

Neural responses to faces reflect social personality traits

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Faces are a developmentally primary and critically important source of social information, and they are processed differently from most other visual percepts. Studies of brain electrophysiology reveal a face-sensitive component, the N170, which is typically enhanced to faces relative to other stimuli. Research in social disabilities suggests that an atypical N170 response in this population may stem from decreased developmental exposure to faces secondary to reduced social interest. Here we examined the relationship between neural responses to faces and social personality characteristics in a normative sample. Participants were pre-screened to identify individuals scoring high on extraversion or introversion. Both groups were presented with upright and inverted face stimuli. An inversion effect, a marker of expertise for faces, was observed in people with high extraversion but not in those with high introversion. These findings suggest that, within typically developing populations, social attitudes are reflected in the neural correlates of face perception.

Keywords: Personality; Extraversion; Social motivation; N170; Event-related potential (ERP/EEG); Face perception.

INTRODUCTION

Faces are highly salient visual stimuli. Efficient analysis of faces likely serves evolutionary importance in terms of perception, interaction, and communication in social situations (Ellis & Young, 1989). Indeed, multiple studies have shown preferential processing of faces throughout development, even in newborn infants (de Haan, Pascalis, & Johnson, 2002). Cognitive theorists have attributed this preference for faces as reflecting an innate functional specialization of the brain (Bruce & Young, 1986); face-specific modules are active within the first months of life and become increasingly attuned to the processing of faces through maturational pruning and experience (Gauthier & Nelson, 2001). Most adults are extraordinarily proficient in face perception (de Haan et al., 2002) and

tend to process and recognize faces more quickly and accurately than other types of visual stimuli (Ellis & Young 1989; Farah, Wilson, Drain, & Tanaka, 1998; Yin, 1969).

Neuroimaging research indicates that face perception is subserved by specialized cortical regions. Spatial imaging studies demonstrate that the presentation of face stimuli selectively activates the fusiform gyrus located in the posterior occipital-temporal cortex (Kanwisher, McDermott, & Chun, 1997; Kanwisher, Stanley, & Harris, 1999). Temporal imaging studies using event-related potentials (ERPs) also reveal particular patterns of brain activity elicited by human faces. When viewing face stimuli, approximately 170 ms post-stimulus onset, a negative deflection of the visual event-related potential waveform is observed, principally over the occipital-temporal areas of the right

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hemisphere (Bentin, Allison, Puce, Perez, & McCarthy, 1996; Rossion et al., 2000; Thierry, Martin, Downing, & Pegna, 2007). This N170 component is enhanced in response to faces compared to nonface or object stimuli (Rossion et al., 2000) but appears insensitive to familiarity (Bentin & Deouell, 2000) and emotional expression (Eimer & Holmes, 2007; Eimer, Holmes, & McGlone, 2003). Consequently the N170 is believed to reflect the earliest stages of face perception, structural encoding (Eimer, 2000b), preceding higher-order processes such as identity recognition. The N170 is elicited by impoverished stimuli, such as schematic faces (Sagiv & Bentin, 2001), and even face-like objects (Churches, Baron-Cohen, & Ring, 2009), but is also sensitive to the visual complexity of face stimuli, responding maximally to face stimuli most closely resembling natural faces (Churches et al., 2009; Sagiv & Bentin, 2001). The neural circuitry reflected in the N170 is honed through developmental experience, and the electrophysiological component follows a protracted developmental course, decreasing in latency until it approximates adult levels in adolescence (Taylor, Batty, & Itier, 2004; Taylor, McCarthy, Saliba, & Degiovanni, 1999).

The face-specificity of the N170 and corresponding hemodynamic measures of activity in the fusiform gyrus is a matter of ongoing debate; behavioral evidence, as well as hemodynamic and electrophysiological imaging studies, suggests that similar processing strategies and brain regions are invoked during processing of nonface stimuli with which individuals have extensive experience, or *perceptual expertise* (Gauthier & Tarr, 1997; Gauthier, Skudlarski, & Anderson, 2000). Additional developmental research is needed to determine whether these brain regions evolved for faces and are co-opted for other stimuli with which individuals develop perceptual expertise (i.e., a domain-specific account) or whether these regions support a particular visual processing strategy irrespective of the visuoperceptual content (i.e., a domain-general account). For both faces and other expert stimuli, one manifestation of the development of expertise is the emergence of an inversion effect. The face inversion effect was first observed as a salient decrement in face recognition when faces are inverted without comparable deficit when objects are inverted (Tanaka & Farah, 1993; Yin, 1969). This phenomenon is presumed to reflect application of a configural processing strategy for faces in contrast to the featural strategy applied to objects; inversion disrupts the prototypic configuration, interfering with application of this specialized processing strategy. This effect has also been demonstrated for nonface expert stimuli, such as dog experts viewing dogs

(Diamond & Carey, 1986). In this way, the inversion effect may be considered an empirical quantification of expertise for a visual stimulus. Experts can be expected to display relatively impaired recognition associated with inversion. In contrast, novices show no such impairment, presumably because these stimuli are perceived on their featural aspects alone.

Consistent with behavioral inversion effects, presentation of inverted faces also affects electrophysiological markers of expertise, eliciting a significantly larger amplitude and longer latency of the N170 component in contrast to upright face stimuli (Bentin et al., 1996; Eimer, 1998, 2000a, 2000b). These differences in the N170 between upright and inverted faces are consistent with the notion that the N170 may be sensitive to the configural properties of faces, which are disrupted when the face is inverted. Interestingly, inverted schematic faces elicit a diminished N170 response compared to upright schematic faces (Sagiv & Bentin 2001), suggesting that structural components, and potentially visual expertise, are important to inversion effects with face stimuli in studies employing the N170 as the dependent measure.

The protracted developmental course reflected in the maturation of electrophysiological markers of face perception, as well as the capacity for face-like neural processing in perceptual expertise, emphasizes the role of experience in the neural specialization associated with face perception. To date, the influence of variability in exposure or expertise with faces and face-related brain activity remains unexplored in typical development. This has, however, been a focus of study in social disability research, with the suggestion that reduced social drive may interfere with development of face expertise resulting in anomalous face perception. Autism spectrum disorder (ASD) is a developmental disorder characterized by deficits in social interaction, communication, and restricted patterns of behavior (American Psychiatric Association, 1994). Though the universality of face processing difficulties in ASD is unclear (Behrmann, Thomas, & Humphreys, 2006; Jemel, Mottron, & Dawson, 2006), many studies indicate impaired face recognition (Klin et al. 1999) and the absence of a behavioral inversion effect in this population (Langdell, 1978). ERP studies have shown slowed processing of faces as reflected in the N170 and a failure to exhibit an N170 inversion effect in ASD participants compared to controls (McPartland, Dawson, Webb, Panagiotides, & Carver, 2004). These findings have been interpreted as secondary effects of a primary deficit in social motivation. From an early age, infants with ASD are not drawn to others and exposure to faces is reduced. This results in a failure to develop typical levels of

expertise for faces and is thus reflected in poor behavioral performance and atypical neural responses to face stimuli (Dawson et al. 2002; Dawson, Webb, & McPartland, 2005).

ASD, of course, represents the extreme end of a theoretical continuum of social motivation and social ability. Research in personality traits indicates significant variance on such factors within the range of typical, or at least subclinical, social function. Indeed, central to personality theory has been the distinction between introversion and extraversion (Jung, 1955; Eysenck & Eysenck, 1964). The Eysenck Personality Questionnaire—Revised (EPQ-R; Eysenck & Eysenck, 1994) was developed as a quantitative self-assessment of this personality attribute, among others. Those scoring high on introversion are characterized as socially inhibited, avoid social situations, and find time spent alone more rewarding than time spent with others; those scoring high on extraversion are instead socially uninhibited, actively seek social engagements, and find this more rewarding than time spent alone. Eysenck proposed a biological basis for this aspect of social drive; this biological model argues that people with lower arousability in the central nervous system require greater external stimulation for optimum arousal, and vice versa (Eysenck & Eysenck, 1964). Gale, Joanne, Morris, Moore, & Forrester (2001) obtained support for this hypothesis in an electroencephalographic (EEG) study that revealed greater magnitude of frontal, temporal, and occipital alpha activity in extraverts compared to introverts. Similarly, Fink (2005) showed that extraverts display less cortical activation than introverts during emotional face processing. Taken together, these findings indicate that introversion–extraversion scores provide a contrasting index of social motivation observable in both behavior and neurophysiology. Though at least one study has failed to demonstrate a relationship between this personality trait and face recognition (Thompson & Mueller, 1984), correlations between introversion and extraversion and early stages of face perception, such as structural encoding, have not been explored. In the present study, we investigated the relationship between introversion and extraversion and neural correlates of face perception in typically developing individuals. Following from the hypotheses put forth to describe atypical social development (Dawson et al., 2005), we predicted that normal variation in social motivation would modulate face perception. Participants scoring high in extraversion or introversion viewed a series of upright and inverted natural and cartoon faces while we simultaneously recorded EEG. We predicted that individuals who scored high on extraversion would

demonstrate higher levels of perceptual expertise, reflected in enhanced ERP indices of expertise. Specifically, we predicted that extraverts would exhibit an N170 inversion effect exceeding that manifest by introverts. For novel, digitized cartoon faces, with which both groups were similarly naïve, we predicted that, as per Sagiv and Bentin (2001), both groups would display an N170 but neither group would display an inversion effect.

METHODS

Participants

Ninety-six college undergraduates (62 female, 34 male) completed the Eysenck Personality Questionnaire Revised Short Scale (EPQ-R; Eysenck, Eysenck, & Barrett, 1985; Eysenck & Eysenck, 1994). The mean EPQ-R score was 6.90 ($SD = 3.83$). Twenty-eight participants scoring in the extreme high (i.e., extravert) and low (i.e., introvert) spectrum as defined by scoring above or below 1 SD of the mean score (6.90 ± 3.83) were invited to participate in the EEG portion of the study. Participants completed a neuropsychological and neurological screening form and were excluded for current or historical trauma or disease that could influence neural response. EEG data from three participants were removed from the analysis owing to more than 25% of EEG channels being marked as bad channels. One further participant was excluded owing to unreported psychopathology evident during the EEG session. Therefore, the final sample included 14 participants in the extraversion group (7 females, 7 males; mean age 23 years) and 10 in the introversion group (7 females, 3 males; mean age 22 years). All participants ($N = 24$; 22 right-handed) had normal or corrected-to-normal visual acuity and were naïve to the purpose of the study. All procedures were approved by the Human Investigation Committee at Yale School of Medicine, and this was in accordance with the Declaration of Helsinki (1975/1983).

Apparatus and stimuli

Stimuli were presented on a Pentium-IV computer controlling a 51 cm color monitor (75 Hz, 1024×768 resolution) running E-Prime 2.0 software (Schneider, Eschman, & Zuccolotto, 2002). Displays were viewed at a distance of 75 cm in a sound-attenuated room, with low ambient illumination. EEG was recorded using NetStation 4.3. A 128 lead Geodesic sensor net (Electrical Geodesics, Inc.; Tucker, 1993) was placed

on the participant's head and fitted according to the manufacturer's specifications. The electrodes were evenly spaced and symmetrically covered the scalp from nasion to inion and from left to right ear. Impedances were kept below 40 k Ω .

All stimuli were presented on a uniform black background. Face stimuli consisted of 60 color digital images (presented at 6.26° by 10.32°; drawn from Tottenham et al. (2009) and Minear and Park (2004)) of frontal face views, all neutral in expression, which were cropped within an oval frame to remove nonface features. These faces were presented both upright and inverted, producing a total of 120 natural face stimuli. Using the Cartoon Wizard program (Chen, Xu, Shum, Zhu, & Zheng, 2001), digitized cartoon faces were generated for each face stimulus (example stimuli are presented in Figure 1). Twenty-five of these faces were shaded red and randomly interspersed to serve as target stimuli. Participants pressed a button on detection of a target, ensuring that they were attending to the faces throughout the EEG session.

Measures

The EPQ-R (Eysenck, Eysenck, & Barrett, 1985; Eysenck & Eysenck, 1994) contains 48 items designed

to assess four personality dimensions: extraversion, neuroticism, psychoticism, and tendency to lie. Only the extraversion subscale was employed in the current study. This subscale contains 12 items, each requiring a "yes" or "no" response. Both the score reliability ($r = 0.82$; Caruso, Witkiewitz, Belcourt-Dittloff, & Gottlieb, 2001) and test-retest reliability ($r = 0.92$; Eysenck & Tambs 1990) for extraversion scores are high. This questionnaire was selected based on this combination of brevity and excellent psychometric properties.

Design and procedure

At the beginning of each trial, a central fixation cross was presented for a time period varying randomly between 500 and 1000 ms. This was followed by the onset of a randomly selected face stimulus for 500 ms and then a 700 ms blank screen. There were 265 trials in total: 60 presenting upright natural faces, 60 presenting upright cartoon faces, 60 presenting inverted natural faces, 60 presenting inverted cartoon faces, and 25 target faces (excluded from data analysis). The experiment took approximately 10 minutes to complete. EEG was recorded continuously throughout each trial.

Data analysis

Data were averaged for each participant by orientation (upright, inverted), face type (natural, cartoon), and hemisphere (left, right) across trials. Averaged data were digitally filtered with a 30 Hz low-pass filter to reduce environmental noise artifacts and transformed to correct for baseline shifts. The window for segmentation of the ERP was set from 100 ms before and 600 ms after stimulus onset. NetStation artifact detection settings were set to 150 μ v for bad channels, 150 μ v for eye blinks, and 100 μ v for eye movements. Channels with artifacts on more than 25% of trials were marked as bad channels and replaced through spline interpolation. Segments that contained eye blinks, eye movement, and those with more than 10 bad channels were also marked as bad and excluded. All participants detected at least 75% of the targets, with both groups obtaining comparable average accuracy of 93%, $t(1, 22) = .31$, $p = .76$. Electrodes of interest were selected based on maximal observed amplitude of the N170 to natural faces and to conform to those used in previous research (McPartland et al., 2004) and the scalp regions characteristically eliciting the N170 (Bentin et al, 1996; Rossion et al, 2000). Data were averaged across six

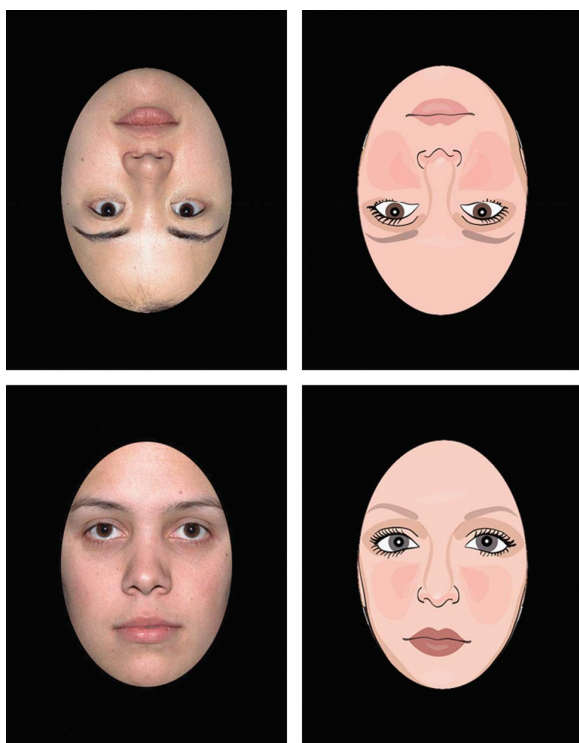


Figure 1. Examples of upright and inverted natural and cartoon face stimuli. Note that faces were presented in full color and only exemplars of female faces are provided here.

electrodes over the left lateral posterior scalp (58, 59, 64, 65, 69, and 70) and six electrodes over the right lateral posterior scalp (90, 91, 92, 95, 96, and 97).

The time window for analysis of the N170 was chosen by visual inspection of the grand averaged data. The resultant time window, extending from 99 to 231 ms post-stimulus onset, was then examined for each subject's individual average to confirm that the component of interest was captured at each electrode for each subject. Peak amplitude and latency to peak measures were averaged across each electrode group within the specified time window and were extracted for each participant.

The N170 amplitudes and latencies to peak were separately analyzed using 3×2 repeated measures analyses of variance (ANOVA). Both analyses had three within-subject factors, each with two levels: face type (natural, cartoon), hemisphere (left, right) and orientation (upright, inverted). Personality group

(extraversion, introversion) was the between-subjects factor. Effect size is presented as partial eta-squared (η^2_{partial}), where .01 represents a small effect size, .06 represents a medium effect size, and .14 represents a large effect size (Kittler, Menard, & Phillips, 2007).

RESULTS

N170 amplitude

N170 amplitudes are presented in Figure 2 as a function of hemisphere, face type, orientation, and personality group. A main effect of hemisphere indicated that the N170 was right lateralized: $F(1, 22) = 4.34, p = .05, MSE = 4.43, \eta^2_{\text{partial}} = .17$. The difference between cartoon and natural faces was not significant: main effect of face type, $F(1, 22) = 2.76, p = .11, MSE = 0.48, \eta^2_{\text{partial}} = .11$. Individuals in the

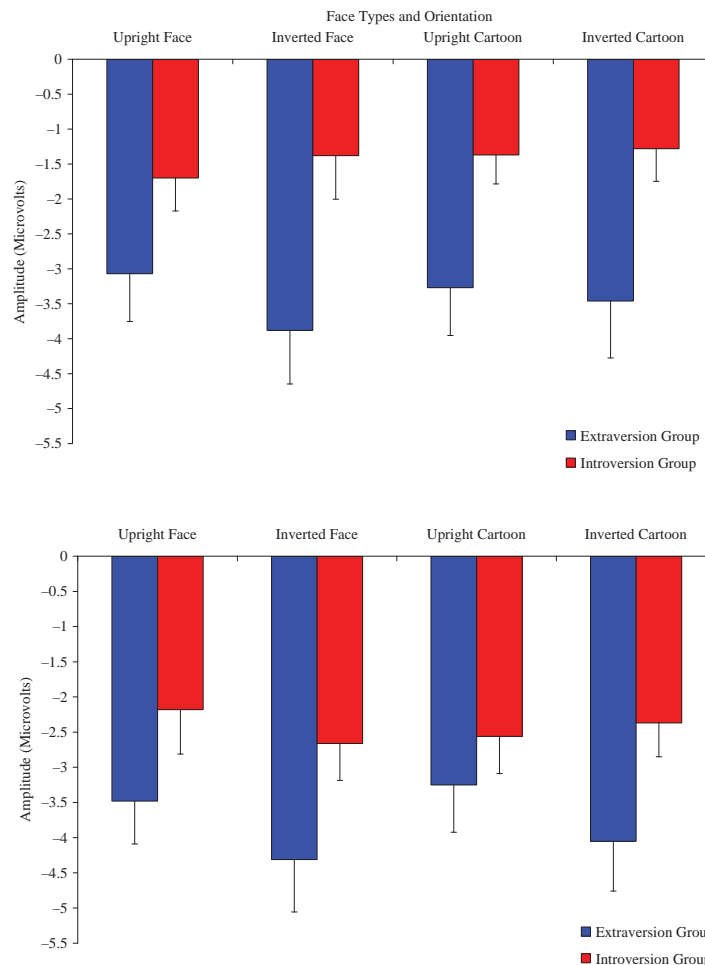


Figure 2. Mean N170 amplitude (μV) for upright and inverted natural and cartoon faces presented as a function of personality type in the left hemisphere (top panel) and the right hemisphere (bottom panel). Error bars represent $\pm 1 SE$.

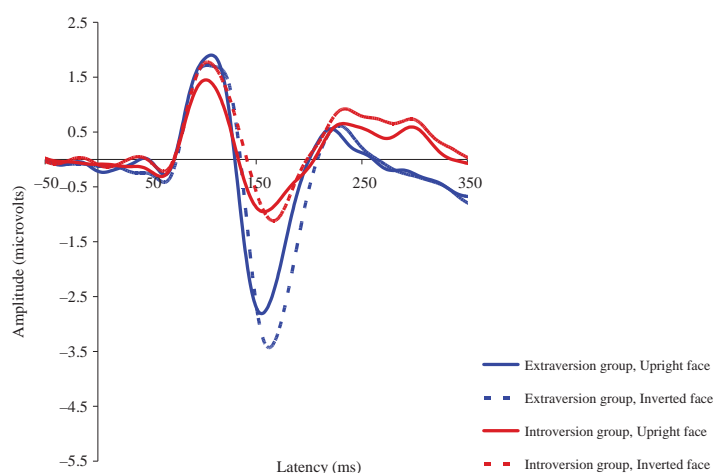


Figure 3. Grand averaged waveforms for introversion and extraversion groups averaged across electrodes of interest in the left and right hemispheres. The figure depicts upright and inverted faces collapsed across natural and cartoon face categories.

extraversion group tended to display larger N170 amplitudes, but this effect did not attain statistical significance: main effect of personality group, $F(1, 22) = 3.84, p = .06, MSE = 35.00, \eta^2_{\text{partial}} = .15$. Consistent with the current literature, we found that N170 amplitude was modulated by face orientation. As reflected in a main effect of orientation, N170 amplitudes were larger in response to inverted vs. upright faces: $F(1, 22) = 6.81, p = .02, MSE = 0.86, \eta^2_{\text{partial}} = .24$, although the inversion effects were not modulated by face type: $F(1, 22) = 0.99, p = .33, MSE = 0.45, \eta^2_{\text{partial}} = .04$. However, this inversion effect significantly interacted with personality type, as shown in a significant personality group by orientation interaction: $F(1, 22) = 5.11, p = .03, MSE = 0.86, \eta^2_{\text{partial}} = .19$. Across face type and hemisphere, individuals in the extraversion group but not the introversion group exhibited discrepant N170 amplitude associated with inversion.

As displayed in Figure 3, N170 amplitude to inverted faces was enhanced in individuals in the extraversion group but not in individuals in the introversion group. In the extraversion group, post-hoc analyses using paired-sample t -tests revealed a significant difference in N170 amplitude between upright and inverted faces (across natural and cartoon faces) in the right hemisphere, $t(13) = 4.43, p = .001$, and a marginal difference in the left hemisphere, $t(13) = 1.91, p = .08$. In the introversion group, there was no inversion effect in either the right hemisphere, $t(9) = 1.21, p = .26$ or the left hemisphere, $t(9) = -.65, p = .53$. No other significant or marginally significant effects were detected for N170 amplitude.

N170 latency

N170 latency tended to be faster in the right hemisphere, though this effect did not attain statistical significance, main effect of hemisphere, $F(1, 22) = 3.79, p = .06, MSE = 325.31, \eta^2_{\text{partial}} = .15$. Analysis of N170 latency effects also revealed an interaction between face type and hemisphere, $F(1, 22) = 5.35, p = .03, MSE = 60.50, \eta^2_{\text{partial}} = .20$, with N170 latency being longer in response to cartoon faces than natural faces in the left hemisphere only. No other significant or marginally significant effects were detected for N170 latency.

GENERAL DISCUSSION

Here we report for the first time the influence of personality traits on face perception as reflected by EEG. The N170 was employed as a neurophysiological marker of face processing in participants scoring high on introversion or extraversion. Though individuals in the extraversion group were comparable to those in the introversion group in terms of general response to faces, only those in the extraversion group showed the expected inversion effect in response to upside-down faces, demonstrating an enhanced N170 relative to upright faces, more prominent in the right hemisphere. In direct contrast with this, those in the introversion group showed no differential sensitivity to inverted faces in either hemisphere. In both personality groups, this inversion effect was not modulated by the natural or cartoon nature of the stimuli presented.

We interpret these findings as consistent with the influence of social motivation on the neural response to faces, that is, a developmental account emphasizing the role of amassed experience over time. The diminished face inversion effect observed in individuals with high introversion scores parallels similar findings in individuals with more pronounced social difficulties (Grelotti, Gauthier, & Schultz, 2002; McPartland et al., 2004). However, unlike individuals with clinical levels of social impairment, those scoring high in introversion in this study did not show an attenuation of the latency of the N170 to upright faces, indicating that the overall efficiency of face processing did not differ as a function of personality type. We interpret this as reflective of differences only at the highest levels of expertise, as manifested in sensitivity to disruption of configural information via inversion. Indeed, the developmental maturation of the N170 follows a protracted course characterized by decreasing latency, only approximating adult parameters around age 14 (Taylor et al., 2004). With respect to both behavior and neural response, the inversion effect is one of the latest developing and most mature manifestations of the development of perceptual expertise for faces. Thus, our current findings suggest differential brain response associated with introversion only at the most subtle levels, an intuitive effect among a high-functioning, typical population. In this instance, the N170 inversion effect appears to be an extremely sensitive measure of inter-individual differences in social perception. Our developmental account is necessarily speculative, as we have assessed the relationship between social personality traits and neural response to faces at a single point in adulthood. We cannot, therefore, determine whether these effects are stable across development or even within an individual adult over time.

An alternative interpretation of our findings is that the observed variation in N170 response reflects current social attitude towards other people rather than a developmental effect. Personality traits of introversion and extraversion are characteristic of differences in social interest, with extraverts seeking out socialization and introverts being less motivated in this regard. It is therefore possible that differences in neural responses reflect variation in salience, reward value, or indirect effects of a person-oriented attentional stance. We find this interpretation of our data less persuasive, as differences emerged only at the most sensitive measure of expertise, the inversion effect. It is unclear why modulation of neural response by social attitudes would manifest only at this level, as opposed to

more extensive effects (e.g., on N170 amplitude or latency to upright face stimuli).

Additional research is required to elucidate the specificity of the observed effects and differentiate between the two interpretations of our findings (social motivation, stimulus salience) presented here. Our interpretation is consistent with prior research demonstrating the face inversion effect to be associated with exposure to faces (Gajewski, Schlegel, & Stoerig, 2008) and a presumption that extraverts will have more exposure to faces; however, the present study has no direct measure of face exposure. Future work could, by assessing self-report of social contact, directly examine this relationship. Conversely, the role of exposure versus social drive could be assessed by examining brain responses in non-extraverts with high levels of face exposure (e.g., an introverted airport security screener). An additional objective of future research will be to directly measure proficiency in face perception (as a reflection of expertise) through behavioral tests assessing accuracy and response time for face identification and categorization tasks.

A third possible interpretation of our results is that the between-group differences observed reflect basic biological differences in the brains of introverts vs. extraverts. This interpretation would be consistent with accounts of basic biological differences between individuals varying in sociability, such as low-level discrepancies in central nervous system arousability (Eysenck & Eysenck, 1964). Again, we find this interpretation less viable given the absence of gross between-group differences in neurophysiological response. We observed differences between introverts and extraverts in particular responses associated with viewing experience, rather than at all levels (e.g., N170 latency to upright faces). We cannot, however, rule out that inversion effects may be more evident in particular personality-derived groups, irrespective of the relationship between social behavior and social stimuli. Future research could examine this hypothesis directly by contrasting inversion effects for face and nonface expert stimuli in groups of introverts and extraverts.

Contrary to our predictions, the inversion effect was not modulated by differences between natural and cartoon face stimuli. Moreover, there was no difference in the N170 elicited between the two face types. In contrast, previous research (Bentin, Sagiv Mecklinger, Friederici, & von Cramon, 2002) found differential N170 sensitivity to inverted schematic faces relative to inverted natural faces. We speculate that, because the cartoon faces employed in the current study were considerably more realistic than

schematic faces used in prior research, participants responded to them as natural faces. In future work, we will examine whether differential response to cartoon vs. natural faces may be a sensitive measure of failure to generalize social information in individuals with clinical levels of social dysfunction; for example, in those with ASD.

There are several limitations of the current study that will be addressed in ongoing and planned research. Social personality traits here were only manipulated by extreme scores of introversion–extraversion but, similarly to autistic symptomatology, these personality traits are likely to exist on a continuum. Therefore, we also plan to correlate neural responses to faces with personality measures across a complete range of scores on this measure of extraversion, examining the relationship between face perception and personality in a dimensional, rather than categorical, fashion. It is possible that unreported psychopathology may have influenced our results; in upcoming studies, we will assess current and lifetime psychopathology to examine this potential contribution to face perception. Finally, because eye movements were not recorded during the EEG, it is possible that between-group differences in viewing patterns to faces (e.g., increased attention to the eyes vs. the mouth) impacted our results. The target detection task ensured maintained visual attention to the face stimuli, and the visual fixation crosshair increased the likelihood of consistent attention between groups. Nevertheless, a focus of our ongoing work is to integrate simultaneous EEG and eye-tracking data so that differences in visual attention can be accounted for in future work. Our limited sample size was adequate to detect between-group differences in inversion effects, but limited statistical power may have prevented detection of other between-group differences (e.g., N170 amplitude to upright faces); it will therefore be essential to replicate these findings in larger samples.

In conclusion, we found the face-elicited N170 response to be influenced by differences in social personality traits. These results highlight the importance of understanding individual differences in social motivation in both typical and atypical populations. Furthermore, the extent to which faces are highly salient visual stimuli may be uniquely determined by personality and individual differences in social motivation.

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