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Event-related potentials index neural response to eye contact

Adam J. Naples*, Jia Wu, Linda C. Mayes, James C. McPartland*

Yale University School of Medicine, Child Study Center, 230 South Frontage Road, New Haven, CT, 06520, United States

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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 500 ms. Furthermore, individual differences in brain response to eye-contact predict meaningful variability in self-reports of social performance.

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 Grünau & Anston, 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 100 ms (Rossion & Caharel, 2011). By 170 ms, 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 N170 s of younger participants is larger in response to eyes alone than to entire faces; this effect is absent by adolescence, during which faces elicit N170 s 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 300 ms. 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, 2011; Tacikowski & Nowicka, 2010) and emotional faces (Lang, Nelson, & Collins, 1990). The P300 is presumed to reflect activity in

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* Corresponding author.
E-mail addresses: adam.naples@yale.edu (A.J. Naples), jia.wu@yale.edu (J. Wu), linda.mayes@yale.edu (L.C. Mayes), james.mcpartland@yale.edu (J.C. McPartland).

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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 et al., 2011), 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 N170 s than eyes closing, and changes in gaze (i.e., direct to averted gaze) elicit differential activity between 300 ms and 500 ms (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, 2004). 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).

1. Method

1.1. Participants

Participants included 15 typically developing adults (10 female; mean age 21.5, range 19–27 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.

1.2. 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 600–1000 ms. 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 80 ms 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 800 ms. 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 Fig. 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 (Fig. 2) to ensure responsive faces even

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

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