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Event-Related Potentials Index Neural Response to Eye Contact

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Abstract

Sensitivity to eye-contact is a foundation upon which social cognition is built. However, there are no known neural markers characterizing response to reciprocal gaze. Using co-registered EEG and eye-tracking, we measured brain activity while participants viewed faces that responded to their looking patterns. Contingent upon participant gaze, onscreen faces opened their eyes or mouths; in this way we measured brain response to reciprocal eye-contact. We identified two ERP components that were largest in response to reciprocal eye-contact: the N170 and the P300. The magnitude of the components' differences between reciprocal eye-contact and mouth movement predicted self-reported social function. Individuals with greater brain response to reciprocal eye-contact reported more normative scores on measures of autistic traits. These results present the first neural markers of eye-contact, revealing that reciprocal eye-contact is identified in less than 500ms. Furthermore, individual differences in brain response to eye-contact predict meaningful variability in self-reports of social performance.

Keywords

Eye-contact; EEG; N170; Face processing

Social interactions rely on the efficient and effective detection and interpretation of communicative information conveyed by the face. The fast-paced and reciprocal nature of social interaction demands that, within moments of seeing another person, one must rapidly recognize identity, facial expression, and gaze to infer affect and intent. Failure or delays in identification of these facial properties will impede adaptive social interaction. Eye-contact is one of the most critical examples of facial communication. Mutual gaze is a salient experience that engages the autonomic nervous system (Nichols & Champnes, 1971) and specific brain systems (Batki, Baron-Cohen, Wheelwright, Connellan, & Ahluwalia, 2000; Farroni, Csibra, Simion, & Johnson, 2002), is detected rapidly (von Grunau & Anston,

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Author Contributions

A.J.N and J.C.M developed the study concept and experimental design. A.J.N and J.W programmed the experiment. A.J.N conducted data analyses and collected data from participants. All authors drafted the manuscript.

1995), and captures and holds attention (Senju & Hasegawa, 2005; Senju & Johnson, 2009) from very early in life (Batki et al., 2000; Farroni et al., 2002). This key social behavior is also highly conserved across primate (Perrett et al., 1985) and non-primate species (Gallup, Cummings, & Nash, 1972). Taken together, this evidence suggests that the neural mechanisms of gaze detection are evolutionarily old and highly selected for.

Given that interpretation of socially meaningful facial communication occurs at a sub-second pace (Deaner & Platt, 2003; Frischen, Bayliss, & Tipper, 2007; Jack, Garrod, & Schyns, 2014), brain imaging techniques with acute temporal resolution, such as electroencephalography (EEG) and magnetoencephalography (MEG), offer unique insight into this dynamic process. These methods reveal brain activity that is sensitive to biologically relevant visual information in less than two-tenths of a second (Bentin, Allison, Puce, Perez, & McCarthy, 1996). Event-related potential (ERP) indices of visual perception reveal that low-level features of a visual stimulus, such as brightness, motion, contrast, and spatial frequency, are encoded by 100ms (Rossion & Caharel, 2011). By 170ms, a negative deflection in the ERP over the right occipitotemporal cortex (N170) distinguishes socially relevant visual information, such as faces (Bentin et al., 1996), eyes (Taylor, Edmonds, McCarthy, & Allison, 2001), and biological movement, from non-social stimuli (Hirai, Senju, Fukushima, & Hiraki, 2005; Puce & Perrett, 2003). The N170 displays larger amplitudes and earlier latencies to faces relative to non-social stimuli (Bentin et al., 1996), with enhanced sensitivity (increased amplitude) to eyes (Kloth, Itier, & Schweinberger, 2013). This sensitivity is especially enhanced during development (Taylor et al., 2001), such that the amplitude of N170s of younger participants is larger in response to eyes alone than to entire faces; this effect is absent by adolescence, during which faces elicit N170s with amplitudes as large as those elicited by isolated eyes. Decomposition of the face perception process with temporal imaging indicates distinct functionality at the P300, a subsequent, positive deflection over the midline scalp at approximately 300ms. Modulations of the P300 are observed in response to socially relevant stimuli, e.g., a participant's own face or name (Gray, Ambady, Lowenthal, & Deldin, 2004; Ninomiya, Onitsuka, Chen, Sato, & Tashiro, 1998; Sugiura et al., 2000; Sui, Zhu, & Han, 2006; Tacikowski, Jednorog, Marchewka, & Nowicka, 2011a; Tacikowski & Nowicka, 2010) and emotional faces (Lang, Nelson, & Collins, 1990). The P300 is presumed to reflect activity in the noradrenergic system, signaling motivational relevance (Nieuwenhuis, Aston-Jones, & Cohen, 2005). While modulations of the P300 are not unique to facial stimuli (Polich, 2007; Pritchard, 1981; Tacikowski, Jednorog, Marchewka, & Nowicka, 2011b), there are few stimuli as naturally salient and motivationally relevant as faces making eye-contact. Thus, the P300, while not specific to face processing, acts as a potent index for socially-relevant information processing.

The preponderance of research on face perception has used experimental designs in which participants view static faces on computer screens. These designs lack ecological validity, as real-life face perception is interactive, embedded in a social context, and mediated by eye-contact. However, several electrophysiological brain imaging studies have used moving stimuli to more closely approximate the naturalistic conditions under which social perception takes place. In dynamic contexts, the N170 is sensitive to facial movement (Puce, Smith, & Allison, 2000): perception of eyes opening elicits larger amplitude N170s than

eyes closing, and changes in gaze (i.e., direct to averted gaze) elicit differential activity between 300ms and 500ms (Carrick, Thompson, Epling, & Puce, 2007). These studies establish that short-latency brain activity is sensitive to visually subtle but socially significant events.

Although research using passive viewing of static or moving facial stimuli has provided a critical foundation for understanding face and gaze perception, there is an increasing recognition that the study of dynamic, reciprocal social processes will benefit from an interactive neuroscience approach (Rolison, Naples, & McPartland, 2015). This connotes moving away from passive, static experimental designs to paradigms that more closely approximate social interaction by incorporating dynamic stimuli that respond contingently to participant behavior (Schilbach, 2016). In this way, prior electrophysiological research in face perception has failed to address the fundamentally interactive character of social behavior; it remains unknown how brain activity unfolds during the time course of a participant-initiated interaction.

The current study addresses this gap in understanding by investigating the neural correlates of face perception in a context that is both dynamic and interactive. An eye-tracker was used to monitor participant visual behavior and to enable dynamic on-screen faces to respond to participant gaze—when participants visually engaged faces, the faces responded with eye-contact or other facial movements. To measure rapid neural responses to these gaze-contingent social simulations, we co-registered the eye-tracker with EEG to record brain responses during interactions with a high level of temporal resolution, focusing on the N170 and P300 due to their significance in prior research. Because the N170 and P300 are early-occurring components that are sensitive to facial movement, we hypothesized that they would be sensitive to reciprocal eye-contact during face-to-face interactions. Secondly, given the centrality of efficient gaze detection to social behavior and its role in disorders affecting social cognition (Hileman, Henderson, Mundy, Newell, & Jaime, 2011; Tsunoda et al., 2012), and evidence that reduced sensitivity to eye-contact is associated with clinically reported social disability (Senju, Tojo, Yaguchi, & Hasegawa, 2005), we predicted that increased neural response, i.e., amplitude, to eye-contact would be correlated with higher levels of self-reported social function. While we did not assess a clinical population, there is increasing evidence that traits associated with social cognition (Lazar, Evans, Myers, Moreno-De Luca, & Moore, 2014) are normally distributed in the population, that meaningful variability exists outside of clinical thresholds (Gottesman & Gould, 2003; Lazar et al., 2014), and that reduced neural sensitivity to social information is associated with increased symptomology (McPartland, Dawson, Webb, Panagiotides, & Carver, 2004b). By measuring the relationship between social function and neural response, we aimed to shed light on the mechanisms that may underlie difficulties in social interactions that span multiple diagnostic categories, such as autism and schizophrenia (Lynn & Salisbury, 2008; Senju et al., 2005).

Method

Participants

Participants included 15 typically developing adults (10 female; mean age 21.5, range 19 to 27 years). Two participants were left-handed, and three participants did not report handedness. An additional 4 participants were excluded for equipment malfunction. Participants were screened by self-report for current or historical brain injury or disease and for normal or corrected-to-normal visual acuity. Social function was assessed using measures specifically designed to assess social function in typically developing, non-clinically ascertained populations (Baron-Cohen et al., 2001; Hurley et al., 2007): the Broad Autism Phenotype Questionnaire (BAPQ) (Hurley, Losh, Parlier, Reznick, & Piven, 2007), which uses three subscales to address pragmatic language use, aloof personality traits, and rigid personality traits, e.g., insistence on sameness and resistance to change of routine, and the Autism Spectrum Quotient (AQ; (Baron-Cohen, Wheelwright, Skinner, Martin, & Clubley, 2001), a self-report measure that measures autistic traits in clinical and non-clinical samples. The subscales for the BAPQ were calculated using the items described in Ingersoll, Hopwood, Wainer, and Donnellan (2011), which yield improved factor separation of the distinct facets of the broad autism phenotype in the typically developing population. Table (1) displays the distribution of the BAPQ subscales and AQ. All participants in this study were below the thresholds associated with a diagnosis of ASD. All procedures were conducted with the understanding and written consent of participants and with approval of the Yale School of Medicine Human Investigation Committee.

Experimental Procedure

Using simultaneous eye-tracking and EEG, we recorded neural response to reciprocal gaze as participants engaged in a simulated face-to-face interaction with onscreen faces that responded to participant-initiated gaze by opening their eyes or mouths. Trials began with a centrally-presented onscreen fixation arrow (pointing up or down) for 600–1000ms. Contingent upon fixation to the arrow, a peripherally presented face with closed eyes and mouth appeared on screen. Fixation arrows cued the participants to look either to the mouth (arrow pointing down) or the eyes (arrow pointing up) of the subsequent face. Contingent upon participant fixation for 80ms to the face (to provide the subjective impression of responsiveness), the face responded by either (a) opening its eyes or (b) opening its mouth, and then remained on screen for 800ms. In this way we display four types of face-to-face interaction: (1) the participant looks to the eyes and the eyes open (reciprocal eye-contact, *eye:eye*), (2) the participant looks to the mouth and the mouth opens (*mouth:mouth*), (3) the participant looks to the mouth and the eyes open (*mouth:eye*), or (4) the participant looks to the eyes and the mouth opens (*eye:mouth*). The trial structure is shown in Figure 1. This design allowed us to assess the specificity of reciprocal eye-contact, i.e., to what extent eye-contact elicits differential neural response relative to other facial movements. The experimental paradigm was programmed in E-prime 2.0 (Psychology Software Tools, Pittsburgh, PA) and consisted of four blocks of 95 trials, with breaks in between blocks. Regions of interest for looking to the eyes or mouth of the face were sufficiently large (Figure 2) to ensure responsive faces even if the eye-tracking calibration degraded over the course of the experiment. To maintain participant engagement, participants were instructed

to press a button when they saw a red target face on the screen. In total, there were 26 target faces distributed across blocks, with 9, 6, 4, and 7 targets respectively across the four blocks. Time between faces appearing on the screen and faces changing in response to participant gaze was 451ms on average. Target trials were excluded from the analysis.

Data Acquisition and Processing

At the start of each session, an individualized head model for each participant was generated using the Smart Eye Pro 5.5 three camera system (www.smarteye.se). After generating the head model, participant gaze was calibrated using a 13-point calibration scheme. Eye-position was sampled at 60Hz and communicated to the experiment presentation computer running the E-prime 2.0 software (Psychology Software Tools, Pittsburgh, PA). Stimuli were presented on a 19-inch LCD monitor (60Hz, 1024 × 768 resolution) at approximately 70cm viewing distance.

EEG recordings were digitally obtained from a 128 Ag/AgCl electrode net with high impedance amplifiers (NetAmps 300 amplifiers; Electrical Geodesics, Inc., Eugene, OR). The net was placed on the participant's head and fitted according to the manufacturer's specifications. Impedances were kept below 40 kOhms. EEG was recorded continuously at 500 Hz with data high-pass filtered at 0.1 Hz and low-pass filtered at 30 Hz offline. Data were re-referenced to an average reference, with Cz serving as the online reference point for all electrodes.

Data were processed using Netstation 4.5 software (Electrical Geodesics, Inc., Eugene, OR). For each participant, EEG was digitally filtered (1 Hz high-pass, 30 Hz low-pass). The EEG was segmented from 100ms before to 500ms after the change of the onscreen face (eyes or mouth opening). Netstation artifact detection voltage limits were set to 100µv for bad channels, 140µv for blinks, and 100µv for saccades. The EGI hydrocel net contains six dedicated electrooculogram (EOG) channels that are used to detect eye movements. These EOG channels are not included in the calculation of the average reference. Channels with artifacts in more than 30% of trials were marked as bad channels and replaced using spherical spline interpolation. Segments containing eye artifacts were excluded. All participants had at least 50% good trials in each condition (~45 trials). Given that our experiment elicited eye movements, we included a large number of trials to permit exclusion of trials with eye artifacts while maintaining enough trials to reliably derivate ERPs of interest (e.g., averages of ~50 trials; Bentin & Deouell, 2000; Itier, Alain, Kovacevic, & McIntosh, 2007). Overall, our participants had a mean of 77 good trials per condition, with a minimum of 48 good trials and a maximum of 89. Data were averaged across eight electrodes over the left (58, 59, 64, 65, 68, 69, 57, 63) and right (90, 95, 96, 94, 99, 100, 91, 89) lateral posterior scalp for the P100 and N170 (these electrodes approximate T5 and T6 in the 10–20 nomenclature), and across six electrodes (62, 72, 78, 77, 61, 67) over midline parietal scalp for the P300 (these electrodes surround Pz in the 10–20 nomenclature). This location for the P300 was chosen as it overlaps with regions described in prior literature on dynamic faces (Carrick et al., 2007; Conty, N'Diaye, Tijus, & George, 2007). P100 and N170 electrodes were selected based on prior research (Cheung, Rutherford, Mayes, & McPartland, 2010; McPartland, Cheung, Perszyk, & Mayes, 2010) and maximal observed

amplitude of the P100, N170, and P300. As our stimuli exhibit subtle visual change, i.e., only mouth or eyes opening instead of an image appearing, we did not see the large amplitude P100 and P300s commonly associated with face perception studies. Time windows for analyzing ERP components were chosen based on prior research and inspection of the grand and individual averaged waveforms. The P100 peak was measured as the maximal amplitude in the time range of 70 to 130ms, the N170 peak was measured as the minimum amplitude in the range of 130 to 225ms, and the P300 was measured as the average amplitude in the range of 350 to 450ms. Amplitude and latency data were analyzed in five separate repeated measures ANOVAs with experimental condition and hemisphere (for N170 and P100) as within-subjects factors. While latency of early ERP components is a critical dependent variable and can reflect meaningful differences between experimental conditions, as well as individual differences (McPartland et al., 2004b), the majority of literature on the N170 focuses on modulations of amplitude (Bentin et al., 1996; Hinojosa, Mercado, & Carretie, 2015). Consequently, our main hypotheses focused on amplitude. Waveforms are shown in Figure 4. Difference scores for correlations between behavioral measures and ERP data were calculated by subtracting the mouth:mouth from the eye:eye condition. For the N170, lower (more negative) difference scores indicate a more negative response at the N170 for reciprocal eye movement. For the P300, larger (more positive) difference scores indicate a more positive response for reciprocal eye movement.

Stimuli

Stimuli consisted of grayscale digital images of neutral faces with their eyes and mouths closed, and open. Faces were generated by the Facegen (Singular Inversions, 2010) software package and rendered using the Softimage (Autodesk, 2011) software package. The stimulus set contained 45 unique identities (25 female and 20 male). By using computer-generated faces, we ensured that movement was constrained to the eyes or the mouth only, and that the eyes and mouth were in the same location across trials. Faces were masked in an oval frame (Gronenschild, Smeets, Vuurman, van Boxtel, & Jolles, 2009) to remove non-face features.

Results

Data were analyzed with separate repeated measures ANOVAs for the P100, N170, and P300 with condition (*eye:eye*, *mouth:mouth*, *mouth:eye*, *eye:mouth*) and hemisphere (for the P100 and N170) as within-subjects factors. For amplitude, there was a main effect of condition on both the N170 $F(3,12) = 22.9$, $p < .001$, and P300 $F(3,12) = 15.6$, $p < .001$. Specifically, eye-contact elicited the largest amplitude response in both the N170 and the P300 (Figure 4). A main effect of hemisphere revealed that the N170 was more negative in the right hemisphere $F(3,12) = 8.3$, $p = .012$. Post-hoc tests revealed that eye-contact was significantly different from all other conditions at the N170 and the P300 (the largest p values were .029 and .047, respectively). Analysis of the P100 revealed a main effect of condition $F(3,12) = 7.48$, $p < .001$, such that P100s were larger in amplitude in reciprocal movement conditions (*eye:eye*, *mouth:mouth*) than non-reciprocal conditions (*eye:mouth*, *mouth:eye*). However, within reciprocal and non-reciprocal conditions, there were no significant differences (e.g., *eye:eye* and *mouth:mouth* were not significantly different at the P100). There was a main effect of both condition and hemisphere on P100 latency $F(3,12)$

$= 3.83, p = .039, F(3,12) = 4.69, p = .048$. Examination of post-hoc tests revealed that the eye:eye condition exhibited an earlier latency than the mouth:eye condition (mean difference $= 5.8\text{ms}, p = .024$). No other pairwise comparisons reached significance; examination of the hemisphere effect revealed that latency in the left hemisphere was faster than that of the right hemisphere (mean difference $= 5.9\text{ms}, p = .048$). Analysis of latency at the N170 revealed no main effect of condition $F(3,12) = 1.49, p = .23$, or hemisphere $F(3,12) = 1.005, p = .33$.

We calculated an index of neural gaze sensitivity at the N170 and the P300 as the difference between response to eye-contact and contingent mouth movement. N170 gaze sensitivity was associated with the pragmatic language ($r = .55, p = .034$) and aloof personality ($r = .56, p = .032$) subscales of the BAPQ, as well as combined aloof and pragmatic scales ($r = .65, p = .009$). The relationship with the rigid personality subscale did not reach significance ($r = .32, p = .247$). P300 gaze sensitivity was associated with AQ score ($r = -.554, p = .032$) (Figure 6). For both components, greater sensitivity to eye-contact predicted more normative social function.

Discussion

Our results reveal a temporally early ERP index for eye-contact. In a simulated social interaction, reciprocal eye-contact elicited enhanced activity at both the N170 and P300 relative to contingent mouth movement or non-reciprocal eye movement. Unlike prior research in static and dynamic face perception, participant gaze elicited the response from onscreen faces, simulating the most basic of social interactions, reciprocal gaze. By extricating passive viewing of direct gaze from interactive eye-contact in this way, these data provide initial evidence for sensitivity of ERP responses to the reciprocal nature of mutual gaze. Sensitivity to eye-contact predicted variability in social function as measured by self-report instruments of social traits, consistent with the practical import of efficient gaze perception. Furthermore, these effects were not attributable to low-level stimulus properties, as P100 differences reflected foveated movement but did not differ between eye and mouth conditions.

The large differences between mouth and eye movement observed here are not reported in passive experiments of dynamic facial movement (Puce & Perrett, 2003; Puce et al., 2000). One of the neural generators of the N170 is the posterior Superior Temporal Sulcus (STS), which is consistently identified as an area sensitive to biological motion (Herrington, Nymberg, & Schultz, 2011; Vaina, Solomon, Chowdhury, Sinha, & Belliveau, 2001). STS activity can also be modulated by social context (Vander Wyk, Hudac, Carter, Sobel, & Pelphrey, 2009). Prior research using fMRI has shown that the STS is sensitive to gaze in social contexts (Pelphrey, Viola, & McCarthy, 2004). Our results show that this sensitivity to social context emerges in the first 200ms of a social interaction. Thus, it is likely that the larger N170 activation associated with reciprocal gaze in this study reflects the joint contribution of dynamic gaze and the interactive context.

The increased activation of the P300 to eye-contact is consistent with findings showing that the mere presence of eye-contact in an interaction is a powerful influence on behavior, guiding how humans attend to and interact with the social world (Laidlaw, Foulsham, Kuhn,

& Kingstone, 2011). Action of the noradrenergic system is widely associated with arousal and salience detection, both of which are modulated by eye-contact and associated with a wide range of psychiatric comorbidities (Berridge & Waterhouse, 2003). Increased P300 amplitude is commonly associated with tasks that require overt responses (Bennington & Polich, 1999). While this experiment does not explicitly require a response, in social contexts, reciprocal gaze is a powerful cue to initiate action and likely contributes to phasic increases in arousal and action preparedness.

We note that we did not observe effects at the P100. The contrast between the P100 and later components suggests influence of eye-contact at face-sensitive components rather than earlier components reflective of low-level visual processing. Activity at the P100 differentiated movement but not the difference between eye vs. mouth movement. This finding suggests that the differences between eye and mouth movement we see in brain activity at the N170 and P300 are specific to the biological relevance of eye-contact rather than the salience of motion.

Reciprocal eye-contact elicits enhanced brain activity, but the size of these effects varies among individuals: our study also reveals relationships between sensitivity to gaze and self-reported social behavior. Participants showing reduced response to eye-contact reported poorer function on the social subscales (aloof personality and pragmatic language) of the BAPQ and on the AQ. Conversely, individuals with greater sensitivity to gaze reported higher levels of social function than individuals with lower sensitivity. As rapid discrimination among socially relevant facial movements is necessary for successful navigation of social interactions, these results suggest that individuals who are less sensitive to eye-contact at these early stages may be at a disadvantage in navigating social interactions. That the N170 correlated with the BAPQ and the P300 with the AQ likely reflects the different dimensions of social function indexed by the separate instruments. The particular subscales of the BAPQ exhibit high levels of internal consistency and may index processes associated with detection of social information, whereas the AQ demonstrates reduced internal consistency but probes a wider range of social situations and indexes variability in motivation and exploration of social contexts. Although efficiency of neural response to faces has long been viewed as reflective of clinical levels of difficulty in social behavior (McPartland, Dawson, Webb, Panagiotides, & Carver, 2004a), our results suggest that differential brain activity may provide inroads into understanding the underlying mechanisms that give rise to differences in reported social function within the normative range.

The current research sheds new light on our understanding of the brain mechanisms that underlie the perception of eye-contact. However, there are several limitations. Our sample size was relatively modest, but prior literature (Bentin et al., 1996) has identified highly reliable face responses in smaller samples sizes. Thus, a sample size of 15 participants was deemed sufficient to observe effects at the ERP components under investigation. Given our modest sample size, we also carried out a bootstrap simulation of our correlational results. With 25,000 bootstrap replications, our N170 correlation remained significant with the following confidence intervals [0.1831, 0.8479]. However, the P300 correlation bootstrap failed to converge (exhibited a bimodal distribution with up to 1,000,000 replicates) and the

confidence intervals crossed 0 $[-0.8976, 0.2526]$. Thus, future research with larger sample sizes is needed to explicate the relationship between the P300, reciprocal social information, and individual differences in social functioning. Secondly, while this experiment simulated the reciprocity of a social interaction, it did not include another physical human being. Nevertheless, this design greatly increased ecological validity as compared to passive paradigms. Additionally, we did not analyze handedness information or educational level of our participants. While our results were primarily right-lateralized, it is possible that the effects manifest in the left hemisphere in some participants. Nevertheless, our findings were supported by a main effect across hemispheres. Future research with a larger sample size will allow us to explicate the role of handedness on the effects observed here. While educational level was not controlled, the participants reflected the composition of typically developing individuals within the community and, while social ability is known to correlate with brain response to faces, there does not appear to be an effect of cognitive ability or impairment on the N170 (Hileman et al., 2011). Again, as our results were supported by within-participant contrasts, our design afforded us some protection from the potential impact of these nuisance variables on our primary dependent measures. Also, as our paradigm intentionally constrained gaze to the eyes or mouths of onscreen faces, we do not explore eye-tracking data. However, we have begun to include free-viewing periods during our experimental paradigms. In this way, future studies will enable us to examine fixation data in relation to neural response. Additionally, future research using this approach could use extended (multi-second) pre-stimulus periods to explore neural underpinnings of anticipation to social interaction, whereas this study only examines response to social stimuli. Finally, while we identified relationships between gaze sensitivity and reports of social function, we did not recruit a clinical population. Despite this limitation, there is increased evidence that (1) variability in social function is associated with multiple clinical categories e.g., autism, schizophrenia, anxiety (Eack et al., 2013), and that (2) subclinical threshold variability may provide a powerful tool for identifying endophenotypes associated with the underlying biology of psychiatric symptomology outside of strict diagnostic categories (Flint & Munafo, 2007).

In summary, our interactive neuroscience approach identified temporally early brain activity that was uniquely enhanced in response to reciprocal eye-contact relative to other forms of facial movement. These differences were not evident at the P100, which is most sensitive to low-level visual changes (Rossion & Caharel, 2011). Additionally, we found that enhanced neural sensitivity to eye-contact predicted stronger social function. These markers are evident at short latency, supporting the rapid, dynamic nature of fluid interpersonal interactions. Insight into the neural mechanisms underpinning eye-contact detection is germane to understanding normative social cognition, as well as psychiatric conditions associated with social dysfunction. Given the specific difficulties associated with dynamic interactive contexts, we believe the approach and markers described here offer great promise for characterizing social processes in psychiatric disorders such as autism, schizophrenia, and social anxiety.

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Highlights

- Brain response to faces that respond to gaze reveal neural markers of eye-contact.
- The N170 and P300 ERPs uniquely distinguish reciprocal eye-contact from other responsive facial movements.
- Individual differences in neural response to eye-contact predict variability in social function.

Figure 1. Participant display with arrow and overlapping regions of interest for eye and mouth conditions. Regions to elicit facial movement were designed to be larger than the target regions to ensure that the face was responsive to participant gaze. In this figure the arrows pointing up and down are overlaid.

Figure 2. Sample trial structure for trials where participant is cued to look to the face's eyes. (A) A blank screen is followed by (B) a centrally presented arrow pointing up or down, cueing participants to look to the eyes of the subsequent face; (C) a peripherally presented face with eyes and mouth closed appears; (D) contingent on participant fixation to the cued region (eyes), the face responds by opening its eyes or mouth.

Figure 3.
Electrodes used for ERP extraction from a 128 Channel EGI Hydrocel net. Blue electrodes show sites for P100 and N170 extraction, dark grey electrodes indicate P300 sites.

Figure 4. Waveforms, averaged across electrodes, depicting the right occipital N170 (a) and central P300 (b).

Figure 5.
Bar charts depicting the right P100, N170, and central P300 amplitude.

Figure 6. Scatterplots depicting the relationship between self-reported autistic traits and sensitivity to eye-contact

Table 1

Descriptive Characteristics of Social Measures

Measure	Minimum	Maximum	Mean	SD
BAPQ rigidity	14	38	23.67	6.04
BAPQ aloof & pragmatic	20	49	37.26	8.44
AQ	2	22	10.93	5.43