NeuroImage 157 (2017) 314–330

Contents lists available at ScienceDirect

NeuroImage

journal homepage: www.elsevier.com/locate/neuroimage

Frontal temporal and parietal systems synchronize within and across brains during live eye-to-eye contact☆

Joy Hirsch[a,b,c,d,*], Xian Zhang[a], J. Adam Noah[a], Yumie Ono[e]

[a] Department of Psychiatry, Yale School of Medicine, New Haven, CT 06511, USA
[b] Department of Neuroscience, Yale School of Medicine, New Haven, CT 06511, USA
[c] Department of Comparative Medicine, Yale School of Medicine, New Haven, CT 06511, USA
[d] Department of Medical Physics and Biomedical Engineering, University College London, UK
[e] Department of Electronics and Bioinformatics, School of Science and Technology, Meiji University, Kawasaki, Kanagawa, Japan

ARTICLE INFO

Keywords:
Two-person neuroscience
Hyperscanning
FNIRS
Eye contact
Interactive Brain Hypothesis
Cross-brain coherence
Social neuroscience

ABSTRACT

Human eye-to-eye contact is a primary source of social cues and communication. In spite of the biological significance of this interpersonal interaction, the underlying neural processes are not well-understood. This knowledge gap, in part, reflects limitations of conventional neuroimaging methods, including solitary confinement in the bore of a scanner and minimal tolerance of head movement that constrain investigations of natural, two-person interactions. However, these limitations are substantially resolved by recent technical developments in functional near-infrared spectroscopy (fNIRS), a non-invasive spectral absorbance technique that detects changes in blood oxygen levels in the brain by using surface-mounted optical sensors. Functional NIRS is tolerant of limited head motion and enables simultaneous acquisitions of neural signals from two interacting partners in natural conditions. We employ fNIRS to advance a data-driven theoretical framework for two-person neuroscience motivated by the Interactive Brain Hypothesis which proposes that interpersonal interaction between individuals evokes neural mechanisms not engaged during solo, non-interactive, behaviors. Within this context, two specific hypotheses related to eye-to-eye contact, functional specificity and functional synchrony, were tested. The functional specificity hypothesis proposes that eye-to-eye contact engages specialized, within-brain, neural systems; and the functional synchrony hypothesis proposes that eye-to-eye contact engages specialized, across-brain, neural processors that are synchronized between dyads. Signals acquired during eye-to-eye contact between partners (interactive condition) were compared to signals acquired during mutual gaze at the eyes of a picture-face (non-interactive condition). In accordance with the specificity hypothesis, responses during eye-to-eye contact were greater than eye-to-picture gaze for a left frontal cluster that included pars opercularis (associated with canonical language production functions known as Broca's region), pre- and supplementary motor cortices (associated with articulatory systems), as well as the subcentral area. This frontal cluster was also functionally connected to a cluster located in the left superior temporal gyrus (associated with canonical language receptive functions known as Wernicke's region), primary somatosensory cortex, and the subcentral area. In accordance with the functional synchrony hypothesis, cross-brain coherence during eye-to-eye contact relative to eye-to-picture gaze increased for signals originating within left superior temporal, middle temporal, and supramarginal gyri as well as the pre- and supplementary motor cortices of both interacting brains. These synchronous cross-brain regions are also associated with known language functions, and were partner-specific (i.e., disappeared with randomly assigned partners). Together, both within and across-brain neural correlates of eye-to-eye contact included components of previously established productive and receptive language systems. These findings reveal a left frontal, temporal, and parietal long-range network that mediates neural responses during eye-to-eye contact between dyads, and advance insight into elemental mechanisms of social and interpersonal interactions.

☆ This work has not been published previously and is not under consideration for publication elsewhere. All authors have approved the manuscript in its present form.

* Correspondence to: 300 George St., Suite 902, New Haven, CT 06511.
E-mail address: joy.hirsch@yale.edu (J. Hirsch).

http://dx.doi.org/10.1016/j.neuroimage.2017.06.018
Received 13 January 2017; Accepted 7 June 2017
Available online 12 June 2017
1053-8119/

Introduction

Eye contact between two humans establishes a universally recognized social link and a conduit for non-verbal interpersonal communication including salient and emotional information. The dynamic exchange of reciprocal information without words between individuals via eye-to-eye contact constitutes a unique opportunity to model mechanisms of human interpersonal communication. A distinctive feature of eye-to-eye contact between two individuals is the rapid and reciprocal exchange of salient information in which each send and receive "volley" is altered in response to the previous, and actions are produced simultaneously with reception and interpretive processes. Common wisdom, well-recognized within the humanities disciplines, regards eye-to-eye contact as a highly poignant social event, and this insight is also an active topic in social neuroscience. It has been proposed that the effects of direct eye gaze in typical individuals involves "privileged access" to specialized neural systems that process and interpret facial cues, including social and communication signals (Allison et al., 2000; Emery, 2000; Ethofer et al., 2011). Support for this hypothesis is based, in part, on imaging studies in which single participants view pictures of faces rather than making real eye-to-eye contact with another individual (Rossion et al., 2003). For example, "eye contact effects" have been observed by comparing neural activity during epochs of viewing static face pictures with either direct or averted gaze during tasks such as passive viewing, identity matching, detection of gender, or discrimination of gaze direction (Senju and Johnson, 2009). Distributed face-selective regions, including the fusiform gyrus, amygdala, superior temporal gyrus, and orbitofrontal cortices, were found to be upregulated during direct gaze relative to indirect gaze. These findings support a classic model for hierarchical processing of static representations of faces with specialized processing for direct gaze (Kanwisher et al., 1997; Haxby et al., 2000; Zhen et al., 2013). The specialized neural impact of direct eye gaze in typical participants (Johnson et al., 2015) underscores the salience of eyes in early development and neurological disorders, particularly with respect to language and autism spectrum disorders (Golarai et al., 2006; Jones and Klin, 2013).

Eye-to-eye contact in natural situations, however, also includes additional features such as dynamic and rapid perception of eye movements, interpretation of facial expressions, as well as appreciation of context and social conditions (Myllyneva and Hietanen, 2015, 2016; and Teufel et al., 2009). A hyperscanning (simultaneous imaging of two individuals) study using fMRI and two separate scanners has shown that responses to eye movement cues can be distinguished from object movement cues, and that partner-to-partner signal synchrony is increased during joint eye tasks (Saito et al., 2010), consistent with enhanced sensitivity to dynamic properties of eyes. Further insight into the social and emotional processing streams stimulated by eye contact originates from behavioral studies where cognitive appraisal of pictured eye-gaze directions has been shown to be modulated by social context (Teufel et al., 2009), and neural responses recorded by electroencephalography, EEG, were found to be amplified during perceptions of being seen by others (Myllyneva and Hietanen, 2016). Modulation of EEG signals has also been associated with viewing actual faces compared to pictured faces and found to be dependent upon both social attributions and the direction of the gaze (Myllyneva and Hietanen, 2015). Extending this evidence for interconnected processing systems related to faces, eyes, emotion, and social context, a recent clinical study using functional magnetic resonance imaging (fMRI) showed symptomatic improvement in patients with generalized anxiety disorder, an affect disorder characterized by negative emotional responses to faces, after treatment with paroxetine that was correlated with neural changes to direct vs averted gaze pictures (Schneier et al., 2011).

Other single brain studies using fMRI and EEG have confirmed that motion contained in video sequences of faces enhances cortical responses in the right superior temporal sulcus, bilateral fusiform face area, and bilateral inferior occipital gyrus (Schultz and Pilz, 2009; Trautmann et al., 2009; and Recio et al., 2011). Dynamic face stimuli, compared to static pictures, have also been associated with enhanced differentiation of emotional valences (Trautmann-Lengsfeld et al., 2013), and these systems were found to be sensitive to the rate of facial movement (Schultz et al., 2013). Moving trajectories of facial expressions morphed from neutral to either a positive or negative valence and recorded by magnetoencephalography (MEG) revealed similar findings with the added observation that pre-motor activity was concomitant with activity in the temporal visual areas, suggesting that motion sensitive mechanisms associated with dynamic facial expressions may also predict facial expression trajectories (Furl et al., 2010). Similar findings have been reported from passive viewing of static and dynamic faces using fMRI, confirming that these effects were lateralized to the right hemisphere (Sato et al., 2004). Overall, these findings establish the neural salience of faces based on single brain responses to either dynamic picture stimuli or to live faces with dynamic emotional expressions, and provide a compelling rationale and background for extending the investigational and theoretical approach to direct and natural eye-to-eye contact between two interacting partners where both single brain and cross-brain effects can be observed.

Recent technical advances in neuroimaging using fNIRS pave the way for hyperscanning during natural and spontaneous social interactions, and enable a new genre of experimental paradigms to investigate interpersonal and social mechanisms (Cheng et al., 2015; Dommer et al., 2012; Funane et al., 2011; Holper et al., 2012; Jiang et al., 2015; Osaka et al., 2014, 2015; Vanutelli et al., 2015; Pinti et al., 2015). These pioneering studies have demonstrated the efficacy of new social and dual-brain approaches, and have given rise to novel research questions that address the neurobiology of social interactions (Babiloni and Astolfi, 2014; García and Ibáñez, 2014; Schilbach et al., 2013, 2014). Concomitant with these technical and experimental advances, a recently proposed theoretical framework, the Interactive Brain Hypothesis, advances the idea that live social interaction drives dynamic neural activity with direct consequences for cognition (Di Paolo and De Jaegher, 2012; De Jaegher et al., 2016). This hypothesis also encompasses the conjecture that social interaction engages neural processes that either do not occur or are less active during similar solo activities (De Jaegher et al., 2010). Supporting observations and experimental paradigms that incorporate real-time interactions to test aspects of this broad hypothesis are nascent but emerging (Konvalinka and Roepstorff, 2012; Schilbach et al., 2013), and highlight new experimental approaches that probe "online" processes, i.e. processes that become manifest when two agents coordinate their visual attention (Schilbach, 2014).

A pivotal aspect of online two-brain investigations relates to the measures of cross-brain linkages. Oscillatory coupling of signals between brains is assumed to reflect cooperating mechanisms that underlie sensation, perception, cognition, and/or action. Cross-brain coherence (a linking indicator) measured by oscillatory coupling between two brains during natural interactive tasks has been reported for both fNIRS (hemodynamic) and EEG (electroencephalographic) signals, and encompasses a wide range of functions. For example, hyperscanning of dyads engaged in cooperative and obstructive interactions during a turn-based game of Jenga using fNIRS revealed inter-brain neural synchrony between right middle and superior frontal gyri during both cooperative and obstructive interaction, and in the dorsomedial prefrontal cortex during cooperative interactions only (Liu et al., 2016). Spontaneous imitation of hand movements between two partners generated EEG signals in the alpha-mu (8–12 Hz) frequency band between right central-parietal regions of the cooperating brains, suggesting that an inter-brain synchronizing network was active during this interaction (Dumas et al., 2010). Behavioral synchrony while playing a guitar in a duet has been shown to produce