Sciences, 112*(25), 7868-7872.

Turner-Brown, L. M., Baranek, G. T., Reznick, J. S., Watson, L. R., & Crais, E. R. (2013). The First Year Inventory: a longitudinal follow-up of 12-month-old to 3-year-old children. *Autism, 17*(5), 527-540.

Turner, M. (1999). Annotation: Repetitive behaviour in autism: A review of psychological research. *Journal of Child Psychology and Psychiatry, 40*(6), 839-849.

Vabalas, A., Gowen, E., Poliakoff, E., & Casson, A. J. (2020). Applying Machine Learning to Kinematic and eye Movement features of a Movement imitation task to predict Autism Diagnosis. *Scientific Reports, 10*(1), 8346.

Van Boxtel, J. J., & Lu, H. (2013). Impaired global, and compensatory local, biological motion processing in people with high levels of autistic traits. *Frontiers in Psychology, 4*, 209.

Van de Cruys, S., Evers, K., Van der Hallen, R., Van Eylen, L., Boets, B., de-Wit, L., & Wagemans, J. (2014). Precise minds in uncertain worlds: Predictive coding in autism. *Psychological Review, 121*(4), 649-675.

Van de Cruys, S., Lemmens, L., Sapey-Triomphe, L. A., Chetverikov, A., Noens, I., & Wagemans, J. (2021). Structural and contextual priors affect visual search in children with and without autism. *Autism Research, 14*, 1484–1495.

Van Der Geest, J. N., Kemner, C., Verbaten, M. N., & Van Engeland, H. (2002). Gaze behavior of children with pervasive developmental disorder toward human faces: a fixation time study. *Journal of Child Psychology and Psychiatry, 43*(5), 669-678.

Van der Hallen, R., Evers, K., Brewaeys, K., Van den Noortgate, W., & Wagemans, J. (2015). Global processing takes time: A meta-analysis on local–global visual processing in ASD. *Psychological Bulletin, 141*(3), 549-573.

van Doorn, J., van den Bergh, D., Böhm, U., Dablander, F., Derks, K., Draws, T., . . . Haaf, J. M. (2021). The JASP guidelines for conducting and reporting a Bayesian analysis. *Psychonomic Bulletin & Review, 28*(3), 813-826.

Van Heijst, B. F., & Geurts, H. M. (2015). Quality of life in autism across the lifespan: A meta-analysis. *Autism, 19*(2), 158-167.

van Swieten, L. M., van Bergen, E., Williams, J. H., Wilson, A. D., Plumb, M. S., Kent, S. W., & Mon-Williams, M. A. (2010). A test of motor (not executive) planning in developmental coordination disorder and autism. *Journal of Experimental Psychology: Human Perception and Performance, 36*(2), 493-499.

Vanvuchelen, M., Roeyers, H., & De Weerdt, W. (2007). Nature of motor imitation problems in school-aged boys with autism: a motor or a cognitive problem? *Autism, 11*(3), 225-240.

Vasa, R. A., Kreiser, N. L., Keefer, A., Singh, V., & Mostofsky, S. H. (2018). Relationships between autism spectrum disorder and intolerance of uncertainty. *Autism Research, 11*(4), 636-644.

Vattikuti, S., & Chow, C. C. (2010). A computational model for cerebral cortical dysfunction in autism spectrum disorders. *Biological Psychiatry, 67*(7), 672-678.

Venter, A., Lord, C., & Schopler, E. (1992). A follow-up study of high-functioning autistic children. *Journal of Child Psychology and Psychiatry, 33*(3), 489-597.

Verhoeven, J. S., De Cock, P., Lagae, L., & Sunaert, S. (2010). Neuroimaging of autism. *Neuroradiology, 52*(1), 3-14.

Vermeulen, P. (2015). Context blindness in autism spectrum disorder: Not using the forest to see the trees as trees. *Focus on Autism and Other Developmental Disabilities, 30*(3), 182-192.

Verstynen, T., & Sabes, P. N. (2011). How each movement changes the next: an experimental and theoretical study of fast adaptive priors in reaching. *Journal of Neuroscience, 31*(27), 10050-10059.

Vilares, I., Howard, J. D., Fernandes, H. L., Gottfried, J. A., & Kording, K. P. (2012). Differential representations of prior and likelihood uncertainty in the human brain. *Current Biology, 22*(18), 1641-1648.

Vilares, I., & Kording, K. (2011). Bayesian models: the structure of the world, uncertainty, behavior, and the brain. *Annals of the New York Academy of Sciences, 1224*(1), 22-39.

Villalobos, M. E., Mizuno, A., Dahl, B. C., Kemmotsu, N., & Müller, R.-A. (2005). Reduced functional connectivity between V1 and inferior frontal cortex associated with visuomotor performance in autism. *Neuroimage, 25*(3), 916-925.

Vine, S. J., Moore, L. J., & Wilson, M. R. (2016). An integrative framework of stress, attention, and visuomotor performance. *Frontiers in Psychology, 7*, 1671.

Vivanti, G., Hocking, D. R., Fanning, P. A., Uljarevic, M., Postorino, V., Mazzone, L., & Dissanayake, C. (2018). Attention to novelty versus repetition: Contrasting habituation profiles in Autism and Williams syndrome. *Developmental Cognitive Neuroscience, 29*, 54-60.

von Hofsten, C., Uhlig, H., Adell, M., & Kochukhova, O. (2009). How children with autism look at events. *Research in Autism Spectrum Disorders, 3*(2), 556-569.

Vossel, S., Mathys, C., Daunizeau, J., Bauer, M., Driver, J., Friston, K. J., & Stephan, K. E. (2014). Spatial attention, precision, and Bayesian inference: a study of saccadic response speed. *Cerebral Cortex, 24*(6), 1436-1450.

Wainwright-Sharp, J. A., & Bryson, S. E. (1993). Visual orienting deficits in high-functioning people with autism. *Journal of Autism and Developmental Disorders, 23*(1), 1-13.

Wainwright, J. A., & Bryson, S. E. (1996). Visual-spatial orienting in autism. *Journal of Autism and Developmental Disorders, 26*(4), 423-438.

Walker, A. R., Luque, D., Le Pelley, M. E., & Beesley, T. (2019). The role of uncertainty in attentional and choice exploration. *Psychonomic Bulletin & Review, 26*(6), 1911-1916.

Wang, S., Jiang, M., Duchesne, X. M., Laugeson, E. A., Kennedy, D. P., Adolphs, R., & Zhao, Q. (2015). Atypical visual saliency in autism spectrum disorder quantified through model-based eye tracking. *Neuron, 88*(3), 604-616.

Wang, Y., Ji, Q., & Zhou, C. (2019). Effect of prior cues on action anticipation in soccer goalkeepers. *Psychology of Sport and Exercise, 43*, 137-143.

Wang, Z., Magnon, G. C., White, S. P., Greene, R. K., Vaillancourt, D. E., & Mosconi, M. W. (2015). Individuals with autism spectrum disorder show abnormalities during initial and subsequent phases of precision gripping. *Journal of Neurophysiology, 113*(7), 1989-2001.

Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience, 5*(6), 598-604.

White, S. W., Oswald, D., Ollendick, T., & Scahill, L. (2009). Anxiety in children and adolescents with autism spectrum disorders. *Clinical Psychology Review, 29*(3), 216-229.

Whyatt, C., & Craig, C. (2013a). Interceptive skills in children aged 9–11 years, diagnosed with Autism Spectrum Disorder. *Research in Autism Spectrum Disorders, 7*(5), 613-623.

Whyatt, C., & Craig, C. (2013b). Sensory-motor problems in Autism. *Frontiers in Integrative Neuroscience, 7*, 51.

Wiggins, J. L., Swartz, J. R., Martin, D. M., Lord, C., & Monk, C. S. (2014). Serotonin transporter genotype impacts amygdala habituation in youth with autism

spectrum disorders. *Social Cognitive and Affective Neuroscience, 9*(6), 832-838.

Wigham, S., Rodgers, J., South, M., McConachie, H., & Freeston, M. (2015). The interplay between sensory processing abnormalities, intolerance of uncertainty, anxiety and restricted and repetitive behaviours in autism spectrum disorder. *Journal of Autism and Developmental Disorders, 45*(4), 943-952.

Williams, A. M., & Davids, K. (1998). Visual search strategy, selective attention, and expertise in soccer. *Research Quarterly for Exercise and Sport, 69*(2), 111-128.

Williams, A. M., Davids, K., Burwitz, L., & Williams, J. G. (1994). Visual search strategies in experienced and inexperienced soccer players. *Research Quarterly for Exercise and Sport, 65*(2), 127-135.

Williams, A. M., Ford, P. R., Eccles, D. W., & Ward, P. (2011). Perceptual-cognitive expertise in sport and its acquisition: Implications for applied cognitive psychology. *Applied Cognitive Psychology, 25*(3), 432-442.

Wilson, M. (2008). From processing efficiency to attentional control: a mechanistic account of the anxiety–performance relationship. *International Review of Sport and Exercise Psychology, 1*(2), 184-201.

Wilson, M. R., Miles, C. A., Vine, S. J., & Vickers, J. N. (2013). Quiet eye distinguishes children of high and low motor coordination abilities. *Medicine & Science in Sports & Exercise, 45*(6), 1144-1151.

Wilson, M. R., & Vine, S. J. (2018). The use of gaze training to expedite motor skill acquisition. In *Handbook of Sport Neuroscience and Psychophysiology* (pp. 237-247): Routledge.

Wing, L., & Gould, J. (1979). Severe impairments of social interaction and associated abnormalities in children: Epidemiology and classification. *Journal of Autism and Developmental Disorders, 9*(1), 11-29.

Wolpert, D. M., Miall, R. C., & Kawato, M. (1998). Internal models in the cerebellum. *Trends in Cognitive Sciences, 2*(9), 338-347.

Wong, A. L., & Shelhamer, M. (2012). Using prediction errors to drive saccade adaptation: the implicit double-step task. *Experimental Brain Research, 222*(2), 55-64.

Wood, G., Miles, C. A., Coyles, G., Alizadehkhaiyat, O., Vine, S. J., Vickers, J. N., & Wilson, M. R. (2017). A randomized controlled trial of a group-based gaze training intervention for children with Developmental Coordination Disorder. *PLoS One, 12*(2), e0171782.

Woodbury-Smith, M. R., Robinson, J., Wheelwright, S., & Baron-Cohen, S. (2005). Screening adults for Asperger syndrome using the AQ: A preliminary study of its diagnostic validity in clinical practice. *Journal of Autism and Developmental Disorders, 35*(3), 331-335.

Wu, S.-W., Delgado, M. R., & Maloney, L. T. (2009). Economic decision-making compared with an equivalent motor task. *Proceedings of the National Academy of Sciences, 106*(15), 6088-6093.

Wulf, G., & Shea, C. H. (2002). Principles derived from the study of simple skills do not generalize to complex skill learning. *Psychonomic Bulletin & Review, 9*(2), 185-211.

Wunsch, K., Pfister, R., Henning, A., Aschersleben, G., & Weigelt, M. (2016). No Interrelation of Motor Planning and Executive Functions across Young Ages. *Frontiers in Psychology, 7*, 1031.

Yanardağ, M., Yılmaz, İ., & Aras, Ö. (2010). Approaches to the teaching exercise and sports for the children with autism. *International Journal of Early Childhood Special Education, 2*(3), 214-230.

Yin, C., Wang, H., Wei, K., & Körding, K. P. (2019). Sensorimotor priors are effector dependent. *Journal of Neurophysiology, 122*(1), 389-397.

Yizhar, O., Fenno, L. E., Prigge, M., Schneider, F., Davidson, T. J., O'shea, D. J., . . . Paz, J. T. (2011). Neocortical excitation/inhibition balance in information processing and social dysfunction. *Nature, 477*(7363), 171-178.

Yon, D. (2021). Prediction and Learning: Understanding Uncertainty. *Current Biology, 31*(1), R23-R25.

Yon, D., & Frith, C. D. (2021). Precision and the Bayesian brain. *Current Biology, 31*(17), R1026-R1032.

Yu, A., & Dayan, P. (2003). Uncertainty, neuromodulation, and attention. *Neuron, 46*, 681-692.

Zago, M., McIntyre, J., Senot, P., & Lacquaniti, F. (2009). Visuo-motor coordination and internal models for object interception. *Experimental Brain Research, 192*(4), 571-604.

Zahabi, M., Abdul Razak, & Mohammed, A. (2020). Adaptive virtual reality-based training: a systematic literature review and framework. *Virtual Reality, 24*(4), 725-752.

Zhang, H., Wu, S.-W., & Maloney, L. T. (2010). Planning multiple movements within a fixed time limit: The cost of constrained time allocation in a visuo-motor task. *Journal of Vision, 10*(6), 1-17.

Appendices

Appendix A. Power Calculations.

A-priori power analyses were performed to determine sample size in each of the studies presented in *Chapters 2-4*. These calculations were conducted using G*Power 3.1 (Faul et al., 2007), with alpha set at $p = 0.05$ and power ($1 - \beta$) at 0.80.

A.1. Determination of Sample Size in Study One

An effect size of $r = .30$ was anticipated for *Study 1*, based on an aggregation of statistical relationships that have previously been observed between autistic-like traits and predictive sensorimotor outcomes (Palmer et al., 2013; Z. Wang et al., 2015; Buckingham et al., 2016). To detect this anticipated effect, it was estimated that 84 participants would be required. However, to account for potential data loss in the study, a total sample of 91 were recruited.

A.2. Determination of Sample Size in Study Two

An moderate effect size of $d = 0.67$ was estimated for between-group comparisons in *Study 2*, in accordance with statistical differences previously documented in clinical motor control research (Schmitz et al., 2003; David et al., 2012; Palmer, Seth, et al., 2015; Z. Wang et al., 2015). Analysis indicated that an overall sample of 56 would be sufficiently powered to detect this effect ($\alpha = .05$ and $1 - \beta = 0.80$) and the study therefore aimed to recruit at least 28 individuals in each participant group.

A.3. Determination of Sample Size in Study Three

Medium-to-large group differences ($d = .78$) were initially estimated for *Study 3*, based on an array of between-group and between-condition differences reported in meta-analyses (Fournier et al., 2010) and volatility-based studies (Vossel et al., 2014; Lawson et al., 2017). On the basis of this anticipated effect size, and the proportion of gaze data that was excluded in *Study 1* (24%, due to poor quality and/or missing cases), it was determined that each group should contain at least 26 participants. However, a larger overall sample was necessary for the correlational analyses in this study ($\alpha = .05$ and $1 - \beta = 0.80$), as relationships between autistic-like traits and sensorimotor measures are generally more moderate in magnitude (see *Section A.1 above*). Therefore, it was deemed that an overall sample of at least 72 participants would be required to detect medium-sized correlations ($r = .32$) akin to those observed in Arthur et al. (2019) and in *Section 2.1.4.1* (re-analysis of Buckingham et al., 2016).

A.4. Determination of Sample Size in Study Four

For the mixed 2x2 design of *Study 4*, a moderate statistical effect was anticipated (*f* = .47). This effect was observed in relation to volatility-related sensorimotor adjustments during *Study 3*, and was consistent (albeit slightly smaller) than the medium interaction effects for reaction time observed in Lawson *et al.* (2017). Though there were no previous data from autistic populations, neurotypical research has demonstrated that the use of explicit cues leads to relatively large improvements in predictive sensorimotor performances (McRobert et al., 2011; Navia et al., 2013; Gredin et al., 2018). So, based on the moderate effect size reported in *Study* 3, and the 8.79% of gaze data excluded from this previous analysis, a sample size of 44 was targeted in this study (i.e., 22 autistic and 22 neurotypical individuals).

Appendix B. Certificates of Ethics Approval.

College of Life and Environmental Sciences
SPORT AND HEALTH SCIENCES

St. Luke's Campus
University of Exeter
Heavitree Road
Exeter
EX1 2LU
United Kingdom

Certificate of Ethical Approval

Proposal Ref No: 2017/M/01

Title: Exploring how autistic traits influence the use of prior knowledge in object lifting

Applicants: Tom Arthur, MSc student, Dr Sam Vine, Dr Gavin Buckingham, Prof Mark Brosnan

The proposal was reviewed by a Representative on the Committee.

Decision: This proposal has been approved until December 2018

Signature:  Date: 20/11/2017

Name/Title of Ethics Committee Reviewer: Dr Melvyn Hillsdon

Your attention is drawn to the attached paper which reminds the researcher of information that needs to be observed when Ethics Committee approval is given.

College of Life and Environmental Sciences
SPORT AND HEALTH SCIENCES

St. Luke's Campus
University of Exeter
Heavitree Road
Exeter
EX1 2LU
United Kingdom

Certificate of Ethical Approval

Proposal Ref No: 180613/B/01

Title: Exploring the use of predictive sensorimotor control in people with Autism Spectrum Disorder.

Applicants: Tom Arthur, Sam Vine, Gavin Buckingham, Mark Wilson, Kate Allen, David Harris

The proposal was reviewed by the Sport and Health Sciences Ethics Committee.

Decision: This proposal has been approved until 01/07/2019

Signature:  Date: 23/11/2019

Name/Title of Ethics Committee Reviewer: Dr Melvyn Hillsdon

Your attention is drawn to the attached paper which reminds the researcher of information that needs to be observed when Ethics Committee approval is given.

College of Life and Environmental Sciences
SPORT AND HEALTH SCIENCES

St. Luke's Campus
University of Exeter
Heavitree Road
Exeter
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United Kingdom

Certificate of Ethical Approval

Proposal Ref No: 190206/B/02

Title: How does predictive control differ in Autism Spectrum Disorder during interceptive motor tasks?

Applicants: Tom Arthur, Sam Vine, Gavin Buckinham, Mark Brosnan, Mark Wilson, Kate Allen, David Harris

The proposal was reviewed by the Sport and Health Sciences Ethics Committee.

Decision: This proposal has been approved until 01/02/2020

Signature:  Date: 20/02/2019

Name/Title of Ethics Committee Reviewer: Dr Melvyn Hillsdon

Your attention is drawn to the attached paper which reminds the researcher of information that needs to be observed when Ethics Committee approval is given.

College of Life and Environmental Sciences
SPORT AND HEALTH SCIENCES

St. Luke's Campus
University of Exeter
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United Kingdom

Certificate of Ethical Approval

Proposal Ref No: 200617/B/01

Title: **How do prior coaching cues affect motor co-ordination in autistic and non-autistic people?**

Applicants: **Tom Arthur**, Sam Vine, Gavin Buckingham, David Harris.

The proposal was reviewed by the College of Life and Environmental Sciences, Sport and Health Sciences Research Ethics Committee.

Decision: This proposal has been approved until 30/06/2021

Signature:  Date: 24/08/2020

Your attention is drawn to the attached paper which reminds the researcher of information that needs to be observed when Ethics Committee approval is given.

Appendix C. Example Informed Consent Form.

Participant Identification Number:

CONSENT FORM

Title of Project: How does predictive control differ in Autism Spectrum Disorder during interceptive motor tasks?

Name of Researcher: Tom Arthur **Please initial box**

1. I confirm that I have read the information sheet dated 23rd January 2019 (version no for the above project. I have had the opportunity to consider the information, ask questions and have had these answered satisfactorily. ☐
2. I understand that my participation is voluntary and that I am free to withdraw at any time without giving any reason and without my legal rights being affected. ☐
3. I understand that relevant sections of the data collected during the study, may be looked at by members of the research team, and individuals from the University of Exeter and Bath, where it is relevant to my taking part in this research. I give permission for these individuals to have access to my records. ☐
4. I understand that taking part involves having my hand-eye movements measured, wearing virtual reality headset and answering some questions ☐
5. I understand that my anonymised data may be used in future reports, articles or presentations by the research team. ☐
6. I give consent for my anonymised data to be uploaded to an online repository for future secondary analysis. ☐
7. I understand that my name will not appear in any reports, articles or presentations. ☐
8. I agree to take part in the above study. ☐

Name of Participant	Date	Signature
Name of researcher taking consent	Date	Signature

When completed: 1 copy for participant; 1 copy for researcher/project file.

Appendix D. Example Participant Information Sheet.

Participant Information Sheet:

How does predictive control differ in Autism Spectrum Disorder during interceptive motor tasks?

Researcher name: Mr Tom Arthur

Invitation and brief summary:

We are inviting people aged 16+ to take part in our research. The aim of this study is to explore how hand-eye co-ordination is used differently between autistic and non-autistic people. Taking part in the study is entirely up to you, so before you decide, it is important for you to understand why the research is being done and what it will involve. Please take the time to read the following information and to discuss it with other people to decide whether you wish to take part or not. Thank you for taking the time to read this information.

Purpose of the research:

This research study is part of a PhD research project funded by the South West Doctoral Training Partnership. Its main purpose is to understand the differences in how autistic people control their movements during interception tasks (e.g., racquet sports, throwing and catching). To do this, we will use scientific and virtual-reality (VR) technology to track your hand and eye movements during a computerised racquetball game. We hope to develop our findings into a coaching strategy that can help overcome movement-related difficulties.

Why have I been approached?

You are being approached about taking part because we are looking for *both* autistic and non-autistic people (aged 16+) to take part in this study.

What would taking part involve?

If you agree to take part you will be asked to complete one session, lasting around 30 mins. This visit will involve two quick movement tasks. Firstly, you will be asked to lift a small number of small objects and say how heavy they feel (by giving a number). During these trials, we will measure the forces that you use for each lift. Next, you will be asked to put on a VR headset and given a game controller (this will be your 'racquet' in the virtual game). Then, after making sure that you feel comfortable with the equipment, we will show you the VR task, which involves hitting bouncing balls with your controller towards a target. After some practice, you will complete your test trials, to see how many times you can hit this target. During all trials, we will measure your eye and hand movements using technology that is built into the VR equipment. You will be offered breaks throughout the session and can rest whenever you like (although

this might increase the time required to complete testing). Prior to the movement tasks we will also ask you to fill a questionnaire, which measures autistic traits, to help with our analysis.

What are the possible benefits of taking part?

The main benefits of the proposed research are educational. We hope our results will be able to guide future coaching and teaching strategies that help autistic people overcome some movement-related difficulties. However, we hope that you will enjoy spending time in our labs and will find the session interesting.

What are the possible disadvantages and risks of taking part?

The majority of the disadvantages and risks associated with this study resemble those found in a typical office environment. Some people do have feelings of motion sickness during VR tasks, but you will be able to stop immediately if you experience any of these effects at any point. You will also be offered regular breaks throughout the session- there's no rush.

What will happen if I don't want to carry on with the study?

You have the right to withdraw yourself and your data from the study at any point. You do not have to give a reason for doing this and you will be able to stop testing immediately. Data will remain anonymous and, if requested, can be destroyed from our analysis.

How will my information be kept confidential?

The University of Exeter processes personal data for the purposes of carrying out research in the public interest. The University will endeavour to be transparent about its processing of your personal data and this information sheet should provide a clear explanation of this. If you do have any queries about the University's processing of your personal data that cannot be resolved by the research team, further information may be obtained from the University's Data Protection Officer by emailing dataprotection@exeter.ac.uk or at www.exeter.ac.uk/dataprotection

If you consent to take part in this study you have a right to privacy. Your name will not appear in any reports, articles or presentations. Instead your data will be linked to an ID number on a password protected database and only these IDs will be used as labels during analysis. All anonymised data will be stored securely and only made available to our research team members, with online files password-protected and hard data (e.g., questionnaires) locked and destroyed once no longer necessary. Your contact details will not be kept for future research projects and will be deleted upon completion of testing.

If you give consent for your data to be uploaded to an online repository, we will aim to publish anonymised data on Open Science Framework for future secondary analysis. Your name will not appear in any of this future work and will be linked to a non-identifiable ID number.

Will I receive any payment for taking part?

If the testing requires you to travel to the University, we can compensate you £5 for your time spent travelling and taking part.

What will happen to the results of this study?

The results will increase our understanding of how movements are controlled differently in autistic people. We will aim to publish the findings in research journals and to present them at conferences in the UK or abroad. Data will always remain anonymous and your name will not appear on any results.

Who is organising and funding this study?

The project is affiliated with the South West Doctoral Training Partnership (SWDTP) and funded by the Economic and Social Research Council (ESRC). The SWDTP brings together academics from the Universities of Bath, Bristol, Exeter, Plymouth and West of England (UWE) to further social sciences research and practice. For more information, please visit their website: https://www.swdtp.ac.uk/

Who has reviewed this study?

All research activity at the University of Exeter and University of Bath is examined and approved by ethics committees to protect your interests. This study has been approved by the Ethics Committee of Sport and Health Sciences, College of Life and Environmental Sciences, University of Exeter and Psychology Ethics Committee, Faculty of Humanities & Social Sciences, University of Bath.

Further information and contact details

If you would like more information or if you have any further questions about the study please contact the investigators using the details below:

Tom Arthur, Principal Investigator
tga202@exeter.ac.uk

Dr Samuel Vine, Project Supervisor (University of Exeter)
S.J.Vine@exeter.ac.uk, 01392 722892

Prof Mark Brosnan, Project Supervisor (University of Bath)
M.J.Brosnan@bath.ac.uk, 01225 386081

Gail Seymour, Research Ethics and Governance Manager
g.m.seymour@exeter.ac.uk, 01392 726621

Appendix E. The 50-item adult Autism Spectrum Quotient (AQ).

	Definitely agree	Slightly agree	Slightly disagree	Definitely disagree
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 to 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 edgewise.				
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 theater than to 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.				

	Definitely agree	Slightly agree	Slightly disagree	Definitely disagree
28. I usually concentrate more on the whole picture, rather than on 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 enjoy doing things alone.				
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 (e.g., types of cars, birds, trains, plants).				
42. I find it difficult to imagine what it would be like to be someone else.				
43. I like to carefully plan any activities I participate in.				
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 people's date of birth.				
50. I find it very easy to play games with children that involve pretending.				

Appendix F. The Social Responsiveness Scale- shortened version.

Please indicate by placing one tick after each of the 11 statements below, how true you think each statement is true of you. If you are unsure about which answer to give- it is hard to pick an answer- **please choose the one** that seems nearest or most appropriate. This can often be the first thing that comes into your mind. There are no right or wrong answers. Please be as honest as you can and do not leave out any questions.

		not TRUE	sometimes TRUE	often TRUE	almost always TRUE
1	I avoid eye contact with other people.				
2	I have difficulty making friends, even when trying my best.				
3	I am sometimes regarded by other people as odd or weird.				
4	I have trouble keeping up with the flow of a normal conversation.				
5	I have difficulty relating to peers.				
6	Compared to others I have a restricted or unusually narrow range of interests.				
7	I have trouble understanding the meaning of other people's tone of voice and facial expressions.				
8	I have trouble concentrating too much on parts of things rather than seeing the whole picture.				
9	I would rather be alone than with others.				
10	I have more difficulty than others do with changes in routine.				
11	I am (or used to be) overly sensitive to sounds, textures or smells.				

Appendix G. The Intolerance of Uncertainty Scale – shortened version.

Please circle the number that best corresponds to how much you agree with each statement.

	Not at all characteristic of me	A little characteristic of me	Somewhat characteristic of me	Very characteristic of me	Entirely characteristic of me
1. Unforeseen events upset me greatly.	1	2	3	4	5
2. It frustrates me not having all the information I need.	1	2	3	4	5
3. Uncertainty keeps me from living a full life.	1	2	3	4	5
4. One should always look ahead so as to avoid surprises.	1	2	3	4	5
5. A small unforeseen event can spoil everything, even with the best of planning.	1	2	3	4	5
6. When it's time to act, uncertainty paralyses me.	1	2	3	4	5
7. When I am uncertain I can't function very well.	1	2	3	4	5
8. I always want to know what the future has in store for me.	1	2	3	4	5
9. I can't stand being taken by surprise.	1	2	3	4	5
10. The smallest doubt can stop me from acting.	1	2	3	4	5
11. I should be able to organize everything in advance.	1	2	3	4	5
12. I must get away from all uncertain situations.	1	2	3	4	5