

Please cite as:

Civile, C., Elchlepp, H., McLaren, R., Galang, C.M., Lavric, A., and McLaren, I.P.L. (2017). The effect of scrambling upright and inverted faces on the N170. *Quarterly Journal of Experimental Psychology*. DOI: 10.1177/1747021817744455

The effect of scrambling upright and inverted faces on the N170

Ciro Civile¹, Heike Elchlepp¹, Rossy McLaren¹, Carl Michael Galang², Aureliu Lavric¹ and I.P.L. McLaren¹

¹School of Psychology, College of Life and Environmental Sciences,
University of Exeter, UK.

²Department of Psychology Neuroscience & Behaviour (PNB)
McMaster University

All correspondence concerning this article should be addressed to:

Ciro Civile or I.P.L McLaren

Washington Singer Laboratories

University of Exeter

Perry Road

Exeter EX4 4QG

c.civile@exeter.ac.uk; i.p.l.mclaren@exeter.ac.uk

Disclosure of Interest

The authors report no conflicts of interest

Abstract

The *face inversion effect* refers to a decrement in performance when we try to recognise familiar faces turned upside down (inverted), compared to familiar faces presented in their usual (upright) orientation. Recently, we have demonstrated that the inversion effect can also be found with checkerboards drawn from prototype-defined categories when the participants have been trained with these categories, suggesting that factors such as expertise and the relationships between stimulus features, may be important determinants of this effect. We also demonstrated that the typical inversion effect on the N170 seen with faces is found with checkerboards, suggesting that modulation of the N170 is a marker for disruption in the use of configural information. In the present experiment, we first demonstrate that our scrambling technique greatly reduces the inversion effect in faces. Following this, we used *Event-Related Potentials (ERPs)* recorded while participants performed an *Old/New recognition study* on normal and scrambled faces presented in both upright and inverted orientations to investigate the impact of scrambling on the N170. We obtained the standard robust inversion effect for normal faces: The N170 was both larger and delayed for normal inverted faces as compared to normal upright faces, whereas a significantly reduced inversion effect was recorded for scrambled faces. These results show that the inversion effect on the N170 is greater for normal compared to scrambled faces, and we interpret the smaller effect for scrambled faces as being due to the reduction in expertise for those faces consequent on scrambling.

Keywords: face inversion effect, N170 peak, scrambled faces, configural processing.

Introduction

Faces are one of our main vehicles for social communication. Face recognition and the interpretation of facial expressions provide us with clues about who we interact with and their motivational and emotional state (Haxby, Hoffman, Gobbini, 2000). Most studies converge to suggest that face recognition relies on holistic/configural cues (there is no consensus on the terminology with these two terms often used interchangeably) whereas this is not the case for many other visual objects that are instead recognised through individual feature-based processing (Tanaka & Farah, 1993; Collishaw & Hole, 2000). Configural face processing most likely involves many different types of processes, all of which converge to allow the extraction of the relations among facial features (Diamond & Carey, 1986, Maurer, LeGrand, & Mondloch, 2002, Civile, McLaren, & McLaren, 2016). The question that then arises is whether these processes are specific to faces, or, if they are deployed in the perceptual analysis of other stimuli that subjects are equally expert with (e.g. artificial categories of objects named Greebles, Gauthier & Tarr, 1997; checkerboards, McLaren, 1997; images of cars and birds, Gauthier, Skudlarski, Gore, & Anderson, 2000). To answer this question, several authors have investigated the effects of distorting configural information in faces and objects stimuli. This is the approach that we take in this paper. We first introduce the face inversion effect and its possible dependence on configural processing. We then consider evidence bearing on this issue and the related issue of the role of expertise in producing the face inversion effect. This quite naturally leads us to the hypothesis that, at least in part, it is our expertise in exploiting configural information in upright faces that produces the inversion effect, and we set out to test this and to establish ERP correlates of the inversion effect that will help us examine this issue.

Recognition of objects that are usually seen in one orientation is sometimes significantly impaired when the same objects are turned upside down, showing how difficult it is to recognise them (Dallet, Wilcox, & D'Andrea, 1968). This was found to be especially true for faces, a phenomenon which is known as the “face inversion effect” (Yin, 1969). Yin (1969) presented participants with upright or inverted pictures of faces, aeroplanes, houses, and other stimuli. Following the study phase participants were then tested with stimuli in the same orientation in a recognition task. The results showed that when the stimuli were studied and tested in an upright orientation, faces were better recognised than other sets of stimuli. Critically, when the same stimuli were presented and tested in an inverted orientation, the recognition of faces was poorer relative to the recognition of other classes of stimuli. This result suggested that faces are “special” (Yin, 1969; Valentine & Bruce, 1986). However, later Diamond and Carey (1986) demonstrated that it was possible to obtain as strong an inversion effect for dog images as for human faces when participants were experts in dog breeds. This finding had a significant impact on the literature and suggested a new interpretation of the face inversion effect based on “expertise” as the key factor that determines our ability to recognise faces.

Diamond and Carey (1986) proposed that there are two types of configural information that we use to recognise faces and objects. The first one is based on *first-order relational* cues between the constituent elements or facial features (e.g. nose always above the mouth, the eyes always above the nose); these identify a stimulus as a face. The second one is based on *second-order relational* cues that capture the small variations in the first-order spatial relationships between features of the base prototype for objects of that type. Their contention was that a large inversion effect can be recorded when the exemplars of the category of stimuli share a base configuration, and participants have gained the necessary expertise to exploit variation in this

configural information. More recently Robbins and McKone (2007) tried to replicate Diamond and Carey's (1986) finding with dog images, however, this time, the results obtained showed a smaller inversion effect for dog images than the inversion effect for human faces. But, although the exact pattern of results from Diamond and Carey's (1986) study was not replicated, and the notion of second-order relations was criticised (e.g. Burton et al., 2015 proposed that second-order relations are a property of the image not of a face) the idea that recognition is linked to expertise for configural information (Diamond & Carey, 1986) remains influential in investigations of face/object recognition. Some of the key behavioural findings are those by Searcy and Bartlett (1996) and Leder and Bruce (1998). These authors used local and configural distortions of face stimuli to investigate the perceptual effects of inversion. Their results showed that distinctiveness impressions caused by distorted configural information (e.g. shortening the distance from mouth to nose) disappeared when faces were presented in an inverted orientation relative to both upright faces and faces distorted in more local aspects (e.g. darker lips, bushier eyebrows, blackening teeth). In a similar vein, Leder, Huber, and Bruce (2001, Exp.1) showed that turning a face upside down leads to a decreased perceptual sensitivity to manipulations of the spatial relationship between the eyes. These studies (see also Maurer et al., 2002, for a review) indicated that inversion strongly affects the use of configural information.

Parallel to the work on the effects of configural distortions on face recognition, some authors investigated the effects of expertise for configural information on novel kinds of stimuli. In particular, Gauthier and Tarr (1997) and McLaren (1997) provided some of the earliest evidence that expertise for prototype defined categories of stimuli (i.e., artificial stimuli named Greebles and checkerboards exemplars that share a configuration) can give participants an advantage in recognition. Gauthier and Tarr (1997) showed that participants were better at

identifying a target feature when it was presented in a familiar (seen before) Greeble configuration than when it was presented in a novel Greeble configuration. McLaren (1997) provided some of the first evidence in support of perceptual learning as a key factor determining the inversion effect. In the relevant study, participants were first trained (the pre-exposure phase) to categorise exemplars drawn from prototype-defined categories of checkerboards that participants had never been exposed to before entering the laboratory. Nevertheless, on a subsequent discrimination task participants showed an increased ability to discriminate between upright (same orientation seen during the pre-exposure phase) exemplars that had not been seen before, but were taken from a familiar (pre-exposed) category of checkerboards, relative to exemplars taken from a novel category of checkerboards (i.e. that had not been previously experienced). Critically, participants showed a clear inversion effect for exemplars from the familiar category, in that they were significantly worse at discriminating new inverted exemplars of that category relative to new upright exemplars. There was no such effect for the exemplars drawn from the novel category. McLaren (1997) interpreted these results as a perceptual learning effect (McLaren, Kaye, & Mackintosh, 1989). Specifically, according to this theory pre-exposure to exemplars taken from a prototype-defined category will lead to a reduction in the salience of the prototypical elements for that category, making these elements less salient. Thus, the elements unique to each exemplar will now be more salient (because they are not encountered very often) and this would allow the participants to better discriminate one (upright) exemplar from another. Importantly, this advantage (the result of perceptual learning) would be lost on inversion resulting in impaired discrimination performance.

A recent study by Civile, Zhao, Ku, Elchlepp, Lavric, and McLaren (2014a), showed that the results obtained by McLaren (1997) transfer to the kind of *old/new recognition memory*

N170 and the Face Inversion Effect

paradigm conventionally used in studies that obtain the inversion effect (Yin, 1969). In Civile, Zhao et al. (2014)'s study, participants were first trained to classify exemplars of two prototype-defined categories (the pre-exposure phase similar to McLaren, 1997), then shown equal numbers of exemplars drawn from either one of the familiar categories or a novel category, half of which were upright and half inverted. They were then tested for recognition of these exemplars after this study phase. The results confirmed the inversion effect for novel checkerboard exemplars taken from a familiar category (experienced during the pre-exposure phase) and the lack of an inversion effect for exemplars drawn from a novel category (not seen during the pre-exposure phase). Taken together, Gauthier and Tarr's (1997), McLaren's (1997), and Civile, Zhao et al. (2014) studies provide support for the Diamond and Carey's (1986) expertise account of face recognition; they have also served as a basis for further investigations of face and object recognition using Electroencephalogram (EEG)-derived event-related potentials (ERPs).

Studies using ERPs are split, in terms of their interpretation of their results, between the specificity and expertise accounts of face recognition already mentioned. Early studies claimed the N170 ERP component to be the neural signature for face stimuli (Bentin, Allison, Puce, Perez, & McCarthy, 1996). The N170 is a negative-polarity ERP deflection (peak) maximal at 150-200ms after the onset of a face stimulus at posterior temporal sites (Bentin et al., 1996; George, Evans, Fiori, Davidoff, & Renault, 1996). The N170 has been found to be elicited by (larger amplitude) images of human faces (or face components like eyes or nose and mouth) but not by animal faces, human hands (Bentin et al., 1996), and objects (e.g. houses, flowers, and tools, Carmel & Bentin, 2002). Since the task adopted for human face stimuli and non-face stimuli was the same, any specific brain response to human faces or components was attributed

N170 and the Face Inversion Effect

to a neural mechanism tuned to detect human physiognomic information (Bentin et al., 1996). In a more recent study, Zion-Golumbic and Bentin (2007) found the N170 to be larger in response to different types of human faces (normal, no contour, scrambled) than watches, indicating that they were all correctly detected as faces. Furthermore, manipulations aimed to affect the configural information of the faces (removal of the contour or scrambling the eyes, nose and mouth) resulted in a delayed and increased N170 peak compared to normal faces. No effects of such manipulations were recorded for images of watches (Zion-Golumbic & Bentin, 2007). Importantly, Bentin et al. (1996, Experiment 3) also recorded a larger (although not significant) N170 for inverted human faces compared to their upright counterparts. Further studies aimed to test this effect of inversion on the N170, and provided additional evidence showing the N170 as being larger in amplitude and longer in latency when responding to inverted compared to upright faces (Rossion et al., 1999; Rossion et al., 2002; Eimer, 2000). Therefore, the argument can be made that if inversion disrupts configural processing, then the effect of inversion on the N170 in some way reflects this disruption (Rossion & Gauthier, 2002).

However, based on the expertise account (Diamond & Carey, 1986), some researchers have claimed that the N170 peak is delayed and larger in response to an inverted face because our expertise for seeing the stimulus' configuration in its usual orientation (upright) is disrupted. Rossion, Gauthier, Goffaux, Tarr and Crommelinck (2002) directly compared ERPs for upright and inverted faces and Greebles during a same/different decision task. Participants were trained in a three-phase experiment in which there was first a baseline phase where ERPs were recorded from responses to faces and Greebles presented in both upright and inverted orientations. This was followed by a training phase using only upright Greebles. Finally, during the final (third) phase of the experiment ERPs were acquired in response to new faces and new Greebles

N170 and the Face Inversion Effect

presented in both upright and inverted orientations. ERPs before the training phase showed that the inversion effect on the N170 mentioned above (more pronounced and delayed N170 for inverted faces compared to upright faces) to be larger for faces than for Greebles. However, after the training with upright Greebles, the inversion effect on the N170 was of a similar magnitude for faces and Greebles. The authors proposed that the mechanisms behind the Face Inversion Effect (FIE) on the N170 can be extended to novel sets of stimuli (that share a configuration) but only when participants have been trained with these stimuli. In a similar vein, Busey and Vanderkolk (2005) showed that fingerprint experts exhibited an effect of inversion in response to images of fingerprints similar to the face inversion effect on the N170. In particular, both inverted faces and inverted fingerprints elicited a significantly delayed N170 compared to upright faces and upright fingerprints in the right parietal-temporal scalp regions.

Furthermore, Civile, Zhao et al. (2014, Experiment 4), found an inversion effect on the N170 for checkerboards drawn from a familiar (seen during the pre-exposure phase) prototype-defined category. Specifically, a larger and delayed N170 was found for inverted familiar checkerboards compared to upright familiar checkerboards (the effect was largest at the temporal-occipital electrode site P08). In conclusion, the results from the studies described above support the view that experience with stimuli possessing configural structure may explain some key phenomena in face recognition. These studies also provided motivation for a departure from the original conceptualisation of the N170 as being specific to faces, toward a position where the inversion-induced enhancement and delay in the N170 can be obtained for at least some non-face categories of stimuli if they are made sufficiently familiar. This is the view of the N170 that we adopted in the study reported here.

The present study set out to directly investigate the link between expertise in using configural information and the face inversion effect originally suggested by Diamond and Carey (1986, for a review of other relevant studies, see Maurer et al., 2002). We first aimed to replicate the typical strong behavioural inversion effect for normal face stimuli. We also contrasted performance with normal faces with performance in a condition where face stimuli were “scrambled” – which serves as our experimental manipulation (Experiment 1). The scrambled stimuli have disrupted configural information (even when upright) caused by the random re-positioning of each of the main facial features (right eye, left eye, mouth, nose, right ear, left ear). This should severely reduce the use of familiar (usually seen within a face) configural information in the upright orientation. Another useful characteristic of these stimuli is that they still contain all the features of faces, and thus are well matched with normal faces for complexity (and lower-level visual characteristics). In the past, other researchers have used manipulated faces to study face recognition and the N170, but all these manipulations suffer from some drawbacks. Some studies have transformed normal and schematic (drawings) of faces by pixelating the images (randomizing the pixels’ spatial positions), thus making the images unrecognizable as faces (Sagiv & Bentin, 2001; Jacques & Rossion, 2004). In other studies, schematic and normal faces were scrambled by dividing a face into patches and shuffling the patches. This manipulation also made the faces hard to recognise as such (Latinus & Taylor, 2006). Finally, some studies scrambled the faces by switching the location of the main features, however, the configural information for the eyes was kept always unaltered (Colishaw & Hole, 2000). For the purpose of the current study, we adopted Civile, McLaren, and McLaren (2014) and Civile, McLaren, and McLaren (2016)’s scrambling manipulation. Thus, we aimed to have a set of stimuli recognisable as being derived from faces which contain the same featural

N170 and the Face Inversion Effect

information as that for normal faces (i.e. nose, ears, mouth, eyes) but in which the configural information involving those main features was disrupted.

Furthermore, we investigated the electrophysiological responses (Experiment 2, EEG) to normal faces in comparison with the responses to scrambled faces and expected to obtain a pattern of results on the N170 that mirrored that for our behavioural results. That is, the inversion effect on the N170 was expected to be substantial for normal faces, and the inversion effect on the N170 for scrambled faces should (to anticipate our results) be reduced. Following the analysis just given, we predicted a larger and delayed N170 for inverted normal faces compared to normal upright faces and predicted smaller differences on the N170 for upright vs. inverted scrambled faces (to accompany the anticipated reduced behavioural inversion effects).

Experiment 1

Method

Materials

The study used a set of 128 male face images standardized to grayscale on a black background using Adobe Photoshop. Gimp 2.6 (Lecarme & Delvare, 2013) software was then used to manipulate the 128 stimuli. Each face stimulus was prepared in four different versions (normal upright, normal inverted, scrambled upright and scrambled inverted), that were used in a counterbalanced fashion across participants so that each face was equally often used in each condition of the experiment. Six facial features were scrambled – the mouth, nose, each ear, and each eye (including the eyebrow). The faces were scrambled by randomly selecting one feature, moving it to the forehead (chosen because this is the widest space inside the face and so can

N170 and the Face Inversion Effect

accommodate any feature). Then, selecting another feature to be moved to the space left empty by the first feature, and so on until all the six facial features were moved. Any distortions produced by this process were then minimized by smoothing. This procedure was applied independently to each face, resulting in multiple spatial configurations of the main facial features in this set of scrambled faces. The stimuli, whose dimensions were 5.63 cm x 7.84 cm, were presented at the resolution of 1280 x 960. The experiment was run using Superlab 4.0.7b. on an iMac computer. Participants sat at about 70 cm away from the screen where the images were presented.

Participants

We recruited 24 (18 female and six male, mean age = 20.04) undergraduate university students with normal or corrected-to-normal vision who participated in the experiment for monetary compensation. They provided written informed consent and the procedures were approved by the institutional ethics committee.

We conducted a post-hoc power analysis using G*power software (Faul, Erdfelder, Lang, & Buchner, 2007). G*Power was used to calculate the Effect Size f (Direct option by inserting the partial η^2 of .30) for the 2 x 2 interaction which gave an f of 0.65. Three measurements were adopted (interaction, inversion effect for normal faces, and inversion effect for scrambled faces). The analysis revealed a statistical power of 0.99 in line with the recommended 0.80 level of power (Cohen, 1988).

Procedure

The experiment consisted of a 'study phase' and an 'old/new recognition phase' (Civile, Zhao et al., Civile, McLaren, & McLaren; Civile, McLaren, & McLaren, 2016). In the study

phase, each participant was shown four different types of face (normal upright, normal inverted, scrambled upright and scrambled inverted) with 16 photos for each face type. In the recognition task, another 64 new faces from the same four face types were added to this set. Each facial stimulus never appeared in more than one condition at a time during the experiment but served at some point in all conditions.

Trial structure

After the instructions, the participants saw a fixation cross in the center of the screen presented for one second. This was followed by a stimulus, presented for three seconds; then the fixation cross was repeated, and another face presented until all 64 facial stimuli had been seen. Once all 64 stimuli had been shown, the program moved to the next set of instructions, which explained the requirements of the old/new recognition task. Participants were told that they were about to see more stimuli presented one at a time in random order. They were asked to press the ‘.’ key if they recognized the stimulus as one shown earlier or to press ‘x’ if they did not. Participants were then shown (in random order) the 64 facial stimuli they had already seen, intermixed with a further 64 previously unseen stimuli.

During the old/new recognition task, after the one-second warning cue, the stimulus was shown for 4 s, and the participant had to respond during this period. If the participant pressed the wrong key (i.e. a key other than ‘x’ or ‘.’) the feedback ‘Wrong key’ was shown for two seconds before the next stimulus appearing on the screen. If the participant was too slow to respond (i.e. took longer than four seconds), the message ‘Too slow’ appeared on the screen. Otherwise, no feedback was given. Since, in the old/new recognition task, there were 128 stimuli to observe, three participant breaks were incorporated. These allowed participants to rest their eyes after they

had viewed 32 facial stimuli. At the end of the experiment, participants were shown a further message thanking them for participating. They were then paid and debriefed.

Results

The data from all the participants were used in the signal detection d' sensitivity analysis of the recognition task (seen and not seen stimuli for each stimulus type) where a $d' =$ of 0.00 indicates chance-level performance (Stanislaw & Todorov, 1999). Reaction times (reported below) revealed no effects of a speed/accuracy trade-off that could have influenced our interpretation of the d' sensitivity data.

Accuracy

We computed a 2 x 2 repeated measure design using *Face Type* (normal, scrambled) and *Orientation* (upright, inverted) as factors. A 2 x 2 ANOVA revealed a significant two-way interaction, $F(1,23) = 9.820$, $MSE = .241$, $p = .005$, $\eta^2_p = .29$, indicating that the inversion effect for normal faces was significantly larger than the inversion effect for scrambled faces. A simple effect analysis showed a significant inversion effect with superior performance for normal upright faces ($M = 1.53$, $SE = 0.17$) compared with normal inverted faces ($M = 0.69$, $SE = 0.09$), $t(23) = 4.706$, $SE = .178$, $p < .001$, $\eta^2_p = .49$, (see Figure 1). No significant inversion effect was found between scrambled upright ($M = 0.42$, $SE = 0.13$) and scrambled inverted ($M = 0.21$, $SE = 0.12$) faces, $t(23) = 1.640$, $SE = .128$, $p = .115$, $\eta^2_p = .10$.

Furthermore, additional analyses showed that normal upright faces were recognised significantly better than scrambled upright, $t(23) = 5.301$, $SE = .200$, $p < .001$, $\eta^2_p = .56$, and scrambled inverted, $t(23) = 6.520$, $SE = .201$, $p < .001$, $\eta^2_p = .64$, faces.

We also report here the complementary measure of bias: Normal inverted, $\beta = 0.91$; Normal upright, $\beta = 1.72$; Scrambled inverted, $\beta = 1.06$; Scrambled upright, $\beta = 1.52$.

Reaction Times

Analyses of the reaction times (RTs) were restricted to correct responses. As for the accuracy results, for RTs as well we computed a 2 x 2 for *Face Type* (normal, scrambled) and *Orientation* (upright, inverted) revealing a significant interaction, $F(1,23) = 7.626$, $MSE = 12962.36$, $p = .011$, $\eta^2_p = .24$. A simple effects analysis showed a significant inversion effect with faster performance for normal upright faces ($M = 1345$ ms, $SE = 56.94$) compared with that for normal inverted faces ($M = 1475$ ms, $SE = 60.17$), $t(23) = 3.034$, $SE = 43.03$, $p = .006$, $\eta^2_p = .28$. No significant inversion effect was found between RTs for scrambled upright ($M = 1650$ ms, $SE = 72.26$) and scrambled inverted ($M = 1652$ ms, $SE = 72.38$) faces, $t(23) = .067$, $SE = 32.84$, $p = .947$, $\eta^2_p = .00$.

Figure 1: About here, please

Discussion

As we predicted, there was a strong inversion effect for normal faces, which was significantly larger than the inversion effect for the scrambled faces. This pattern of results shows that we have, at the least, severely reduced the inversion effect typically seen with normal faces using our scrambling manipulation. Our result is consistent with the hypothesis that participants, when presented with scrambled faces, thus disrupting familiar configural information, would, at least in part, have reduced expertise for those upright faces. We should also point out that despite the low scores for the scrambled faces, we have previously been able

N170 and the Face Inversion Effect

to detect a highly significant inversion effects at this level of d' (see Civile, Zhao et al, 2014), suggesting that it is not simply a scaling effect we are observing here.

Importantly, we notice that despite being not significant, we find a numerical inversion effect for scrambled faces. We also performed a Bayesian analysis based on the procedures outlined by Dienes (2011). This used the effect in the normal faces as the prior, setting the standard deviation of $p(\text{population value}|\text{theory})$ to the mean for the inversion effect in this condition. We then calculated Bayes factors using a one- tailed distribution for our theory (because it does not predict a reversal of the inversion effect, only that it might be diminished) and a mean of 0. This gave a Bayes factor (B) of 1.07 for the inversion effect obtained with scrambled faces. This is not smaller than .3 thus, it does not support the null hypothesis. Instead, it provides equivocal evidence for any inversion effect. Thus all we can be sure of here is that the effect is smaller than that with normal faces, not that it has been eliminated entirely.

In the following experiment, we investigated the effects of inversion and our scrambling manipulation on the N170 peak. We predicted we would find the typical inversion effect on the N170 for normal faces i.e. larger and delayed peak for inverted faces compared to that for upright faces. Critically, we expected to find a reduced inversion effect on the N170 for scrambled faces, that is, a reduced difference in amplitude or latency between upright and inverted scrambled faces.

Experiment 2

Method

Materials

The study used a set of 320 pictures of faces in total, half female and half male. The stimuli were manipulated and scrambled in the same way as in Experiment 1.

Participants

As for Experiment 1, we recruited 24 (17 female and seven male, mean age = 20.87) undergraduate university students with normal or corrected-to-normal vision who participated in the experiment for monetary compensation. All the participants were right-handed. They provided written informed consent and the procedures were approved by the institutional ethics review board.

Procedure

This was the same as that in Experiment 1, except that the number of trials was increased for this experiment to allow better averaging of our ERP components. In the study phase, each participant was shown four different types of the face (normal upright, normal inverted, scrambled upright and scrambled inverted) with 40 photos for each face type (half male and half female). In the test phase, another 160 novel stimuli of the same four types were added to this set. Each stimulus never appeared in more than one condition at a time during the experiment but served at some point in all conditions.

EEG Recordings

The EEG was sampled continuously during both the study and test phases at 500 Hz with a band-pass of 0.016-100 Hz, the reference at Cz and the ground at AFz using 64 Ag/AgCl active electrodes and BrainAmp amplifiers. There were 61 electrodes placed on the scalp in an extended 10-20 configuration plus one on each earlobe (references during online recording). Their impedances were kept below 10 k Ω .

Data Processing and Analysis

EEG data processing was performed in MATLAB with the open-source EEGLAB (Delorme & Makeig, 2004) and ERPLAB (Lopez-Calderon & Luck, 2014) toolboxes. The data

N170 and the Face Inversion Effect

were filtered off-line using a noncausal Butterworth bandpass filter (half-amplitude cutoffs at 0.1 and 20 Hz, 24 dB/octave roll-off). All scalp electrodes were referenced off-line to a common average reference. This was used according to previous studies in the field investigating the N170 for normal vs scrambled upright faces (Towler, Parketny, & Eimer, 2016), and for normal faces vs objects (e.g. Greebles; Rossion et al., 2002; cars, Goffaux, Gauthier, & Rossion, 2003). To correct for blink artefacts, independent component analysis (ICA)¹ was applied to the continuous data after the deletion of sections containing extreme values (Jung et al., 2000). Remaining artefacts exceeding ± 100 mV in amplitude or containing a change of over 100 mV in a period of 50 ms were rejected (in ERPLAB this function is named Simple Threshold Voltage, Luck, 2005). Artefact-free data were then segmented into epochs ranging from 250 ms before to 800 ms after stimulus onset for all conditions (Zion-Golumbic & Bentin, 2007).

N170 Analysis

ERPs were created by averaging the segmented trials (and baseline corrected) according to the four stimulus' conditions in each phase of the experiment (study and recognition). The absolute peak of the N170 was determined using the ERPLAB Measurement Tool based on the option to select the most negative peaks between 150 and 220 ms. Subsequent visual scrutiny was applied to ensure that the values represented real peaks rather than end points of the epoch (Zion-Golumbic & Bentin, 2007). N170 latency and amplitude analyses were restricted to electrode PO8, (over the right temporal hemisphere) which often in the literature has shown bigger effects on the N170 (Rossion & Jacques, 2008).

¹ In Part A of our *supplemental material* document we provided additional EEG data processing and analyses without the ICA. The effects obtained are very similar to ones here reported.

P100 Analysis

A similar additional analysis was performed on amplitudes and latencies of the P1 (the most positive in the range 100-170 ms) in order to determine whether the obtained inversion effect differences between normal vs scrambled faces on the N170 could be starting earlier and therefore might not reflect the influence of our scrambling manipulation on the N170.

Results

Behavioural Results

As in Experiment 1, the data from all the participants were used in the signal detection d' analysis of the recognition task. Reaction times (reported below) revealed no effects of a speed/accuracy trade-off that could have influenced our interpretation of the d' sensitivity data.

Accuracy

We conducted a 2 x 2 repeated measures ANOVA with factors *Face Type* (normal, scrambled) and *Orientation* (upright, inverted). It revealed a significant two-way interaction, $F(1,23) = 23.07$, $MSE = .178$, $p < .001$, $\eta^2_p = .50$, replicating the finding from Experiment 1 that the inversion effect in normal faces was significantly larger than that in scrambled faces. A simple effects analysis showed a significant inversion effect with greater performance for normal upright faces ($M = 1.40$, $SE = 0.108$) compared with normal inverted faces ($M = 0.59$, $SE = 0.101$), $t(23) = 6.339$, $SE = .128$, $p < .001$, $\eta^2_p = .63$, (see Figure 2). Simple effects analyses showed similar recognition performance for both scrambled upright ($M = 0.41$, $SE = 0.07$) and scrambled inverted ($M = 0.43$, $SE = 0.09$) faces, $t(23) = 0.163$, $SE = .098$, $p = .872$, $\eta^2_p = .00$.

Furthermore, as in Experiment 1, additional analyses showed that normal upright faces were recognised significantly better than scrambled upright, $t(23) = 8.432$, $SE = .117$, $p < .001$, $\eta^2_p = .75$, and scrambled inverted, $t(23) = 6.821$, $SE = .142$, $p < .001$, $\eta^2_p = .66$, faces.

N170 and the Face Inversion Effect

We report here the complementary measure of bias: Normal inverted, $\beta = 1.07$; Normal upright, $\beta = 1.71$; Scrambled inverted, $\beta = 1.43$; Scrambled upright, $\beta = 1.44$.

Reaction Times

As for Experiment 1, analyses of the reaction times (RTs) were restricted to correct responses. We computed a 2 x 2 for *Face Type* (normal, scrambled) and *Orientation* (upright, inverted) revealing a significant interaction, $F(1,23) = 5.503$, $MSE = 20246.87$, $p = .028$, $\eta^2_p = .19$. A simple effects analysis showed a significant inversion effect with faster performance for normal upright faces ($M = 1333$ ms, $SE = 53.48$) compared with that for normal inverted faces ($M = 1423$ ms, $SE = 62.48$), $t(23) = 3.940$, $SE = 22.79$, $p = .001$, $\eta^2_p = .40$. No significant inversion effect was found between RTs for scrambled upright ($M = 1577$ ms, $SE = 81.88$) and scrambled inverted ($M = 1531$ ms, $SE = 81.15$) faces, $t(23) = -.868$, $SE = 53.56$, $p = .395$, $\eta^2_p = .03$.

Figure 2: About here, please

ERPs Results

Study Phase

N170 Peak Latency. A 2 x 2 repeated measure ANOVA revealed a significant interaction between *Face Type* and *Orientation*, $F(1,23) = 28.076$, $MSE = 14.84$, $p < .001$, $\eta^2_p = .55$. A simple effects analysis showed a significant inversion effect on the N170 for normal faces, with latencies to normal inverted faces ($M = 196$ ms, $SE = 3.35$) being significantly delayed compared to latencies for normal upright faces ($M = 185$ ms, $SE = 2.94$), $t(23) = 7.807$, $SE =$

N170 and the Face Inversion Effect

1.40, $p < .001$, $\eta^2_p = .72$. A reduced inversion effect was found for scrambled faces with scrambled inverted ($M = 196$ ms, $SE = 3.40$) nevertheless showing a reliable delay compared to scrambled upright faces ($M = 193$ ms, $SE = 3.45$), $F(1,23) = 2.821$, $MSE = 0.94$, $p = .010$, $\eta^2_p = .25$. (see Figure 3, Panel A).

Additional analyses showed that the N170 latency for scrambled upright, $t(23) = 2.987$, $SE = 2.73$, $p = .007$, $\eta^2_p = .27$, and scrambled inverted, $t(23) = 4.276$, $SE = 2.53$, $p < .001$, $\eta^2_p = .44$, faces were both significantly delayed compared to normal upright faces.

P100 Peak Latency. We conducted the same analyses as for the N170 peak latency. A 2 x 2 repeated measure ANOVA revealed a significant interaction between *Face Type* and *Orientation*, $F(1,23) = 14.04$, $MSE = 20.43$, $p = .001$, $\eta^2_p = .37$. A simple effect analysis showed latencies to normal inverted faces ($M = 153$ ms, $SE = 2.42$) being significantly delayed compared to latencies for normal upright faces ($M = 144$ ms, $SE = 2.42$), $t(23) = 4.723$, $SE = 1.88$, $p < .001$, $\eta^2_p = .49$. No significant inversion effect was found for scrambled faces with scrambled inverted ($M = 152$ ms, $SE = 2.81$) only numerically showing a slight delay compared to scrambled upright faces ($M = 150$ ms, $SE = 2.60$), $F(1,23) = 1.523$, $MSE = 1.31$, $p = .14$, $\eta^2_p = .09$. This pattern of results on the P100 peak latency could suggest that the latency effects found for the N170 might be due earlier effects (for similar effects on the P100 peak latency see Zion-Golumbic & Bentin, 2007). Hence, just like in Zion-Golumbic and Bentin (2007)'s study, we explored the effects for our stimuli on the 170 peak latency by subtracting the P100 latencies. Once this was done, a significant interaction between *Face Type* and *Orientation*, $F(1,23) = 28.07$, $MSE = 14.84$, $p < .001$, $\eta^2_p = .55$ was still found. A simple effects analysis showed a significant inversion effect for normal faces, $t(23) = 5.234$, $SE = 1.71$, $p < .001$, $\eta^2_p = .54$. There was now no significant inversion effect for scrambled faces, $F(1,23) = .770$, $MSE = .86$, $p = .44$, $\eta^2_p = .02$. This analysis

N170 and the Face Inversion Effect

reassured us that, although some early effects were present, the main effects found for the N170 peak latency persisted even when these earlier effects were allowed for.

N170 Peak Amplitude. A 2 x 2 repeated measure ANOVA revealed a significant interaction, $F(1,23) = 14.264$, $MSE = 1.14$, $p = .001$, $\eta^2_p = .38$. A simple effect analysis showed a significant inversion effect for normal faces, with amplitudes for inverted normal faces ($M = 1.65\mu V$, $SE = 0.84$) being larger (closer to being negative) compared to amplitudes for upright normal faces ($M = 2.84\mu V$, $SE = 0.83$), $t(23) = 3.257$, $SE = .363$, $p = .003$, $\eta^2_p = .31$. No significant effect of inversion was found for amplitudes in response to upright ($M = 3.02\mu V$, $SE = 0.79$) and inverted ($M = 3.48\mu V$, $SE = 0.66$) scrambled faces, $t(23) = 1.448$, $SE = .322$, $p = .16$, $\eta^2_p = .08$ (see Figure 3, Panel A).

Additional analyses showed that the N170 peak for normal inverted faces was significantly more negative than that for scrambled inverted faces, $t(23) = 5.045$, $SE = .364$, $p < .001$, $\eta^2_p = .52$, and scrambled upright faces, $t(23) = 3.350$, $SE = .409$, $p = .003$, $\eta^2_p = .32$.

P100 Peak Amplitude. A 2 x 2 repeated measure ANOVA revealed no interaction between *Face Type* and *Orientation*, $F(1,23) = 1.435$, $MSE = 1.41$, $p = .24$, $\eta^2_p = .05$.

Old/New Recognition Phase

N170 Peak Latency. Here as well, the 2 x 2 repeated measure ANOVA revealed a significant interaction between *Face Type* and *Orientation*, $F(1,23) = 12.002$, $MSE = 45.90$, $p = .002$, $\eta^2_p = .34$. A simple effects analysis showed a significant inversion effect on the N170 for normal faces, with latencies to normal inverted faces ($M = 193$ ms, $SE = 2.49$) being significantly delayed compared to latencies for normal upright faces ($M = 183$ ms, $SE = 3.23$), $t(23) = 5.598$,

N170 and the Face Inversion Effect

SE = 1.74, $p < .001$, $\eta^2_p = .57$. No significant inversion effect was found for scrambled inverted ($M = 190$ ms, $SE = 3.09$) vs scrambled upright faces ($M = 189$ ms, $SE = 2.72$), $F(1,23) = .085$, $SE = 1.96$, $p = .93$, $\eta^2_p = .00$. (see Figure 3, Panel A).

In the recognition task we also found that scrambled upright, $t(23) = 3.084$, $SE = 1.97$, $p = .005$, $\eta^2_p = .29$, and scrambled inverted, $t(23) = 3.281$, $SE = 1.90$, $p = .003$, $\eta^2_p = .31$, faces were significantly delayed on the N170 peak compared to normal upright faces. Thus, as in the study phase, the normal inverted faces and two sets of scrambled faces tended to group together regarding latencies and were all significantly different to the normal upright faces.

P100 Peak Latency. A 2 x 2 repeated measure ANOVA revealed no interaction between *Face Type* and *Orientation*, $F(1,23) = 1.51$, $MSE = 77.04$, $p = .23$, $\eta^2_p = .06$.

N170 Peak Amplitude. A 2 x 2 repeated measure ANOVA revealed a non-significant interaction, $F(1,23) = 2.573$, $MSE = 1.98$, $p = .12$, $\eta^2_p = .10$. Although the interaction is not significant, a simple effects analysis showed a significant inversion effect for normal faces, with amplitudes for inverted normal faces ($M = 1.30\mu\text{V}$, $SE = 0.86$) being larger (closer to being negative) compared to amplitudes for upright normal faces ($M = 2.26\mu\text{V}$, $SE = 0.86$), $t(23) = 2.835$, $SE = .337$, $p = .009$, $\eta^2_p = .25$. No effect of inversion was found for amplitudes in response to upright ($M = 2.59\mu\text{V}$, $SE = 0.89$) and inverted ($M = 2.69\mu\text{V}$, $SE = 1.01$) scrambled faces, $t(23) = .093$, $SE = .355$, $p = .92$, $\eta^2_p = .00$, (see Figure 3, Panel A).

Additional analyses showed that the N170 peak for normal inverted faces was significantly more negative than that for scrambled inverted faces, $t(23) = 4.276$, $SE = .300$, $p < .001$, $\eta^2_p = .44$, and scrambled upright faces, $t(23) = 4.061$, $SE = .324$, $p < .001$, $\eta^2_p = .41$.

P100 Peak Amplitude. A 2 x 2 repeated measure ANOVA revealed no interaction between *Face Type* and *Orientation*, $F(1,23) = .994$, $MSE = 1.12$, $p = .34$, $\eta^2_p = .03$.

Figure 3: About here, please

Discussion

The behavioural results from Experiment 2 confirm what we previously found in Experiment 1: the inversion effect in the normal faces was significantly larger than that in the scrambled faces. These results support the claim that disruption of configural information (by scrambling) leads to a quite severe reduction of the inversion effect for scrambled faces. We further analysed this effect by calculating the Bayes factor for scrambled faces. We did this by using the same procedure adopted in Experiment 1 (i.e. using as a prior the inversion effect for normal faces). This resulted in a Bayes factor of 0.14; for upright vs inverted scrambled faces in Experiment 2. This factor is substantially less than 1, providing some support for the null (for Bayes factor calculator see Dienes, 2011) however, it does not establish it (which it would if less than .1).

The results from the ERPs provide similar results to the behavioural ones. In the *study phase*, a greater inversion effect on the N170 (delayed and larger N170 for inverted faces compared to that for upright faces) was found for normal faces compared to that for scrambled faces. We then calculated the Bayes factor for the inversion effect on the N170 for scrambled faces (here we also used the inversion effect for normal faces as prior). For the latencies, we obtained a B of 8.86, whereas for the amplitudes we found a B of 0.76. These just confirm that disrupting the configural information by scrambling the main features within it, does reduce the inversion effect compared to normal faces, however, there is still some additional information (e.g. single feature orientation information, Civile, McLaren, & McLaren, 2014) leading to some

inversion effect (either numerical or significant) for scrambled faces. We shall return to this in our General Discussion.

The ERPs from the *old/new recognition* task showed a similar pattern of results to that found in the study phase. Hence, a greater inversion effect on the N170 was found for normal faces compared to scrambled faces for the latencies. Also, for the amplitudes (despite the interaction not being significant) there was a trend in the same direction. Bayes factor analyses showed a B of 0.21 for the scrambled faces inversion effect latencies and a B of 0.38 of for the amplitudes.

General Discussion

In the Experiments reported in this paper we investigated the link between configural processing, expertise and the face inversion effect (Diamond & Carey, 1986). In particular, our aim was to investigate whether the loss of familiar configural information brought about by the scrambling manipulation would strongly reduce the face inversion effect observed in performance and the N170 brain potential.

The behavioural results from Experiment 1 and 2 confirmed that we can obtain the usual inversion effect for normal faces and that this inversion effect is significantly reduced for scrambled faces. These results are consistent with our hypothesis that participants, when presented with upright scrambled faces, would have less applicable expertise with which to exploit the configural information contained in those faces. When the same scrambled faces are presented inverted, participants will suffer less decrement in performance consequent on their inability to make use of this configural information than would be the case for normal faces. Hence, we observe a reduced inversion effect for scrambled faces. In this sense, our behavioural results support Diamond and Carey's (1986) position. The inversion effect can be explained (at

least in part) by our ability to extract variations in the configural information for categories of stimuli that share a configuration and are sufficiently familiar.

Another aspect of our behavioural results (Experiment 1 and 2) that deserves comment is the fact that performance on the scrambled faces, whether upright or inverted, was very similar to that on normal inverted faces, and worse than to upright normal faces. At first sight, this seems at odds with the results in Civile, McLaren, and McLaren (2014). The authors reported a highly significant inversion effect with scrambled faces, but note that they used a configural “template” for the scrambled faces shown to their participants. Each participant saw a certain type of scrambled face that always had the facial features in the same position, albeit one different to the position in normal faces. We hypothesize that this configural structure was important in allowing a highly significant inversion effect to manifest in these experiments. It was not the only factor, however. Civile, McLaren, and McLaren (2014) also used scrambled faces which had 50% of their facial features inverted as controls in their experiment. This eliminated the inversion effect and strongly suggested that the orientation of individual features was also contributing to the inversion effect in the scrambled faces. Upright scrambled faces showed better performance than these 50% feature-inverted and scrambled faces, but inverted scrambled faces were significantly worse than this control set.

The scrambled faces used in the current experiment have a randomly chosen configuration that varies from stimulus to stimulus, and this may be the key factor that reduced the inversion effect with these stimuli. The individual feature orientations were not altered as part of this scrambling process, such that they are all upright in the upright faces, and all inverted in the inverted faces. Clearly, if individual feature orientation could, on its own, drive the inversion effect then we would expect to see a highly significant effect (perhaps even

N170 and the Face Inversion Effect

comparable to that for normal faces) with the present stimuli. Furthermore, there is the possibility that some of the configural information contained within each individual feature (e.g. the spatial relationships between the eye brows and the eyes or between the lower and upper mouth lips) could still have an effect in causing the inversion effect. We conclude that it is the combination of a set configuration and individual feature orientation that is crucial in generating an inversion effect with scrambled faces. The performance level with our randomly scrambled faces will reflect both the loss of expertise in dealing with these stimuli, their increased variability relative to normal faces (which are constrained to have a set configuration) and the loss of fine-grain information as a result of the smoothing process used in scrambling. Seen from this perspective, the issue is more one of why the performance with normal inverted faces is almost as bad. They also suffer from the loss of expertise, but their variability is only that of normal faces, and they have not been subject to the same smoothing process. Here we can appeal to the finding first made by McLaren (1997) and established in Civile, Zhao et al., (2014), that novel inverted stimuli drawn from a prototype-defined familiar category suffer from a disadvantage relative to controls. Thus, we see the approximate behavioural agreement regarding performance between normal inverted faces and the scrambled faces as something of an accident brought about by a combination of different factors.

The ERP results in Experiment 2 provide some intriguing similar results to our behavioural findings. In both the *study phase* and the *old/new recognition task*, the N170 peak latencies showed a highly significant inversion effect (longer latencies for inverted faces compared to upright faces) for normal faces, which contrasted with a reduced inversion effect for scrambled faces. Furthermore, we have noted (see additional analyses) that the latencies for normal inverted faces, scrambled upright and scrambled inverted faces were all significantly

N170 and the Face Inversion Effect

delayed compared to the latencies for normal upright faces. This result matches our behavioural results (Experiment 1 and 2), in the sense that we observed significantly higher performance for normal upright faces compared to the performance for all the other faces (see additional analyses for the behavioural results). Thus, in addition to the modulation of the inversion effect and its reduction, these results (both behavioural and electrophysiological) are consistent with the idea that disrupting expertise by either inversion (in the case of normal faces) or scrambling (both upright and inverted scrambled faces) can lead to reduced recognition performance and a delayed N170 response. These results are in agreement with our predictions, specifically with the idea that the delay of the N170 peak is due to the difficulty that participants encountered when the usual familiar configuration was altered in some way (Halit, de Haan, Johnson, 2000; Rossion & Gauthier, 2002). Our results also would seem to match (at least in part) Zion-Glumbic and Bentin (2007)'s results. The authors found that when configural information was disrupted by the scrambling manipulation, a delayed N170 peak was recorded for scrambled upright faces (the inversion effect was not tested) compared to that for normal upright faces. In addition, no difference on the N170 amplitudes was found for normal vs scrambled upright faces.

Perhaps the most striking result from the ERP amplitudes is that normal inverted faces show an enhanced N170 compared to all other stimulus types. Why do the amplitudes group the scrambled faces with the normal upright faces, when the latencies group the scrambled faces with the normal inverted faces? Perhaps we have evidence here for dissociable, multiple processes contributing to the inversion effect. In the case of the latencies, given the grouping with normal inverted faces, it is plausible to interpret the delay in the N170 as reflecting the difficulty in using familiar configural information as we have already said. We speculate that the effect of scrambling on N170 amplitudes has a different source. Something like this pattern of

N170 and the Face Inversion Effect

results has previously been found in other studies that investigated the expertise account of the face inversion effect. Civile, Zhao et al. (2014) investigated the ERPs to upright and inverted checkerboards drawn from familiar (seen during pre-exposure) and novel prototype-defined categories². The authors found that the N170 peak amplitudes during the study phase for inverted checkerboards from a familiar category were more negative compared to the other stimulus type conditions that showed similar amplitudes, i.e. that upright checkerboards from a familiar category and novel checkerboards grouped together. A similar pattern can also be seen in Rossion et al. (2002)'s study on Greebles before training on the Greebles. In that phase, the N170 peak amplitudes were more negative for normal inverted faces compared to normal upright faces, and the upright and inverted Greeble stimuli showed amplitudes that were more similar to the normal faces. Thus, our results together with those previously found in the literature seem to support the idea that novel sets of stimuli (checkerboards, Greebles, scrambled faces) elicit an N170 peak amplitude more similar to normal upright faces than that elicited by normal inverted faces, even though their performance to these stimuli is more like that to normal inverted faces.

Given that this is a reliable pattern of results, then, the question remains of what might cause it. Our suggestion is that the enhanced N170 amplitude acts as a marker for the component of the inversion effect referred to earlier, that is, the significant disadvantage suffered by inverted checkerboard exemplars drawn from familiar, prototype-defined categories relative to controls, which has an analogue in the result found by Civile, Zhao et al. (2014) comparing scrambled faces that have a set configuration to 50% feature-inverted and scrambled faces (Civile, McLaren, & McLaren, 2014). In effect, we are asserting that the grouping of normal upright

² In Part B of our *supplemental material* document we have offered an alternative way to process and analyse the EEG data similar to that adopted by Civile, Zhao et al. (2014). This was done to allow a closer comparison between the two studies despite adopting very different stimuli (faces, checkerboards).

N170 and the Face Inversion Effect

faces and both sets of scrambled faces found here reflects the fact that none of them suffers from this disadvantage. The argument here is that the normal inverted faces possess all the spatial relations of a normal face, but presented in an orientation that not only makes it difficult to make use of them, but imposes an additional cost as well. This cost is not present in either the normal upright faces (where the learned configuration is exploited appropriately) or the two sets of scrambled faces (where there is no learned configuration in the first place).

In conclusion, in the two experiments reported here, we have provided some evidence in support of the idea that it is our ability to use configural information that plays a key role in determining the inversion effect. In particular, that once our expertise in exploiting the configural information within a face has been disrupted by the scrambling manipulation, the inversion effect is reduced. Furthermore, we have shown how correlates of these effects on behavioural recognition performance can also be found in the ERP N170 component.

Acknowledgments

This project has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No 743702 awarded to Ciro Civile.

References

- Bell, A. J., and Sejnowski, T. J. (1995). An information-maximization approach to blind separation and blind deconvolution. *Neural Computation*, 7, 1129–1159.
- Bentin, S., Allison, T., Puce, A., Perez, E., and McCarthy, G. (1996). Electrophysiological studies of face perception in humans. *Journal of Cognitive Neuroscience*, 8, 551-565.
- Busey, T., and Vanderkolk, J. (2005). Behavioural and electrophysiological evidence for configural processing in fingerprint experts. *Vision Research*, 45, 431-448.
- Burton, A. M., Schweinberger, S. R., Jenkins, R., & Kaufmann, J. M. (2015). Arguments against a configural processing account of familiar face recognition. *Perspectives on Psychological Science*, 10, 482–496.
- Carmel, D., and Bentin, S. (2002). Domain specificity versus expertise: factors influencing distinct processing of faces. *Cognition*, 83, 1-29.
- Civile, C., McLaren, R., and McLaren, I.P.L. (2016). The face inversion effect: Roles of first and second-order relational information. *The American Journal of Psychology*, 129, 23-35.
- Civile, C., Zhao, D., Ku, Y., Elchlepp, H., Lavric, A., and McLaren, I.P.L. (2014a). Perceptual learning and inversion effect: Recognition of prototype-defined familiar checkerboards. *Journal of Experimental Psychology; Animal Learning and Cognition*, 40, 144-161.
- Civile, C., McLaren, R., and McLaren, I. P. L. (2014b). The face inversion effect: Parts and wholes. *The Quarterly Journal of Experimental Psychology*, 67, 728–746.
- Cohen, J. (1988). *Statistical power analysis for the behavioural sciences* (2nd ed.). HillSEale, NJ: Lawrence Earlbaum Associates.

N170 and the Face Inversion Effect

- Collishaw, M., and Hole, G. (2000). "Featural and configurational processes in the recognition of faces of different familiarity". *Perception*, 29, 893–909.
- Dallett, K., Wilcox, S., and D'Andrea, L. (1968). Picture memory experiments. *Journal of Experimental Psychology*, 76, 312-320.
- Delorme, A. and Makeig, S. (2004) EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of Neuroscience Methods*, 134, 9–21
- Diamond, R., & Carey, S. (1986). Why faces are and are not special: An effect of expertise. *Journal of Experimental Psychology: General*, 115, 107-117.
- Dienes, Z. (2011). Bayesian versus orthodox statistics: Which side are you on? *Perspectives on Psychological Science*, 6, 274–290.
- Eimer, M. (2000). The face-specific N170 component reflects late stages in the structural encoding of faces. *Neuroreport*, 11, 2319-2324.
- Faul, F., Erdfelder, E., Lang, A., and Buchner, A. (2007). G*Power3: A flexible statistical power analysis program for the social, behavioural, and biomedical sciences. *Behaviour Research Methods*, 39, 175–191.
- Gauthier, I., Skudlarski, P., Gore, J. C., and Anderson, A. (2000). Expertise for cars and birds recruits brain areas involved in face recognition. *Nature Neuroscience* 3, 191–197.
- Gauthier, I., and Tarr, M. (1997). Becoming a “Greeble” expert: exploring mechanisms for face recognition. *Vision Research*, 37, 1673-1682.
- George, N., Evans, J., Fiori, N., Davidoff, J., and Renualt, B. (1996). Brain events related to normal and moderately scrambled faces. *Cognitive Brain Research*, 4, 65-76.

N170 and the Face Inversion Effect

Goffaux, V., Gauthier, I., and Rossion, B. (2003). Spatial scale contribution to early visual differences between face and object processing. *Brain Research, Cognition Brain Research*, 16, 416–424

Halit, H., de Haan, M., Johnson, M.H., 2000. Modulation of event-related potentials by prototypical and atypical faces. *NeuroReport* 11, 1871–1875.

Haxby, J., Hoffman, E., and Gobbini, M. (2000): The distributed human neural system for face perception. *Trends in Cognitive Science*, 4, 223–233.

Jacques, C., and Rossion, B. (2004) Concurrent processing reveals competition between visual representations of faces. *Neuroreport*, 15, 2417–2421

Jung, T., Makeig, S., Westerfield, M., Townsend, J., Courchesne, E., Sejnowski, T., 2001. Analysis and visualization of single-trial eventrelated potential. *Human Brain Mapping*, 14, 166 – 185.

Latinus, M., and Taylor, M. (2006). Face processing stages: impact of difficulty and the separation of effects. *Brain Research*, 1123, 179–187.

Leder, H., and Bruce, V. (1998). Local and relational aspects of face distinctiveness. *The Quarterly Journal of Experimental Psychology*, 51, 449 – 473.

Leder, H., Huber, O., and Bruce, V.(2001). Configural features in the context of upright and inverted faces. *Perception* 30, 73–83.

Lecarme, O., and Delvare, K. (2013). The book of GIMP: The complete guide to nearly everything. San Francisco, CA: No Starch Press.

Lopez-Calderon, J., & Luck, S.J. (2014). ERPLAB: an open-source toolbox for the analysis of event-related potentials. *Frontiers in Human Neuroscience*, 8, 1–14.

N170 and the Face Inversion Effect

Luck S. J. (2005). *An Introduction to the Event-Related Potential Technique* 2nd Edn

Cambridge, MA: MIT Press

Maurer, D., Le Grand, R., and Mondloch, C. (2002). The many faces of configural processing.

Trends in Cognitive Science, 6, 255-260.

McLaren, I.P.L. (1997). Categorisation and perceptual learning: An analogue of the face

inversion effect. *The Quarterly Journal of Experimental Psychology*, 50, 257-273.

McLaren, I.P.L., Kaye, H. & Mackintosh, N.J. (1989). An associative theory of the

representation of stimuli: Applications to perceptual learning and latent inhibition. In

R.G.M. Morris (Ed.) *Parallel Distributed Processing - Implications for Psychology and*

Neurobiology. Oxford, Oxford University Press.

Robbins, R., and McKone, E. (2007). No face-like processing for objects-of-expertise in three

behavioural tasks. *Cognition*, 103, 34-79.

Rossion, B., and Gauthier, I. (2002). How does the brain process upright and inverted faces?

Behavioural and Cognitive Neuroscience Reviews, 1, 62-74.

Rossion, B., Delvenne, J., Debatisse, D., Goffaux, V., Bruyer, R., Crommelinck, M., and

Guerit, M. (1999). Spatio-Temporal localization of the face inversion effect: an event-

related potentials study. *Biological Psychology* 50, 173-189.

Rossion, B., Gauthier, I., Goffaux, V., Tarr, M., and Crommelinck, M. (2002). Expertise training

with novel objects leads to face-like electrophysiological responses. *Psychological*

Science, 13, 250-257.

N170 and the Face Inversion Effect

- Rossion B. and Jacques C. (2008). Does physical interstimulus variance account for early electrophysiological face sensitive responses in the human brain Ten lessons on the N170. *Neuroimage*, 39, 1959–1979.
- Searcy, J., and Bartlett, J.(1996). Inversion and processing of component and spatial-relational information in faces. *Journal of Experimental Psychology: Human Perception and Performance*, 22, 904 – 915.
- Sagiv, N., and Bentin S. (2001). Structural encoding of human and schematic faces: holistic and part-based processes. *Journal of Cognitive Neuroscience*, 13, 937-951.
- Stanislaw, H., and Todorov, N. (1999). Calculation of signal detection theory measures. *Behaviour Research Methods, Instruments, and Computers*, 31, 137–149
- Tanaka, J., and Farah, M. (1993) Parts and wholes in face recognition. *Quarterly Journal of Experimental Psychology*, 46, 225–245.
- Towler, J., Parketny, J., & Eimer, M. (2016). Perceptual face processing in developmental prosopagnosia is not sensitive to the canonical location of face parts. *Cortex*, 74, 53–66
- Valentine, T., and Bruce, V. (1988). Mental rotation of faces. *Memory & Cognition*, 16, 556-566.
- Yin, R. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81, 141-145.
- Zion-Golumbic, E., and Bentin, S. (2007). Dissociated neural mechanisms for face detection and configural encoding: Evidence from N170 and Gamma-band oscillation effects. *Cerebral Cortex*, 17, 1741–1749

Figure 1

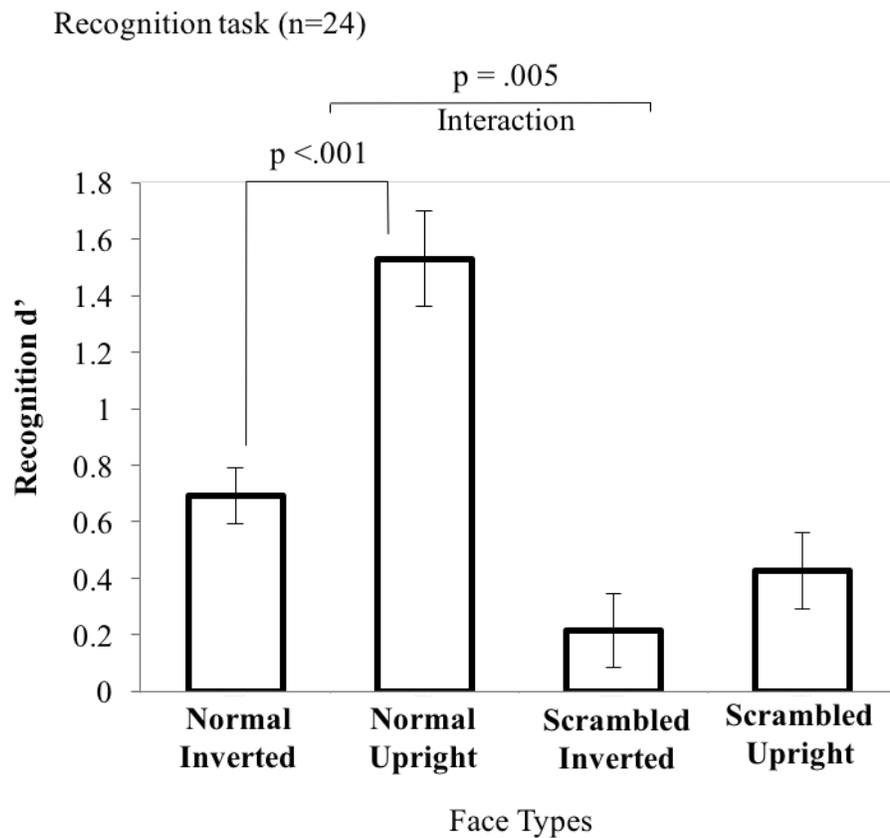


Figure.1. The X axis shows the four different stimulus conditions, whereas the Y axis shows the d' means for each of the four facial conditions in the old/new recognition task of Experiment 1. Error bars are SEM.

Figure 2

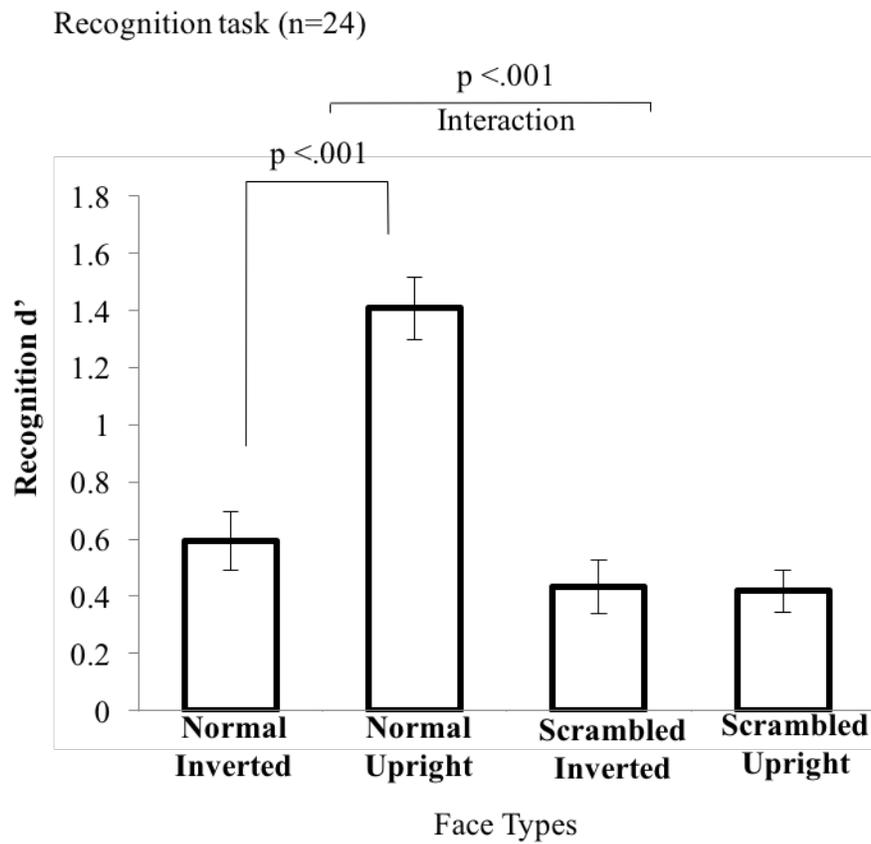


Figure.2. The X axis shows the four different stimulus conditions, whereas the Y axis shows the d' means for each of the four facial conditions in the old/new recognition task of Experiment 2. Error bars are SEM.

Figure 3

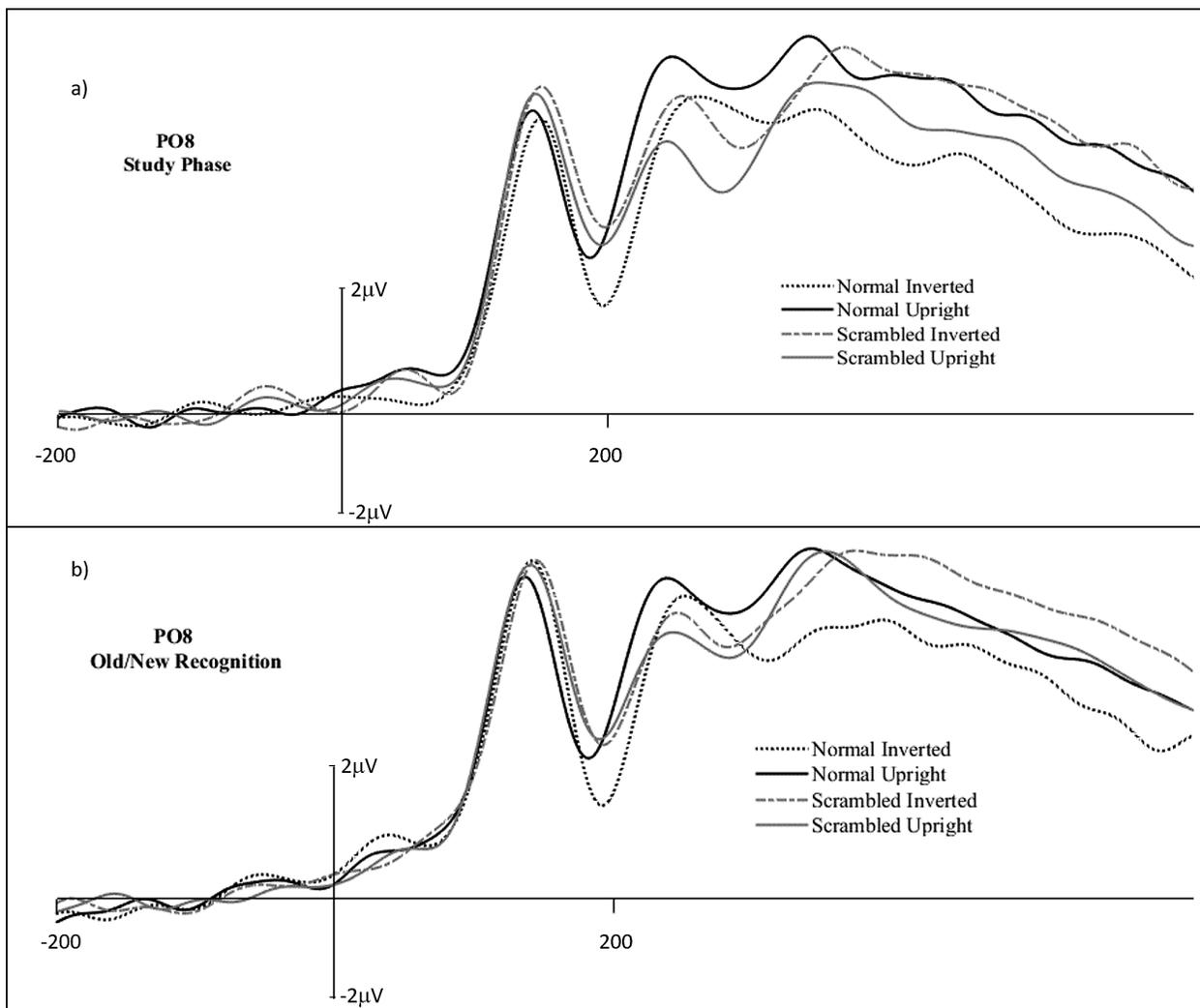


Figure 3. Panel (a): waveforms at electrode P08 for the study phase. Panel (b): waveforms at electrode P08 for the recognition task. In both panels, the X-axis shows the elapsed time after a stimulus was presented and the Y-axis shows the ERP amplitudes (μV).