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Neural substrates of shared attention as social memory: A hyperscanning functional magnetic resonance imaging study

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ABSTRACT

During a dyadic social interaction, two individuals can share visual attention through gaze, directed to each other (mutual gaze) or to a third person or an object (joint attention). Shared attention is fundamental to dyadic face-to-face interaction, but how attention is shared, retained, and neutrally represented in a pair-specific manner has not been well studied. Here, we conducted a two-day hyperscanning functional magnetic resonance imaging study in which pairs of participants performed a real-time mutual gaze task followed by a joint attention task on the first day, and mutual gaze tasks several days later. The joint attention task enhanced eye-blink synchronization, which is believed to be a behavioral index of shared attention. When the same participant pairs underwent mutual gaze without joint attention on the second day, enhanced eye-blink synchronization persisted, and this was positively correlated with inter-individual neural synchronization within the right inferior frontal gyrus. Neural synchronization was also positively correlated with enhanced eye-blink synchronization during the previous joint attention task session. Consistent with the Hebbian association hypothesis, the right inferior frontal gyrus had been activated both by initiating and responding to joint attention. These results indicate that shared attention is represented and retained by pair-specific neural synchronization that cannot be reduced to the individual level.

Introduction

Social interactions enable us to evaluate what the mental states and intentions of others might be. Importantly, the type of social experience is fundamentally different when we directly interact with others (second-person view) rather than merely observing them (spectator view; Schilbach et al., 2013). Social interactions have been postulated to have three prominent characteristics (Schilbach et al., 2013). First, there are different roles for the interacting individuals (e.g., initiator and responder at the simplest level). Second, sharing of attention, intention, and motivation are created de novo within an interaction, which are critical for the progress and continuation of the interaction itself. Finally, there is a context for the interaction based on past events and experience. Shared attention, or coordinated visual attention during face-to-face interaction, such as joint attention and mutual gaze (Emery, 2000), is a typical and fundamental process that fulfils the above three characteristics.

Humans use eye gaze to detect another individual's focus of attention, orient their own attention to the same locus, and draw inferences regarding the other individual's goals (Allison et al., 2000; Calder et al., 2007; Nummenmaa and Calder, 2009). Mutual gaze provides a communicative link between humans by sharing the message of "I am attending to you" (Farroni et al., 2002; Schilbach, 2015). Joint attention (JA) coordinates attention between partners to share an awareness of objects or events (Mundy et al., 1986). There are two types of JA: Initiating

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JA (IJA) is the ability to create spontaneously a shared point of reference using mutual gaze, and by alternating gaze between objects and other individuals; and responding JA (RJA) is the ability to follow the direction of the initiator's gaze in order to share attention towards the object (Mundy et al., 2009). Thus IJA, RJA, and mutual gaze are tightly linked (Emery, 2000; Perrett and Emery, 1994) and function to share attention within a dyad or to a third object. The importance of mutual gaze and JA in the development of social cognition has been stressed (Mundy and Newell, 2007). However, it is unknown if the attention shared between interactants is retained as social memory (Oullier et al., 2008), nor its neural substrates. As shared attention is an interactively constituted phenomenon which cannot be reduced to responses at the individual level, hyperscanning is really needed to depict its neural mechanisms and the hypothesized memory trace (Konvalinka and Roepstorff, 2012; Schilbach, 2015).

A previous hyperscanning functional magnetic resonance imaging (fMRI) study showed inter-individual neural synchronization within the right inferior frontal gyrus (IFG) during JA after the removal of common effects of task (Saito et al., 2010). JA is regarded as a two-way behavioral stimulus-to-brain coupling phenomenon, such that the behavior of one person is coupled to the brain activation of the other, and vice versa (Hari et al., 2009). Thus neural synchronization in the right IFG may represent inter-individual shared attention as a ‘readiness potential’ for subsequent gaze based interaction (Schilbach, 2015).

Inter-individual neural synchronization can be understood based on the premise that the perceptual system of one brain can become coupled to the motor system of another (Dumas, 2011; Jacob, 2009; Schippers and Keysers, 2011) through Hebbian association. This Hebbian account was previously invoked to explain automatic mimicry (Keysers and Perrett, 2004; Del Giudice et al., 2009; Sasaki et al., 2012). That is, the basis of automatic mimicry is motor and perception action representations becoming tightly linked in such a way that perceiving another person's action activates the same representations as performing the action. It was argued that the action representation, or motor-perceptual common representation, could be formed as an internal model through Hebbian associations trained during motor execution (Keysers and Perrett, 2004; Del Giudice et al., 2009). Given that we continuously monitor our own actions, their sensory consequences are systematically and synchronously paired with motor commands. This predicts the emergence of Hebbian connections that link motor programs to sensory consequences (forward internal models), and vice versa (inverse internal models), even during social interaction (Wolpert et al., 2003): In social Hebbian connections, one's own motor programs are linked to the sensory consequences provided by another's actions. We applied this motor-perceptual common representation account to attention control. Our hypothesis was that the training of joint attention, JA causes a social Hebbian association between initiating and responding joint attention, IJA and RJA. This is because the control of directing attention toward a third object for initiating JA is temporally linked to sensory consequences of the partner's response of directing attention to the same object, that is, RJA. Thus, social Hebbian association could link the neural activities induced by IJA to those by induced by RJA of the partner, resulting in neural synchronization. If this is true, then both IJA and RJA should activate the right IFG, and the synchronization should be retained as social memory after the JA experience.

To quantify interpersonal aspects of the social interaction such as shared attention, finding adequate and useful behavioral markers is critical (Schilbach, 2014). Attentional coordination during shared attention is in the spatial domain. Less explicitly included in the shared attention is the common “time window” of the attention directed to each other during mutual gaze, that precedes the JA. To perform a JA task, the initiator is required to confirm that the partner is attending to the initiator during a preceding eye contact condition, and the responder is required to attend to the initiator's eye movements. Thus, they are to share an attentional temporal window.

Eye-blinks are known to define the attentional temporal window. Demands for attentional resources modulate the rate of eye-blinks (Bentivoglio et al., 1997; Shultz et al., 2011), and the timing of eye-blinks is associated with implicit (Herrmann, 2010) and explicit (Orchard and Stern, 1991) attentional pauses in task content. Eye-blinks of participants are synchronized while viewing the same video stories (Nakano et al., 2009), and between listener and speaker in face-to-face conversation (Nakano and Kitazawa, 2010). Considering that blinks define the attentional “window”, synchronization of eye-blinks between face-to-face interactants can be taken as an index of shared attention. Once a Hebbian association is established, the initiation of eye-contact between the previously trained pair will induce the control–response linkage in the attentional domain that can be measured via eye-blink synchronization.

Accordingly, our hypothesis was that shared attention during a JA task would be represented by blink synchronization and retained as the social memory, and that this social memory would be represented by enhanced inter-individual neural synchronization in the right IFG. We also expected the right IFG to be activated by both RJA and IJA. To test these hypotheses, we conducted hyperscanning fMRI during a JA task, and during mutual eye gaze both before and after the JA task (Fig. 1A). Three fMRI experiments were carried out. In Experiment 1, participants performed real-time mutual gaze (MG1 condition, Fig. 1A) followed by the JA tasks (Figs. 1B to D) on Day 1; on Day 2 of Experiment 1, participants again underwent the real-time mutual gaze condition (MG2 condition, Fig. 2A). There was a control condition in which participants believed that they were performing real-time interaction using eye contact, but in actuality they watched a video recorded on Day 1 (VIDEO condition, Fig. 1A). Experiment 2 was a 2-day hyperscanning fMRI study consisting of the real-time mutual gaze task without JA on Day 1. In Experiment 3, participants completed the MG1 and JA tasks as in Experiment 1 on Day 1, but on Day 2 they performed the real-time mutual gaze task with a new partner different from the partner they had on Day 1.

Material and methods

Participants

A total of 96 volunteers participated. Prior to the experiment, we assigned participants of the same gender to pairs. Participants were not mutually acquainted prior to the start of the experiment. All participants except one were right-handed according to the Edinburgh Handedness Inventory (Oldfield, 1971). None of the participants had a history of neurological or psychiatric illness. The protocol was approved by the ethical committee of the National Institute for Physiological Sciences (Okazaki, Japan), and the experiments were undertaken in compliance with national legislation and the Code of Ethical Principles for Medical Research Involving Human Subjects of the World Medical Association (the Declaration of Helsinki). All participants gave their written informed consent to participate in the study.

Experimental setup

To measure neural activation during the online exchange of eye signals between pairs of participants, we used a hyperscanning paradigm with two MR scanners (Magnetom Verio 3 T, Siemens, Erlangen, Germany), installed side-by-side in parallel to minimize interference between magnetic fields. The two MR scanners shared one control room, and the onset of scanning was synchronized by an external trigger that was generated by in-house MS-DOS software. To enable reciprocal face-to-face interaction, the two MRI scanners were used alongside online video cameras and infrared eye-tracking systems (NAC Image Technology Inc., Tokyo, Japan). The infrared camera captured images of each participant's face including the eyes and eyebrows, which were transferred to a personal computer (Dimension 9200, Dell

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