Chapter 11
Shared Attention and Interindividual Neural Synchronization in the Human Right Inferior Frontal Cortex

Norihiro Sadato

Abstract During a dyadic social interaction, two individuals can share visual attention through gaze, directed to each other (eye contact) or to a third person or an object (joint attention). Eye contact and joint attention are tightly coupled to generate the state of shared attention across individuals. Hyperscanning fMRI conducted with pairs of adults during joint attention tasks showed interindividual neural synchronization in the right inferior frontal gyrus. To explore how joint attention generates the state of shared attention, and whether its memory trace persists during a subsequent eye-contact condition, two-day hyperscanning fMRI study was conducted, 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 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, which was positively correlated with interindividual 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. These results indicate that shared attention is represented and retained by pair-specific neural synchronization during mutual gaze that cannot be reduced to the individual level. This interbrain effect highlights the role of the right inferior frontal gyrus in the execution and learning of attentional coordination and sharing attention between self and others.

Keywords Inferior frontal gyrus • Hyperscanning functional MRI • Joint attention • Mutual gaze • Eye blink • Social cognition • Action representation • Hebbian association

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N. Sadato (✉)
National Institute for Physiological Sciences, 38 Nishigonaka, Myodaiji, Okazaki,
Aichi 444-8585, Japan
e-mail: sadato@nips.ac.jp

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11.1 Shared Attention Critical for Social Interaction

11.1.1 Social Interaction, Social Attention, and Shared Attention

Humans can detect another person's focus of attention, orient own attention to the same location, and draw inferences regarding the other's goals using mainly through eye-gaze information (Allison et al. 2000; Calder et al. 2007; Nummenmaa and Calder 2009). This capability, known as social attention, is particularly important when during direct interaction with others. Face-to-face social interaction has three prominent characteristics (Schilbach et al. 2013). First, different roles for the interacting individuals emerge, such as initiator and responder. Second, sharing of attention, intention, and motivation are created de novo within an interaction and are critical for 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 mutual gaze and joint attention (Emery 2000), is a typical and fundamental process that fulfills the above three characteristics (Koike et al. 2016).

11.1.2 Mutual Gaze

Mutual gaze provides a communicative link between humans by sharing the message "I am attending to you" (Farroni et al. 2002; Schilbach 2015). As gaze direction explicitly indicates the attentional target, mutual gaze is regarded as shared attention directed toward one another. Human infants and adults interact with one another dyadically by looking, touching, smiling, and vocalizing toward each other in turn-taking sequences, called protoconversations, during which infants gaze into the eyes of the partner (Hobson 2002; Trevarthen 1979, 1993). This face-to-face visual engagement, mutual gaze, is a universal feature of adult–infant interactions that represents mutual attentiveness and enhances positive emotional states (Keller et al. 1988). Thus, mutual gaze is implicated in the sharing of various psychological states.

11.1.3 Joint Attention

Joint attention (JA) coordinates attention between partners to share an awareness of objects or events (Mundy et al. 1986). The importance of JA in the development of social cognition, as well as development of language, has been stressed (Mundy and Newell 2007). As an early-onset interactive process that leads to various kinds of social learning (Mundy and Newell 2007), it emerges as early as 6–12 months of age (Corkum and Moore 1998). Two types of joint attention are known: Initiating 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 to share attention toward an object (Mundy et al. 2009).

11.1.4 Link Between Mutual Gaze and Joint Attention

The shared space of the common psychological ground resulting from mutual gaze may provide a communicative context. An adult's initial eye contact or mutual gaze prior to looking at an object is a critical cue that can establish joint attention with infants as young as 9 months old (Striano and Reie 2006). Mutual gaze therefore provides a communicative context for joint attention (Farroni et al. 2002). Thus IJA, RJA, and mutual gaze are tightly linked (Emery 2000; Perrett and Emery 1994) and function to share attention within a dyad or toward a third object.

11.2 Neural Substrates of Social Attention

11.2.1 Isolated Brain Approaches

Eye Gaze

The neural substrates of social attention have been studied extensively, particularly using eye-gaze paradigms. Bilateral removal of the superior temporal sulcus (STS) region in macaques impairs perception of gaze direction without affecting perception of facial identity (Heywood and Cowey 1992). Recent human functional MRI (fMRI) studies have identified the involvement of the posterior STS (pSTS) in social perception through eye movement (Allison et al. 2000). Gaze processing extends beyond the STS to include the amygdala (George et al. 2001; Kawashima et al. 1999) and the inferior temporal (Wicker et al. 1998), parietal (Calder et al. 2007; Hoffman and Haxby 2000; Wicker et al. 1998; Mosconi et al. 2005; Hooker et al. 2003), medial prefrontal and anterior cingulate cortices (Calder et al. 2002), and other frontal regions (Mosconi et al. 2005; Hooker et al. 2003; Bristow et al. 2007). These different regions seem to process different aspects of the visual and social properties of gaze. Other regions of relevance include temporal areas implicated in face perception, frontoparietal attention regions, and areas implicated in emotion and social cognition (Nummenmaa and Calder 2009). For example, Sato et al. (2009) showed that automatic attentional shifts triggered by gaze, gestures, and symbols commonly activated the pSTS, the inferior parietal lobule, the inferior frontal gyrus, and the occipital cortices in the right hemisphere. This evidence indicated that the pSTS is related to the attentional shift per se. Recently, a combined fMRI–diffusion tensor imaging study by Ethofer et al. (2011) showed that dynamic gaze shifts toward an observer enhanced functional connectivity between the right pSTS and right anterior insula which, abutting the lower inferior frontal gyrus, plays a crucial role as part of the ventral attention system that is recruited by salient stimuli (Corbetta et al. 2008). Calder et al. (2002) reported that without making an explicit judgment, effects were observed in the anterior rostral portion of the medial prefrontal cortex (arMFC), when comparing an averted eye-gaze condition with a direct-gaze condition. They suggest that the activation of the arMFC is related to the implicit interpretation of averted gaze regarding the shift of an avatar's attention, which is a process that recruits the theory of mind module postulated by Baron-Cohen (1995). Thus, research in gaze processing is now outlining the neural basis of social attention, the cognitive components of which include the directing of social attention, attention shifting, processing of emotional reactions, and attribution of mental states (Saito et al. 2010).

Joint Attention

There are several neuroimaging studies of joint attention. Williams et al. (2005) used an RJA task that focused on the sharing of attention toward objects. In a joint attention condition, an avatar's gaze and the movement of a set of dot stimuli was concordant, whereas it was discordant in a non-joint attention condition. Corresponding regions of brain activation were in the anterior and posterior cingulate cortices. Laube et al. (2011) showed that the right pSTS and the right fusiform gyrus were involved in both processing of head- and eye-gaze direction during RJA. Using live interaction joint attention tasks, Redcay et al. (2010, 2012) showed activation in the ventromedial prefrontal cortex for RJA and intraparietal sulcus and middle frontal gyrus for IJA. Overlap for both IJA and RJA was observed in the dorsal medial prefrontal cortex, right inferior frontal gyrus, and right pSTS. Utilizing a virtual reality paradigm and functional MRI, Schilbach et al. (2010) showed that IJA and RJA are accompanied by activation of overlapping but partially independent neural networks. Unique activation for IJA was reported in the ventral striatum bilaterally, and unique activation for RJA was reported within the ventral medial prefrontal cortex. The extent to which the neural substrates of IJA and RJA are functionally segregated remains controversial.

11.2.2 Need for Hyperscanning to Identify the Neural Substrates of Shared Attention

Until recently, the neural substrates of cross subject sharing of attention were hardly known. This is because much of the previous work on social attention has measured the responses of an individual brain to shared attention stimuli. However, since shared attention arises from the dynamic interaction of two agents, simultaneous measurement of the brain activities of two persons engaged in actual eye contact and joint attention is critical, because shared attention is an interactively constituted phenomenon which cannot be reduced to responses at the individual level (Konvalinka and Roepstorff 2012; Schilbach 2015). There have been several studies that investigated the flow of information between the brains of two partners by scanning participants one after another during offline interactions (pseudo hyperscanning, Anders et al. 2011; Konvalinka and Roepstorff 2012; Schippers et al. 2010; Stephens et al. 2010, for review). However, this technique cannot capture mutual influence *during* the interaction, which may be represented by interindividual neural synchronization (Astolfi et al. 2010; Cui et al. 2012; Dumas et al. 2010; Jiang et al. 2012; Muller et al. 2013; Osaka et al. 2014; Saito et al. 2010; Sänger et al. 2013; Tanabe et al. 2012; Yun et al. 2012).

The brain could be conceptualized as a discrete functional system, with external factors modulating rather than determining the operation of the system. In contrast, another way to conceptualize the brain is that it is an input–output system primarily driven by interaction with the external world (Fox et al. 2007). Support for the intrinsic perspective on brain function comes from studies of brain activity present even in the absence of task performance or stimuli, called intrinsic brain activity. This intrinsic brain activity is not random noise but is specifically correlated between related neurons (Tsodyks et al. 1999) and cortical columns (Kenet et al. 2003) and within widely distributed neuroanatomical systems (Biswal et al. 1995; Fox et al. 2005; Greicius et al. 2003; Hampson et al. 2002; Lowe et al. 1998). Given this spatial organization at multiple levels, intrinsic brain activity might have an important role in coordination of neuronal processing within the brain (Fox et al. 2007). Expanding this concept, intersubject synchronization might represent the intersubjective sharing of psychological states during eye contact. To evaluate intersubject synchronization, however, it is critical to exclude the possibility that the observed neural synchronization simply reflects similarity in their behavior (Konvalinka and Roepstorff 2012).

11.2.3 Interindividual Neural Synchronization at Right IFG During JA

Hyperscanning fMRI with JA

Based on this conceptualization and caveat, Saito et al. (2010) conducted hyperscanning fMRI of paired subjects (Montague et al. 2002) while they were engaged in joint attention tasks, with eye contact as the baseline. Saito et al. (2010) reported neural synchronization by intersubject correlation of the "innovations" which are the residual time courses of the neural activities obtained by modeling out the task-related effects and other confounding effects (Fig. 11.1). Given the linear addition of task-related activity on top of the persistent resting spontaneous activity

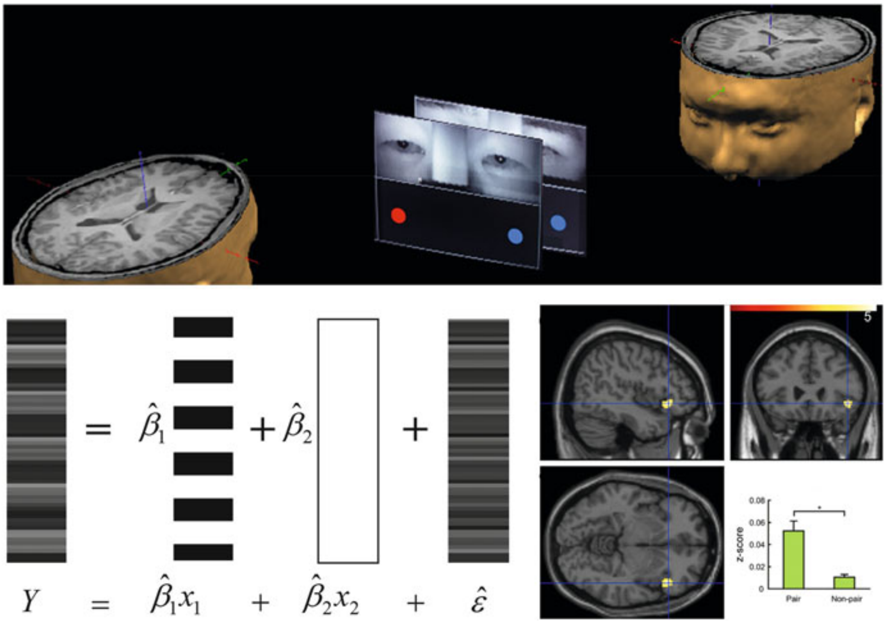

Fig. 11.1 (*Top*) schematic diagram of the "hyperscan." Double-video systems implemented on two MRI scanners captured video images of each participant's eyes and eyebrows, which were transferred to the screen splitter that bound them to the computer-generated visual stimuli. The combined images were projected onto the screen in front of the counterpart through the projector. The other participant's eyes were presented on the upper half of the screen, and computer-generated images of balls were displayed at both ends of the screen in the lower half. The timing of the MRI scanning and the stimulus presentation were synchronized by the pulse signal from the controller of the double-video system to the two MRI scanners and the PC for the presentation of visual stimuli. (*Bottom left*) general linear model showing that the observed time series of the BOLD signal in the given voxel (Y) is the linear sum of the task-related activities (x1), constant term (x2), and the innovation (ε). (*Bottom right*) significant positive correlations of the innovation between the paired subjects who had been "face-to-face" during fMRI compared with the non-paired subjects. Images are superimposed on three orthogonal sagittal, transaxial, and coronal sections of T1-weighted high-resolution MR images. The *blue lines* in each section cross in the right IFG (44, 26, –6). The *color scale* indicates the *t* values. Standardized correlation value (z-score) of the pair and non-pair group. *Error bars* indicate the standard error of the mean (Modified from Saito et al. 2010)

(Fox et al. 2006), the adequate removal of task-induced variance in functional connectivity should yield a correlation profile similar to "continuous" resting-state data. Fair et al. (2007) speculated that interregional correlations might be altered during task states such that correlated spontaneous neural activity is strengthened in task-induced areas and weakened in non-task-induced areas. Thus, the innovation is a useful source of intrinsic dynamic information within different brain regions (Riera et al. 2004; Fair et al. 2007). Saito et al. (2010) made use of the correlations between pairs of innovations at voxels in different brain regions to construct measures that reflect interpersonal influences. As the baseline of JA is the eye-contact condition, the interpersonal correlation of the innovations of the paired persons, compared with those of the non-paired persons, represented the eye-contact effect. The advantage of the innovation approach is that it eliminates the effect of task, and therefore any remaining intersubjective correlation of the innovation data is not caused by task similarity across partners.

Interindividual Neural Synchronization at Right IFG During Joint Attention

A comparison of “pair” and “non-pair” correlations of the innovations showed that the correlation of the right IFG ($x = 44$, $y = 26$, $z = -6$, MNI coordinate) between the two brains was more prominent in the “paired” group than in a dummy “non-paired” group (Fig. 11.1 bottom right). The peak correlation corresponds to Brodmann area 47 adjacent to the anterior insular cortex (Saito et al. 2010). As mutual gaze implies the sharing of the intentional relation from the self to the agent (“I look at you”), and from the agent to the self (“You look at me”), the between-subject correlation of the innovation suggests that the right IFG is related to the between-subject sharing of the intentional relation. This sharing might create a context that enhances the detection of the communicative intent emitted with the eye movement (Frith and Frith 2006), making possible collaborative activities with shared goals (in the case of joint attention, looking at the same objects). The neural synchronization of the right IFG might represent the innate self-other equivalence in intention in action (Meltzoff 2007), which in turn provides a “like-me” framework. Within the “like-me” framework, it has been argued that internal representations of actions are shared between the self and others (shared action representations) and that this integration of information about one’s own actions, and those of others, might involve the IFG. Recently, de Vignemont and Haggard (2008) argued that shared action representations are represented within the motor system. Within the hierarchical model of motor control, shared action representations involve intentional representations of action prior to the dispatch of a motor command. Shared action representations allow the observer to internalize someone else’s actions as if he or she were the agent, and not just an external witness, providing the first-person perspective (de Vignemont and Haggard 2008). Saito et al. (2010) concluded that the right IFG may be the site of the neural representation of the “shared space of common psychological ground” mediated by eye gaze.

11.2.4 Hebbian Association Causes Synchronization of the Right IFG

What Does the Neural Synchronization Represent?

In the context of shared action representations, interindividual 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 et al. 2010;

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 the process by which motor and perceptual action representations become tightly linked in such a way that perceiving another person's action activates the same representations as performing the action. It has been argued that action representations, or perceptuo-motor common representations, can 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; Treur 2011). In social Hebbian connections, one's own motor programs are linked to the sensory consequences provided by another's actions. Koike et al. (2016) applied this motor-perceptual common representation account to attention control. Their hypothesis was that the training of joint attention causes a social Hebbian association between initiating and responding joint attention, IJA and RJA, respectively. 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 this synchronization should be retained as social memory after the JA experience.

Behavioral Markers of Shared Attention: Blink

To quantify interpersonal aspects of the social interaction such as shared attention, finding 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 (Koike et al. 2016). 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 (Koike et al. 2016).

Hyperscanning fMRI with Mutual Gaze of Pre- and Post-JA Task

Hypothesis

Koike et al. (2016) hypothesized that shared attention during a JA task would be represented by blink synchronization and retained as a social memory and that this social memory would be represented by enhanced interindividual neural synchronization in the right IFG. Based on the Hebbian account, they also expected the right IFG to be activated by both RJA and IJA.

Experimental Setup

To test these hypotheses, Koike et al. (2016) conducted hyperscanning fMRI during a JA task and during mutual eye gaze both before and after the JA task (Fig. 11.2a). Three fMRI experiments were carried out. In Experiment 1, 34 (17 pairs) participants performed real-time mutual gaze (MG1 condition, Fig. 11.2a) followed by the JA tasks (Figs. 11.2b–d) on day 1; on day 2, participants again underwent the real-time mutual gaze condition (MG2 condition, Fig. 11.2a). 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. 11.2a). Experiment 2 was a 2-day hyperscanning fMRI study with 30 participants consisting of the real-time mutual gaze task without JA on day 1. In Experiment 3, 32 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.

Eye-Blink Synchronization

In Experiment 1, the mutual gaze condition on day 1 (MG1) with an unknown partner did not elicit significant eye-blink synchronization (Fig. 11.3a). On day 2, during the mutual gaze condition (MG2), eye-blink synchronization was significant (Fig. 11.3a), and eye-blink synchronization in MG2 was significantly more prominent than during MG1 (Fig. 11.3a). Without online interaction between participants (VIDEO condition, watching the video recorded during the MG1), eye-blink synchronization was not significant (Fig. 11.3a). The difference in eye-blink synchronization between the MG2 and VIDEO conditions was also statistically significant (Fig. 11.3a).

There was a significant interindividual eye-blink synchronization even during JA tasks between paired partners (real pair) compared with eye-blink

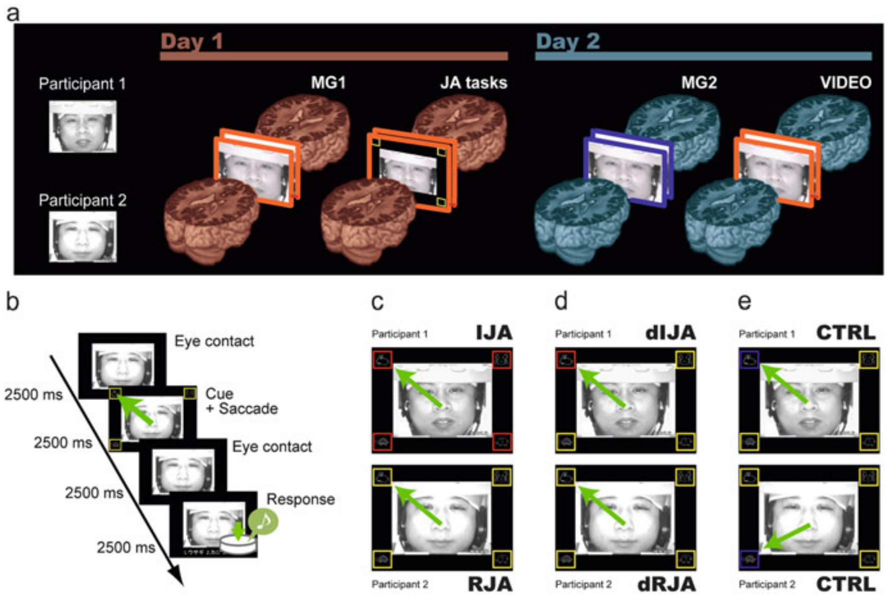

Fig. 11.2 (**a**) Time line of Experiment 1. Image of the brain schematically indicates fMRI data obtained in day 1 (*orange*) during real-time eye contact through video (*orange frame*, MG1) and during joint attention task (*red frame*, JA tasks). In day 2, fMRI data (*blue brains*) was obtained during real-time eye contact through video (*blue frame*, MG2) and during watching the face video of the partner on day 1 (*orange frame*, VIDEO). (**b**) Time course of JA tasks. (**c**) Settings of IJA/RJA. The "all-four red" cue prompted the participant 1 to freely select one of the objects and shift his/her gaze on it. At the same time, identical objects with yellow frame were presented to the counterpart, participant 2. This "all-four-yellow" cue prompted the participant 2 to shift his/her gaze to the object that participant A attended to (*Green arrows*). Once the objects disappear, the participants are required to return back to the eye-contact situation for 2,500 ms. Then the names of four objects were presented under the live image of partner's face. Using a *button*, participants were required to select the name of the object that they had watched. Sound effect feedback was used to inform whether or not they successfully shared their attention to one object. (**d**) Designated-choice IJA/RJA (dIJA/dRJA). One red frame object and three yellow frame objects were presented to participant 1 who has to shift eye gaze toward the red target. (**e**) Control (CTRL) task. Both of them have to shift eye gaze individually toward the blue target without caring about partner's eye movement (Modified from Koike et al. 2016)

synchronization between randomly selected participants (pseudo pair, Fig. 11.3b). The strength of eye-blink synchronization during JA was positively correlated with enhanced eye-blink synchronization during MG2 compared with MG1 (Fig. 11.3c).

Neural Synchronization

During the mutual gaze condition on day 1 (MG1), interindividual neural synchronization was found in the middle occipital gyrus and MTG (Fig. 11.3d) adjacent to the right EBA (white outline in Figs. 11.3d–f). During the mutual gaze condition on

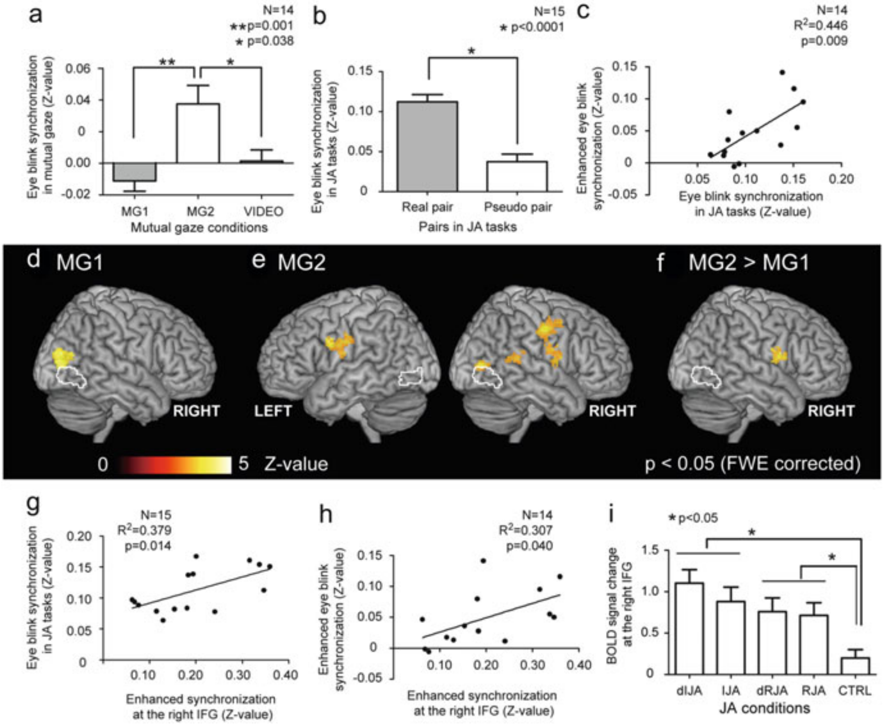

Fig. 11.3 Interindividual eye-blink and neural synchronization. (**a**) The eye-blink synchronization between paired participants during the MG1, MG2, and VIDEO conditions. (**b**) Eye-blink synchronization in the JA task between paired participants (real pair) and two participants who were not paired but performed JA tasks with the same temporal parameters (pseudo pair). (**c**) Correlation between eye-blink synchronization during JA tasks and enhancement of eye-blink synchronization from MG1 to MG2. (**d**) Interindividual neural synchronizations before (MG1), **e** after JA task (MG2), and (**f**) their increment were superimposed on the 3D surface of a template brain. *White contour* indicates functionally defined extrastriate body area (EBA). The enhancement of neural synchronization at the right IFG cluster defined by MG2-MG1 (**f**) was correlated with (**g**) eye-blink synchronization during JA tasks and with (**h**) enhanced eye-blink synchronization. (**i**) Task-related activation of the right IFG during JA task. *Error bars*, standard error of the mean (s.e.m.) (Modified from Koike et al. 2016)

day 2 (MG2), interindividual synchronization extended anteriorly to the right posterior superior temporal sulcus, bilateral IFG, and ventral premotor cortex (Fig. 11.3e). The enhancement in interindividual synchronization during MG2 compared with MG1 was statistically significant only in the right IFG (Fig. 11.3f).

Relationship Between Neural and Behavioral Synchronization

The enhancement of interindividual neural synchronization in the right IFG was significantly correlated with eye-blink synchronization during JA tasks (Fig. 11.3g) and with the enhancement of eye-blink synchronization (Fig. 11.3h). Consistent with the social Hebbian learning hypothesis, the right IFG was activated by both IJA and RJA, while no activation was found during the control condition (Fig. 11.3i).

The Learning Effect Was Task and Pair Specific

Without JA experience (Experiment 2), no enhancement of behavioral synchronization was observed. Even following JA (Experiment 3), synchronization was not enhanced when the partner was swapped. In parallel with the behavioral data, there was no enhancement of interindividual neural synchronization in the right IFG.

Eye-Blink Synchronization During JA

The JA task caused blink synchronization. To successfully conduct the task, participants had to coordinate the timing of opening and closing their window of attention with their partner's, resulting in eye-blink synchronization (task effect). Consistent with the task effect, significant eye-blink synchronization was also observed in the pseudo pair (Fig. 11.3b). As the task design was identical across the pairs, this indicates that the JA task aligned the attentional window within the dyad. Therefore, any difference in blink synchronization between real and pseudo pairs (Fig. 11.3b) constitutes a pair-specific effect. There was no eye-blink synchronization during first mutual gaze (MG1), reflecting no commonly shared task that can provide cues for eliciting similar behavior. Thus, eye-blink synchronization during mutual gaze which emerged after the JA task (Fig. 11.3a) does not reflect a task effect. The lack of eye-blink synchronization in the VIDEO condition confirms the importance of online mutual interaction for the emergence of eye-blink synchronization during MG2. Furthermore, the strength of eye-blink synchronization during JA was positively correlated with enhanced eye-blink synchronization during MG2 (Fig. 11.3c). Given constant task effects in synchronization during JA, this correlation indicates that blink synchronization during MG2 is affected by the pair-specific effect of blink synchronization during JA. In other words, the shared attention induced by JA was retained as a pair-specific "social" memory and represented by enhanced synchronization during mutual gaze.

Enhanced Neural Synchronization in IFG During Mutual Gaze After JA

Across the whole brain, only the right IFG showed enhanced neural synchronization following JA (MG2–MG1, Fig. 11.3f), whereas no synchronization was observed during VIDEO. Enhanced synchronization in the right IFG was positively correlated with eye-blink synchronization during JA tasks and with the enhancement of eye-blink synchronization. Finally, the right IFG was activated by both IJA and RJA. These findings indicate that the right IFG is related to the generation of shared attention through social Hebbian association during JA and to its retention that is evoked by mutual gaze.

The Role of Right IFG in Shared Attention

In general, the IFG is linked to several executive processes of the social stimuli, such as controlling, overriding, or inhibiting behavioral and emotional responses (Aron et al. 2004; Dillon and Pizzagalli 2007; Mitchell 2011), as well as mirroring (Leslie et al. 2004), empathizing (Schulte-Rüther et al. 2007), or imitating the behavior of another individual (Lee 2006). The IFG is also related to a unification of different types of sensory information to perform these executive processes (Frühholz and Grandjean 2013). The right IFG is an interface between self and other, especially during social situations. The right IFG is involved in unconscious incorporation of facial information of one's partner (Leslie et al. 2004) and in distinguishing self-related facial information from that of others (Sugiura et al. 2005). Furthermore, the right IFG is involved in the release of attention that is linked to spontaneous eye blinks (Nakano et al. 2013). The release of attention activates the default-mode network that is associated with internal processing while suppressing the dorsal attentional network (Nakano et al. 2013). As the right IFG and adjacent anterior insula switch between central-executive and default-mode networks (Sridharan et al. 2008), neural synchronization in the right IFG may represent synchronized shifting of attention toward self and others (Pfeiffer et al. 2013).

The right IFG was activated by both responding and initiating JA (Fig. 11.3i), consistent with previous studies (Redcay et al. 2012; Saito et al. 2010; Williams et al. 2005). Furthermore, neural synchronization of the right IFG occurred spontaneously during MG2. These findings are in line with the notion that mirror neuron properties of the right IFG and ventral premotor cortex (Gallese et al. 1996; Rizzolatti et al. 1996; Keysers et al. 2010) are caused by social Hebbian learning (Keysers and Perrett 2004; Wolpert et al. 2003) which binds self-derived behavior to that of others through online interaction (Mundy and Newell 2007; Treur 2011). The present study suggests that the right IFG was affected by social Hebbian association which binds self-derived directed attention (Tomasello and Carpenter 2007) to that of others.

Enhanced interindividual neural synchronization in the right IFG was statistically significant even after the removal of the eye-blink-related activation (Koike et al. 2016). Thus, the neural synchronization of the right IFG is not related to the blink per se but represents learned shared attention. Considering shared attention is to be understood as a complementary action due to its social salience, relevance in initiating communication, and joint action (Pfeiffer et al. 2013), the present finding is consistent with a previous study by Newman-Norlund et al. (2007) who showed the right IFG is more active during complimentary as compared to imitative actions.

11.3 Neural Synchronization in the "Social Default Mode"

Koike et al. (2016) showed enhanced synchronization of eye blinks within a dyad that was not attributable to similarity in their behavior but was instead due to the pair-specific relation (Konvalinka and Roepstorff 2012). Regarding the interindividual functional connectivity by means of neural correlation, Koike et al. (2016) treated the two brains as a spontaneous "two-in-one" system during the mutual gaze condition that can be regarded as a "social default mode," as the activity of an individual brain consists of spontaneously organized networks during the resting state (Fox et al. 2005, 2006). Right middle temporal gyrus (MTG) showed significant and consistent interindividual synchronization during mutual gaze (Fig. 11.3d, e). Unlike the right IFG, there was no learning effect (Fig. 11.3f). As no interindividual neural synchronization occurred during the VIDEO condition, MTG synchronization should have emerged as a result of online mutual interaction during mutual gaze. The EBA are known to receive both sensory inputs of others' body information (Downing et al. 2001) and efference copies (Astafiev et al. 2004; Orlov et al. 2010); thus, the adjacent MTG may conceivably receive information about self and other's eye blinks. Consistent with this notion, MTG has a role in detecting contingency between own and partner's behavior (Redcay et al. 2010). Given that the summation of inputs to the MTG region is identical between the two participants, even pairs of new partners synchronize their visual area activation (Koike et al. 2016).

In contrast, in the right IFG, interindividual connectivity became more conspicuous after partners became familiar with one another, i.e., after the JA training (Fig. 11.3f), and the connectivity profiles showed pair specificity. Thus, the property of the two-in-one system during the social default mode reflects the relationship between two participants, as the property of an intra-brain network reflects the mental state during a no-task condition or default mode (Yan et al. 2009). Mutual gaze underlies almost all face-to-face social interactions. Therefore, the effect of mutual gaze should be carefully considered to explore interindividual networks involved in face-to-face communication. Further investigation of this two-in-one system, during minimum task constraints, i.e., mutual gaze, might help to reveal the functional roles of interindividual neural synchronization, as default-mode network studies in the resting state have shed light on task-related brain networks (Fox et al. 2005, 2006).

11.4 Conclusion

The enhancement of behavioral and interindividual neural synchronization of the right IFG during mutual gaze after a JA task represents a pair-specific construct of shared attention that cannot be reduced to the individual level. As default-mode network studies on the resting state have shed light on state-related brain activities (Fox et al. 2005), further investigation of interindividual neural interaction will help to reveal the neural underpinnings of the state of interacting persons (Konvalinka and Roepstorff 2012).

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