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The Interacting Body: Intra- and Interindividual Processes During Imitation

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Cognition involving others, or social cognition, is often conceptualized as the solitary, third-person computation of mental states. Relatively, little attention has been paid to how individuals use their cognitive capacities at the behavioral and brain levels in social exchanges. We introduce imitation as a valuable model of dynamic social interactive phenomena and describe laboratory procedures for studying it in behavioral and neuroimaging contexts. We review research that reveals behavioral and neural synchronization of individuals engaged in imitation. In the latter case, brain activity is correlated in imitative partners, but the pattern expressed by an individual depends on the individual's role (i.e., model or imitator). We link these findings to theoretical notions about mirroring and mentalizing brain systems and then describe how mirroring and mentalizing support the notion of prospective cognition, even in basic forms of communication such as reciprocal imitation.

Keywords: imitation; EEG; fMRI; synchrony; interbrain

Traditional research in cognitive science has often been grounded in the view that an individual constitutes a "lone cognizer." Based on the analogy that the brain works like a computer, individuals have been perceived as solitary information processing systems that take in information from the environment. In recent decades, cognitive science has placed increasing attention on social cognition (cognition involving others), an important

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aspect of which is cognition that takes place during real-time social exchanges. Unfortunately, inquiry into social cognition often retains the lone cognizer perspective. In many cognitive neuroscience studies using functional magnetic resonance imaging (fMRI) to study social cognition, for instance, brain activity is recorded during the presentation of photos or video clips describing social situations. Such procedures may document the brain regions that are activated in certain social situations, but they do not clarify what happens in the brain during social exchanges (Amodio & Frith, 2006; Gallese, Keysers, & Rizzolatti, 2004; Pfeiffer, Timmermans, Vogeley, Frith, & Schilbach, 2013).

Inspiration for an alternative approach to social cognition comes from developmental psychology, in which, beginning in the 1970s, attention turned to studying real-time dynamic interactions involving two or more partners (e.g., see Scheflen, 1982). This focus on live interaction requires an emphasis on dyadic variables (Nadel & Camaioni, 1993) such as imitation (Kugiumutzakis, 1993; Nadel-Brulfert & Baudonnière, 1982), joint attention (Mundy, Kasari, & Sigman, 1992), and covariation in partner actions and cognitions, various aspects of which have been referred to as coregulation (Fogel, 1993), synchrony (Trevarthen, 1977), and harmonization (Stern, 1977). Importantly, cognition in dynamic interactions is constantly evolving (Varela, 1984) and to sustain covariation, members of an interaction must engage anticipatory processes. As a result, social cognition is prospective cognition.

The increasing recognition that social cognition is interactive and socially situated (e.g., Dumas, 2011; Schilbach, 2010) has forced social neuroscientists to update their theoretical frameworks. An illustrative theoretical view is the interactive brain hypothesis of Di Paolo and De Jaegher (2012), which extends the enactive perspective on cognition, which grounds cognition in the coupling between living sentient beings and their environment (Varela, Thompson, & Rosch, 1991), into the social realm. Enactive theories see nonsocial cognition as inherent in, or inextricably embedded in, functional relations between organisms and the environment. Social cognition, similarly, is seen as inseparable from the social environment. Interaction is constitutive of social brain mechanisms, and meaning is generated through interaction (see also De Jaegher, 2009).

In line with dynamical systems theory, enactive accounts focus on *synchronization* as a key feature of cognition. Synchronization means the coregulation of tempo and is considered as one of the most pervasive nonlinear phenomena in nature (Pikovsky, Rosenblum, & Kurths, 2003). Cell assemblies synchronize at the neural scale (Bressler & Kelso, 2001; Fries, 2005; Varela, Lachaux, Rodriguez, & Martinerie, 2001), and at the behavioral scale, interactional synchrony is an important regulator of social exchanges.

INTERACTIONAL MODELS OF SOCIAL COGNITION DEMAND NEW METHODS

A focus on interaction also demands the updating of methods used to study social cognition. The most pressing challenge involves how to design experimental situations involving a live social context. Concerning synchrony, a pioneering effort in developmental psychology involved the use of microanalysis by Condon and Sander (1974). Using detailed coding of face-to-face interactions in which an adult spoke to a neonate, they found that the neonate's movements synchronized with the rhythm of the adult's speech. Subsequent studies have suggested that reciprocity (i.e., mutual influence) is the critical feature of these effects (Murray & Trevarthen, 1985).

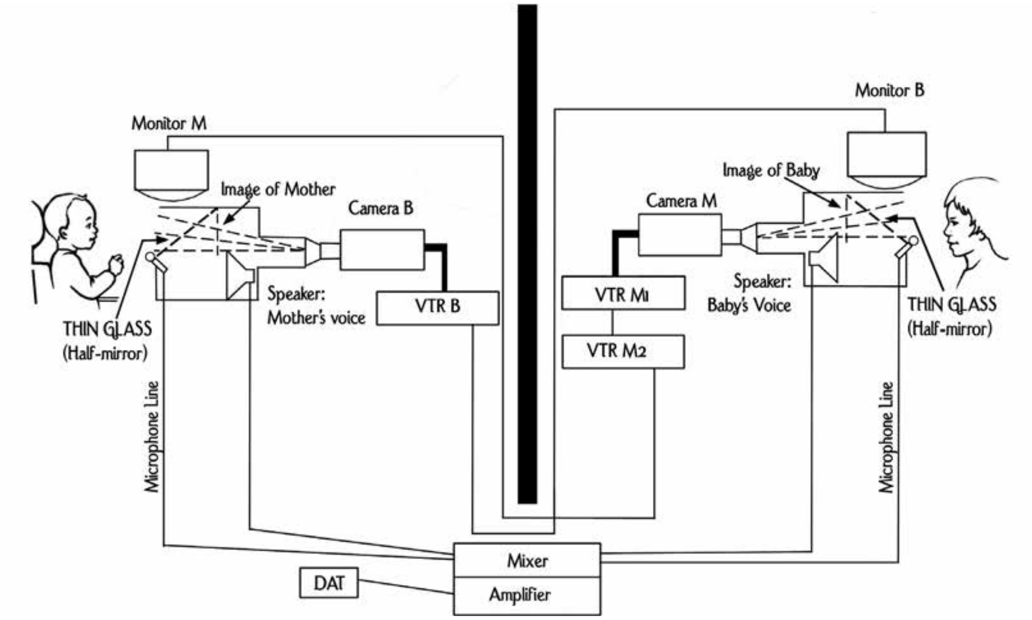

FIGURE 1. Double video system of Nadel et al. (1999). At each station, audio and video of one dyad member can be captured and relayed in real time to the other dyad member's station. At the infant's station, recorded audio and video of the mother can be substituted for the live feed. Audio and video recording permit detailed descriptive analysis of the infant's reactions. VTR = video tape recorder; DAT = digital audio tape.

Reciprocity was featured prominently in an experiment by Nadel, Carchon, Kervella, Marcelli, and Réserbat-Plantey (1999) in which, during an initial phase, mothers and their infants could interact through a double camera system (see Figure 1). Each of several mother–infant dyads was allowed to interact through the system, which allowed for a detailed description of dyad dynamics. The role of reciprocity was evaluated by temporarily substituting recorded mother communication for live input, which functionally desynchronized the dyad, because the mother could not react contingently to the infant's sounds and actions. Results showed how disorganizing a rupture of synchrony can be for 2-month-olds (Nadel et al., 1999; Nadel, Soussignan, Canet, Guillaume, & Gérardin, 2005; Soussignan, Nadel, Canet, & Gérardin, 2006): The infants stopped smiling, looked away, and became upset. When the live feed of mother communication was restored, the mood and behavior recovered. This investigation provided an early demonstration that synchrony is an integral feature of communication.

In social neuroscience, the challenge of developing methods to track social interaction is magnified because of the practical constraints of working with neuroimaging equipment (Hari & Kujala, 2009). Typical neuroimaging methods reflect the lone cognizer perspective in that they involve the recording of brain activity in one individual, but the technique known as *hyperscanning* allows for simultaneous recording (through fMRI or electroencephalography [EEG]) of brain activity in multiple participants, facilitating both within- and between-brain analyses (Babiloni et al., 2006; Montague et al., 2002). Hyperscanning is a potentially powerful tool for two-body neuroscience research, and several studies have employed it to record brain activity in social contexts.

It is important to note that a recording technique alone does not solve the problem of how to embed a live social interaction in the experimental context. Several hyperscanning studies, although not capturing the dynamic nature of naturalistic social interactions, have succeeded in documenting the possibility of interindividual correlations in brain activity. For example, correlated brain activity has been observed in individuals experiencing the same perceptual context (Hasson, Nir, Levy, Fuhrmann, & Malach, 2004) and in guitarists whose playing was guided by the same metronome (Lindenberger, Li, Gruber, & Müller, 2009). Such individuals are not interacting. Correlated brain activity was evident in individuals playing the game of charades (Schippers, Roebroeck, Renken, Nanetti, & Keysers, 2010), but in charades, the "social" role fulfilled by each individual is highly structured and not reciprocal (e.g., one person gestures while the other guesses). Correlated activity, particularly in brain areas associated with reward prediction, has been observed in individuals during economic exchanges (Babiloni et al., 2006; King-Casas et al., 2005; Montague et al., 2002). However, the tasks employed in economic studies are highly structured and incorporate ritualized turn-taking.

A genuine social interactive context involves spontaneous social coordination (i.e., reciprocal influence) taking place at minute time scales. Hyperscanning EEG, with its millisecond time scale of measurement, is especially well-suited to examining such relationships. Tognoli, Lagarde, DeGuzman, and Kelso (2007) demonstrated the efficacy of hyperscanning EEG in studying the spontaneous motor coordination of two individuals. They found, in the parietal region, a rhythmic activity in the 10Hz range of the EEG spectrum (called the phi complex) that was modulated by the intentional coordination of movements of the two subjects. Although the type of interaction examined in this study was nonverbal, it qualifies as social according to the definition offered earlier.

INCORPORATING REAL-LIFE SOCIAL INTERACTIONS IN A NEUROIMAGING EXPERIMENT

Here begins our own story. Our interdisciplinary group has embarked on a series of innovative studies that were inspired by the developmental research described previously and employs double video technology coupled with hyperscanning techniques. To evaluate neural synchrony during real-life social interactions, we have focused our attention on synchronic imitation.

Reciprocal Imitation as a Model of Social Interaction

Imitation has received relatively little attention in the study of children's development, education, and therapy. Traditionally, imitation has been thought of as a rather simple component of the imitator's learning mechanisms (Piaget, 1962; Tomasello, 1999), and indeed, literally from birth, imitation enriches an individual's motor repertoire with gestures and actions that are acquired from watching other people (Kugiumutzakis, 1993; Meltzoff & Moore, 1983; Soussignan, Courtial, Canet, Danon-Apter, & Nadel, 2011). Yet careful examination indicates that imitation, occurring in live social contexts, is *interactive*. Studies of preverbal typical infants (Nadel, 1986; Nadel-Brulfert & Baudonnière, 1982; Nadel & Pezé, 1993) and nonverbal children with autism (Nadel, 2006; Nadel & Butterworth, 1999; Nadel et al., 2000) show that imitation has two sides to it: We imitate others, but others also imitate us. Imitation thus qualifies as social in the manner under this discussion.

But there is more. Our own studies (cited earlier) show that young children use imitation to initiate and maintain contact with their preverbal peers. That is, long before verbal

FIGURE 2. Coregulating synchrony.

communication becomes sophisticated, imitation provides us a medium for turn-taking and social synchrony that is integral to later verbal communication. Our experimental setting contained two identical sets of 10 attractive objects (e.g., umbrellas, hats, sunglasses, etc.; see Figure 2). Pairs of young acquainted children aged 2–4 years met in this setting, without an adult present, and were not given any special instructions. The children were free to use any of the objects in any manner they preferred. They could play with an individual item, or with combinations of items, that did or did not correspond to an item in the other child's possession, and the manner in which they used the objects was not externally constrained in any way. By far, the most frequent outcome, however, was picking up the same object that the other child had chosen and using it in the same manner as the other child. We stress that it is not important whether the acts imitated were already in the children's motor repertoire.

Although this process may have spawned acquisition of motor skills, according to the traditional view of imitation, whether or not the imitated acts were already in the imitator's motor repertoire is probably not the most important feature of these interactions. Lakin and Chartrand (2003) suggest that something more general and important is learned through imitative exchanges: The person who is imitated comes to understand the capacity to influence people, and reciprocal imitation cements social relationships by fostering liking and affiliation.

Also apparently critical to imitative exchanges is a fine-grained system of turn-taking. The synchrony in this system is temporally sensitive: A child who is late to perform tends to speed up while the partner slows down. The children alternate imitating and being imitated and employ role-reversing gestures to enforce turn-taking. For instance, a child may offer the partner an object that she or he has chosen as a way to take the floor and become the model. Overall, imitation incorporates synchrony and turn-taking and constitutes a system of communication.

Thus, it appears that imitation serves (a) the traditionally recognized function of promoting skill acquisition and (b) a previously unacknowledged communicative function. A particularly striking illustration of the communicative function can be seen in children with autism, who, although described as typically deficient in social interaction and often inattentive to others' social behaviors, are sensitive to being imitated. The critical experiment (Nadel et al., 2000) and replications (Field, Field, Sanders, & Nadel, 2001; Heimann, Laberg, & Nordöen, 2006) placed a child in a room with two identical sets of objects and an unacquainted adult. In the initial stage of the experiment, the adult sat still with an unexpressive face and no obvious sign of interest in the child, who proceeded to explore the room and its contents without obvious interest in the adult. A few moments later, the adult approached the child and began imitating the child's actions in a playful way. In some cases, the child began to imitate the adult's actions (if they were in the child's existing motor repertoire). When the adult returned to the still position, the child approached the adult, offering toys and showing signs of affection. This response shows that children with autism understand the social nature of an imitative exchange, expect the exchange to remain reciprocal, and benefit from the same imitation-driven cementing of social relationships that is seen in persons without autism.

Overall, our research documents that imitation involves social coordination taking place at minute time scales. This makes imitation a useful model for examining possible neural synchrony that occurs when individuals in a social interaction negotiate and coregulate complementary roles.

Brain Recordings During Reciprocal Imitation

Our studies employ imitation as a free interaction. The procedure allows partners to see each other's hand gestures through a double video arrangement (Nadel et al., 1999) while brain activity is recorded. Specifically, we modified the double video system depicted in Figure 1 to allow for interaction between a participant in an fMRI scanner and an experimenter outside the scanner room (see Figure 3).

Individual fMRI Findings. There were 23 healthy young women who participated in the scanner. They were scanned while performing hand gestures according to two conditions: free movement or instructed imitation. During free movement, the women were told that

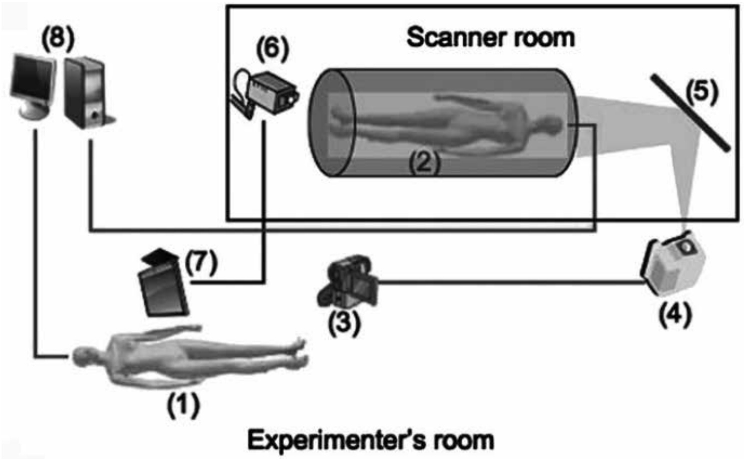

FIGURE 3. The fMRI imitation platform. Experimenter (1) and subject in the scanner (2) lay in the same position. The experimenter's hand movements were recorded by video camera (3) and, via a projector (4) outside the scanner room, displayed to the subject via a mirror behind the scanner (5). Subject's hand movements were recorded using an fMRI-compatible video camera (6) and displayed to the experimenter via a monitor (7). A computer (8) automatically delivered auditory instructions regarding start and end of blocks. Adapted from "Reciprocal imitation: Toward a neural basis of social interaction," by S. Guionnet, J. Nadel, E. Bertasi, M. Sperduti, P. Delaveau, and P. Fossati, 2012, *Cerebral Cortex*, *22*(4), pp. 971–978.

they could do what they liked with their hands, including performing their own gestures or imitating the gestures that they saw on the video monitor. During instructed imitation, subjects were asked to imitate the hand gestures shown on the monitor.

During free episodes, a frame-by-frame analysis of synchronized videos of the partners allowed movements to be categorized as imitation, modeling (being imitated), or own movement for comparison with corresponding brain activations. Imitation was recorded when the hand gestures of the two subjects showed a similar morphology (waving, swinging, describing a circle, etc.) and a similar direction (up, down, right, left, etc.). The subject initiating the gesture was identified as the model, and the follower was labeled the imitator. As we have found in our studies with children, the imitative behavior occurred frequently (about 77% of the time).

Periods of free movement and instructed imitation alternated in a counterbalanced order. Comparison of periods of imitation during free movement, to the instructed imitation condition, revealed a replication of previous findings suggesting the existence of an imitative neural network (Iacoboni et al., 1999; Molenberghs, Cunnington, & Mattingley, 2009) and also revealed involvement of the dorsolateral prefrontal cortex and other regions that are involved in social anticipation, thus verifying that imitation is an example of prospective social cognition. Our fMRI work thus supported the notion that imitation is a useful model for two-body neuroscience, but the results remained computed at the individual level.

EEG Hyperscanning Results. We have undertaken genuine two-body neuroscience using EEG hyperscanning methodology. Instead of a subject and an experimenter following a protocol, the dyads were composed of two unacquainted subjects seated in separate experimental cabins and viewing each other's hand gestures (see Figure 4, Panel A). For a fine-grained analysis of synchrony, imitation, and turn-taking, the free imitation blocks were analyzed with the ELAN software. Synchrony was assessed when the hands of the two participants started and ended a

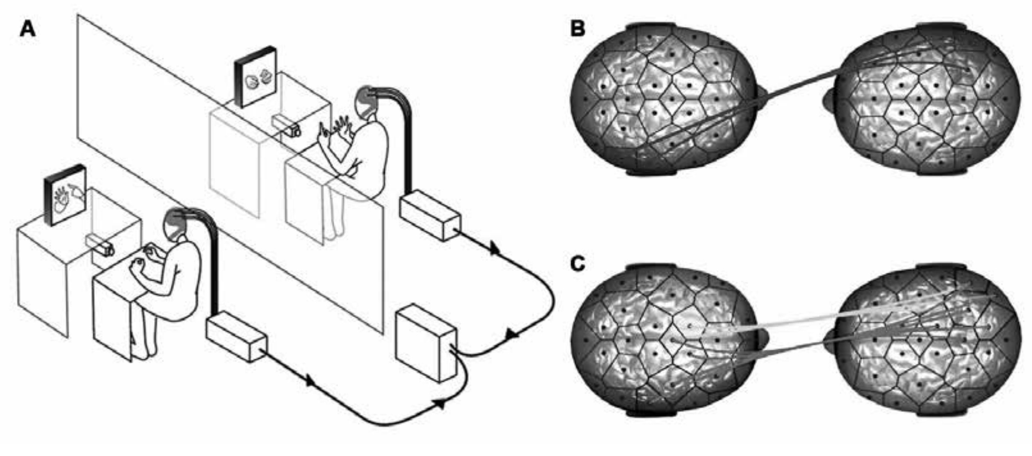

FIGURE 4. Panel A: schematic of the dual EEG/behavior platform. Panel B: interbrain synchrony in the alpha–mu band (8–12 Hz) between right centroparietal regions of the model (left) and imitator (right). Panel C: synchrony involving the beta (light grey lines, 13–30 Hz) and gamma (dark lines, 31–48 Hz) band clusters between frontocentral and right parietooccipital regions. Adapted from "Inter-brain synchronization during social interaction," by G. Dumas, J. Nadel, R. Soussignan, J. Martinerie, and L. Garnero, 2010, *PloS One, 5*(8), p. e12166.

gesture simultaneously thus showing a coordinated rhythm. Dyads engaged in imitation (i.e., made hand gestures of similar morphology) roughly 65% of the time and synchronized hand movements (i.e., gestures began and ended at the same time but did not necessarily share the same morphology) about 78% of the time. Within each dyad, we observed a spontaneous emergence of a balanced turn-taking between the role of model and imitator within each dyad.

EEG hyperscanning showed emergent synchronization of brainwaves in subjects who were engaged in spontaneous imitation with interactional synchrony (Dumas, Nadel, Soussignan, Martinerie, & Garnero, 2010). This interbrain relationship was strongly present in the alpha–mu frequency band where it symmetrically linked the right parietal regions of the two subjects (Figure 4, Panel B). Interestingly, the phi neuromarker of social coordination has been observed in this range of rhythmic activity at this same neural location (Tognoli et al., 2007). The relevant parietal regions have been traditionally associated with attentional processes (Battelli, Pascual-Leone, & Cavanagh, 2007; Battelli, Walsh, Pascual-Leone, & Cavanagh, 2008), temporal processing (Busch, Dubois, & VanRullen, 2009; VanRullen, Pascual-Leone, & Battelli, 2008), and sensorimotor information (Pineda, 2005). Interbrain synchronization of right parietal regions in this range of rhythmic activity suggest a link between interindividual coordination and the intraindividual temporal estimation and anticipation necessary for an effective alternation of roles (Wilson & Wilson, 2005).

Interbrain synchronization was also observed in higher frequency bands, although not between homologous brain regions (Figure 4, Panel C). In the model, frontal regions were implicated, perhaps reflecting planning and control (Miller & Cohen, 2001). In the imitator, activity was localized over parietooccipital regions, which usually are associated with visual perception of biological motion (Grèzes et al., 2001; Pavlova, Guerreschi, Lutzenberger, & Krägeloh-Mann, 2010). Finally, brainwaves of individuals differed depending on whether the individual was serving as model or imitator (Dumas, Martinerie, et al., 2012).

Discussion: Even Basic Social Interaction Involves Prospective Cognition

Social interaction is a special case of social cognition. Some forms of social cognition can take place without the interactive participation of a partner, as in an imagined conversation or the processing of social information from another's video-recorded speech. In these cases, the individual is the unit of analysis. In social interaction, however, a dyad is the foundation for emergent social phenomena. One cannot take turns without the agreement and collaboration of a partner. One cannot jointly focus attention without the coordinated attention of a partner. And one cannot develop behavioral synchrony without continuous and reciprocal temporal modulation involving a partner. Turn-taking, joint attention, and synchrony constitute three dynamic aspects of the embodied dyadic process of social interaction, and all three are exemplified in simple form by gestural imitation at the level of both the brain and behavior.

Our work on imitative interaction reveals symmetrical and asymmetrical neural activities during imitation, the latter of which differentiate the imitator from the model (see Figure 5). Our findings are consistent with the notion of a Mirror Neuron System (MNS), which assumes the use of similar parietofrontal network for perceived, imagined, and produced actions (Rizzolatti & Sinigaglia, 2010). The putative MNS has been suggested as the mechanism for grasping other individuals' motor goals and intentions. This system is thought to operate either alone (Becchio et al., 2010) or in conjunction with a mentalizing system, composed of the temporoparietal junction and the midline structures for inferential and reflective

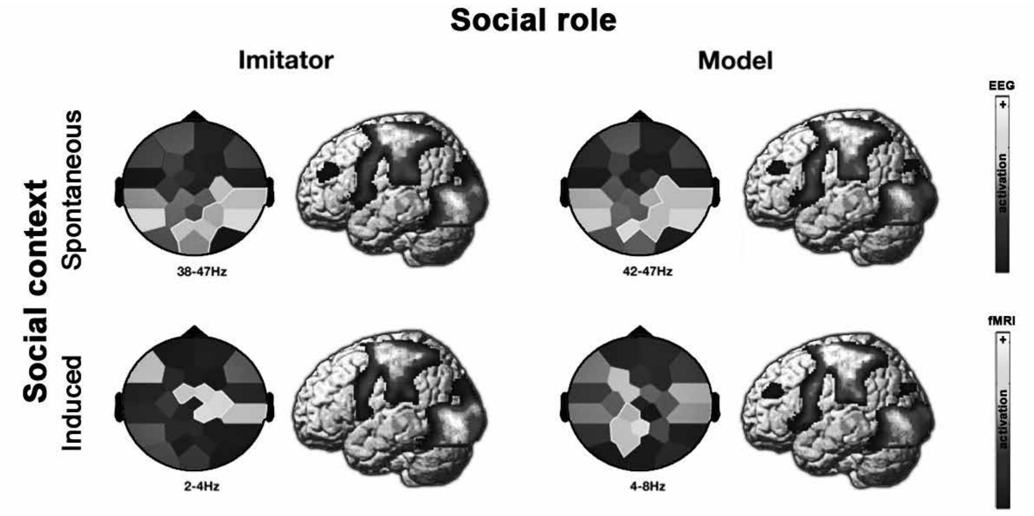

FIGURE 5. Dissociation of brain activities related to the social context and social role. During spontaneous imitation, the co-ownership of action in imitator and model is reflected by symmetric activation in the gamma frequency band over parietal regions. These effects are evident in results from EEG (2-D topographic maps; Dumas, Martinerie, et al., 2012) and fMRI (3-D brain reconstructions; Guionnet et al., 2012). Symmetry is absent during induced imitation, which produced topographical differences in delta/theta activity.

processes, that is activated when inferences are made about intentions referring to volitional or epistemic mental states (Amodio & Frith, 2006).

Our results contribute to the assumptions of MNS by showing a fine-grained temporal interplay of brain activities in areas implicated in motor planning and mentalizing during social perception. In a recent study of the functional connectivity of the mirror system, we found a strong coupling between the MNS and the mentalizing system for both imitating and being imitated conditions (Sperduti, Guionnet, Fossati, & Nadel, in press). Such coupling indicates an involvement of prospective cognition in the two partners, for the hallmark of mirroring systems is their involvement in both perception and planning. If two persons are "perceiving" each other during interaction, they are, in essence, mutually, continuously shaping one another's planning. Given such perception is in terms of planning, it entails an anticipatory edge that derives from the planning content. The perceptions are, in short, inherently prospective.

Phenomena such as turn-taking, joint attention, and synchrony are further consistent with the notions of prospective cognition (Critchfield & Jordan, 2014) because they are multiscale, in that they operate at various different organizational levels (Maturana & Varela, 1987; Thompson & Varela, 2001) simultaneously. In our hyperscanning studies, a bidirectional coupling emerged between the participants. The behavior of each influenced the behavior of the other, and interbrain synchronization reflected their cognitive entanglement. Such synchronization may facilitate the transmission of information between two interacting brains in much the same way communication occurs between interacting regions of a single brain. Similar processes may operate at the larger scale of collective cognition (Bahrami et al., 2010; Dumas, 2011; Kelso, Dumas, & Tognoli, 2013; Pérez-Escudero & de Polavieja, 2011; Woolley, Chabris, Pentland, Hashmi, Malone, 2010): Although each individual remains a separate entity at the physical level, a certain degree of similarity remains necessary at both biological (Dumas, Chavez, et al., 2012) and cultural (Allen & Williams, 2011) levels to allow the group interaction to emerge.

Our results are further consistent with the notions of prospective cognition, in that a critical component of any social interaction is a complementary, contingent oscillation between social roles. This means that if one person must be the model and the other must be the imitator, there needs to be asymmetric action processing in the interacting partners. However, this asymmetry must entail active coregulation (Fogel, 1993) because turn-taking requires anticipation of the other's pending switch in role. Our laboratory findings suggest this aspect of an ongoing social interaction should involve both the mirror and the mentalizing systems. The mirror system would be involved in the understanding and anticipation of action schemes leading to synchrony, whereas the mentalizing system would allow monitoring another's intention so as to produce fine-grained role switching. In functional terms, anticipation is at work at both scales and is the main organizer of the dynamic coproduction that is social interaction.

REFERENCES

Allen, M., & Williams, G. (2011). Consciousness, plasticity, and connectomics: The role of intersubjectivity in human cognition. *Frontiers in Psychology*, *2*, 20. http://dx.doi.org/10.3389/fpsyg. 2011.00020

Amodio, D. M., & Frith, C. D. (2006). Meeting of minds: The medial frontal cortex and social cognition. *Nature Reviews Neuroscience*, *7*(4), 268–277.

Babiloni, F., Cincotti, F., Mattia, D., Mattiocco, M., De Vico Fallani, F., Tocci, A., . . . Astolfi, L. (2006). Hypermethods for EEG hyperscanning. *Conference Proceedings: Annual International Conference of the IEEE Engineering in Medicine and Biology Society*. *1*, 3666–3669.

Bahrami, B., Olsen, K., Latham, P. E., Roepstorff, A., Rees, G., Frith, C. D. (2010). Optimally interacting minds. *Science, 329,* 1081. http://dx.doi.org/10.1126/science.1185718

Battelli, L., Pascual-Leone, A., & Cavanagh, P. (2007). The 'when' pathway of the right parietal lobe. *Trends in Cognitive Sciences*, *11*(5), 204–210.

Battelli, L., Walsh, V., Pascual-Leone, A., & Cavanagh, P. (2008). The 'when' parietal pathway explored by lesion studies. *Current Opinion in Neurobiology*, *18*(2), 120–126.

Becchio, C., Cavallo, A., Begliomini, C., Sartori, L., Feltrin, G., & Castiello, U. (2010). Social grasping: From mirroring to mentalizing. *NeuroImage*, *61*(1), 240–248. http://dx.doi.org/10.1016/j.neuroimage.2012.03.013

Bressler, S. L., & Kelso, J. A. (2001). Cortical coordination dynamics and cognition. *Trends in Cognitive Sciences*, *5*(1), 26–36.

Busch, N. A., Dubois, J., & VanRullen, R. (2009). The phase of ongoing EEG oscillations predicts visual perception. *The Journal of Neuroscience*, *29*(24), 7869–7876.

Condon, W. S., & Sander, L. W. (1974). Neonate movement is synchronized with adult speech: Interactional participation and language acquisition. *Science*, *183*(4120), 99–101.

Critchfield, T. S., & Jordan, J. S. (2014). Prospective cognition in education and enculturation: An overview. *Journal of Cognitive Education and Psychology*, *13*(2), 139–146.

De Jaegher, H. (2009). Social understanding through direct perception? Yes, by interacting. *Consciousness and Cognition*, *18*(2), 535–542.

Di Paolo, E., & De Jaegher, H. (2012). The interactive brain hypothesis. *Frontiers in Human Neuroscience, 6,* 163. http://dx.doi.org/10.3389/fnhum.2012.00163

Dumas, G. (2011). Towards a two-body neuroscience. *Communicative & Integrative Biology*, *4*(3), 349–352.

Dumas, G., Chavez, M., Nadel, J., & Martinerie, J. (2012). Anatomical connectivity influences both intra- and inter-brain synchronizations. *PLoS One*, *7*(5), e36414. http://dx.doi.org/10.1371/journal.pone.0036414.g008

Dumas, G., Martinerie, J., Soussignan, R., & Nadel, J. (2012). Does the brain know who is at the origin of what in an imitative interaction? *Frontiers in Human Neuroscience*, *6*, 128. http://dx.doi.org/10.3389/fnhum.2012.00128

Dumas, G., Nadel, J., Soussignan, R., Martinerie, J., & Garnero, L. (2010). Inter-brain synchronization during social interaction. *PloS One*, *5*(8), e12166.

Field, T., Field, T., Sanders, C., & Nadel, J. (2001). Children with autism display more social behaviors after repeated imitation sessions. *Autism*, *5*, 317–323.

Fogel, A. (1993). *Developing through relationships*. Chicago, IL: University of Chicago Press.

Fries, P. (2005). A mechanism for cognitive dynamics: Neuronal communication through neuronal coherence. *Trends in Cognitive Sciences*, *9*(10), 474–480.

Gallese, V., Keysers, C., & Rizzolatti, G. (2004). A unifying view of the basis of social cognition. *Trends in Cognitive Sciences*, *8*(9), 396–403.

Grèzes, J., Fonlupt, P., Bertenthal, B., Delon-Martin, C., Segebarth, C., & Decety, J. (2001). Does perception of biological motion rely on specific brain regions? *NeuroImage*, *13*(5), 775–785.

Guionnet, S., Nadel, J., Bertasi, E., Sperduti, M., Delaveau, P., & Fossati, P. (2012). Reciprocal imitation: Toward a neural basis of social interaction. *Cerebral Cortex*, *22*(4), 971–978.

Hari, R., & Kujala, M. V. (2009). Brain basis of human social interaction: From concepts to brain imaging. *Physiological Reviews*, *89*(2), 453–479.

Hasson, U., Nir, Y., Levy, I., Fuhrmann, G., & Malach, R. (2004). Intersubject synchronization of cortical activity during natural vision. *Science*, *303*(5664), 1634–1640.

Heimann, M., Laberg, K.E., & Nordöen, B. (2006). Imitative interaction increases social interest and elicited imitation in non-verbal children with autism. *Infant and Child Development*, *15*, 297–309.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical mechanisms of human imitation. *Science*, *286*(5449), 2526–2528.

Kelso, J. A. S., Dumas, G., & Tognoli, E. (2013). Outline of a general theory of behavior and brain coordination. *Neural Networks, 37,* 120–131. http://dx.doi.org/10.1016/j.neunet.2012.09.003

King-Casas, B., Tomlin, D., Anen, C., Camerer, C. F., Quartz, S. R., & Montague, P. R. (2005). Getting to know you: Reputation and trust in a two-person economic exchange. *Science*, *308*(5718), 78–83.

Kugiumutzakis, G. (1993). Intersubjective imitation in early mother-infant interaction. In J. Nadel & L. Camaioni (Eds.), *New perspectives in early communicative development* (pp. 36–59). London, United Kingdom: Routledge.

Lakin, J. L., & Chartrand, T. L. (2003). Using nonconscious behavioral mimicry to create affiliation and rapport. *Psychological Science*, *14*, 334–339.

Lindenberger, U., Li, S. C., Gruber, W., & Müller, V. (2009). Brains swinging in concert: Cortical phase synchronization while playing guitar. *BMC Neuroscience*, *10*(1), 22.

Maturana, H. R., & Varela, F. J. (1987). *The tree of knowledge: The biological roots of human understanding*. Boston, MA: Shambhala.

Meltzoff, A. N., & Moore, M. (1983). Newborn infants imitate adult facial gestures. *Child Development*, *54*, 702–709.

Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202.

Molenberghs, P., Cunnington, R., & Mattingley, J. B. (2009). Is the mirror neuron system involved in imitation? A short review and meta-analysis. *Neuroscience & Biobehavioral Reviews*, *33*(7), 975–980.

Montague, P. R., Berns, G. S., Cohen, J. D., McClure, S. M., Pagnoni, G., Dhamala, M., & Fisher, R. E. (2002). Hyperscanning: Simultaneous fMRI during linked social interactions. *NeuroImage*, *16*(4), 1159–1164.

Mundy, P., Kasari, C., & Sigman, M. (1992). Nonverbal communication, affective sharing, and intersubjectivity. *Infant Behavior & Development*, *15*, 377–381.

Murray, L., & Trevarthen, C. (1985). Emotional regulation of interactions between two-month-olds and their mother. In T. M. Field & N. A. Fox (Eds.), *Social perception in infants* (pp. 177–197). Norwood, NJ: Ablex.

Pérez-Escudero, A., & de Polavieja, G. G. (2011). Collective animal behavior from bayesian estimation and probability matching. *PlosOne Computationa Biology, 7,* e1002282.

Nadel, J. (1986). *Imitation et communication entre jeunes enfants.* Paris, France: Presses Universitaires de France.

Nadel, J. (2006). Does imitation matter to children with autism? In S. Rogers & J. Williams (Eds.), *Imitation and the development of the social mind: Lessons from typical development and autism* (pp. 118–137). New York, NY: Guilford Press.

Nadel, J., & Butterworth, G. (Eds.). (1999). *Imitation in infancy*. Cambridge, United Kingdom: Cambridge University Press.

Nadel, J., & Camaioni, L. (Eds.). (1993). *New perspectives in early communicative development*. London, United Kingdom: Routledge.

Nadel, J., Carchon, I., Kervella, C., Marcelli, D., & Réserbat-Plantey, D. (1999). Expectancies for social contingency in 2-month-olds. *Developmental Science, 2,* 164–174.

Nadel, J., Croué, S., Kervella, C., Mattlinger, MJ, Canet, P., Hudelot, C., . . . Martini, M. (2000). Do children with autism have expectancies concerning human behavior? *Autism, 4,* 133–145.

Nadel, J., & Pezé, A. (1993). What makes immediate imitation communicative in toddlers and autistic children? In J. Nadel & L. Camaioni (Eds.), *New perspectives in early communicative development.* London, NY: Routledge.

Nadel, J., Soussignan, R., Canet, P., Guillaume, L., & Gérardin, P. (2005). Two-month-old infants of depressed mothers show mild, delayed and persistent change in emotional state after non-contingent interaction. *Infant Behavior and Development, 4,* 418–425

Nadel-Brulfert, J., & Baudonnière, P. M. (1982). The social function of reciprocal imitation in 2-year-old peers. *International Journal of Behavioral Development, 5,* 95–109.

Pavlova, M., Guerreschi, M., Lutzenberger, W., & Krägeloh-Mann, I. (2010). Social interaction revealed by motion: Dynamics of neuromagnetic gamma activity. *Cerebral Cortex, 20*(10), 2361–2367.

Pfeiffer, U. J., Timmermans, B., Vogeley, K., Frith, C. D., & Schilbach, L. (2013). Towards a neuroscience of social interaction. *Frontiers in Human Neuroscience, 7,* 22. http://dx.doi.org/10.3389/fnhum.2013.00022

Piaget, J. (1962). *Play, dreams and imitation in childhood.* New York, NY: Norton.

Pikovsky, A., Rosenblum, M., & Kurths, J. (2003). *Synchronization: A universal concept in nonlinear sciences* (Vol. 12). Cambridge, United Kingdom: Cambridge University Press.

Pineda, J. A. (2005). The functional significance of mu rhythms: Translating "seeing" and "hearing" into "doing." *Brain Research Reviews, 50*(1), 57–68.

Rizzolatti, G., & Sinigaglia, C. (2010). The functional role of the parieto-frontal mirror circuit: Interpretations and misinterpretations. *Nature Reviews Neuroscience, 11*(4), 264–274.

Scheflen, A. (1982). Comments on the significance of interaction rhythms. In M. Davis (Ed.), *Interaction rhythms: Periodicity in communicative behavior* (pp. 13–32). New York, NY: Human Sciences Press.

Schilbach, L. (2010). A second-person approach to other minds. *Nature Reviews Neuroscience, 11*(6), 449.

Schippers, M. B., Roebroeck, A., Renken, R., Nanetti, L., & Keysers, C. (2010). Mapping the information flow from one brain to another during gestural communication. *Proceedings of the National Academy of Sciences, 107*(20), 9388–9393.

Soussignan, R., Courtial, A., Canet, P., Danon-Apter, G., & Nadel, J. (2011). Human newborns match tongue protrusion of disembodied human and robotic mouths. *Developmental Science, 14,* 385–394. http://dx.doi.org/10.1111/j.1467-7687.2010.00984.x

Soussignan, R., Nadel, J., Canet, P., & Gérardin, P. (2006). Sensitivity to social contingency and positive emotion in 2-month-olds. *Infancy, 10,* 123–144.

Sperduti, M., Guionnet, S., Fossati, P., & Nadel, J. (in press). Mirror Neuron System and Mentalizing System connect during online social interaction. *Cognitive Processing.*

Stern, D. (1977). *The first relationship: Infant and mother*. Cambridge, MA: Harvard University Press.

Thompson, E., & Varela, F. J. (2001). Radical embodiment: Neural dynamics and consciousness. *Trends in Cognitive Sciences*, *5*(10), 418–425.

Tognoli, E., Lagarde, J., DeGuzman, G. C., & Kelso, J. A. (2007). The Phi complex as a neuromarker of human social coordination. *Proceedings of the National Academy of Sciences*, *104*(19), 8190–8195.

Tomasello, M. (1999). *The cultural origins of human cognition*. Cambridge, MA: Harvard University Press.

Trevarthen, C. (1977). Descriptive analyses of infant communicative behaviour. In H. R. Schaffer (Ed.), *Studies of infant-mother interaction. The Loch Lomond Symposium*. (pp. 227–270). London, United Kingdom: Academic Press.

VanRullen, R., Pascual-Leone, A., & Battelli, L. (2008). The continuous wagon wheel illusion and the ‘when’ pathway of the right parietal lobe: A repetitive transcranial magnetic stimulation study. *PloS One*, *3*(8), e2911.

Varela, F. J. (1984) Two principles for self-organization. In H. Ulrich & G. Probst (Eds.), *Self-organization and management of social systems* (pp. 25–33). Berlin: Springer Verlag.

Varela, F. J., Thompson, E. T., & Rosch, E. (1991). *The embodied mind: Cognitive science and human experience*. Cambridge, MA: MIT Press.

Varela, F., Lachaux, J. P., Rodriguez, E., & Martinerie, J. (2001). The brainweb: Phase synchronization and large-scale integration. *Nature Reviews Neuroscience*, *2*(4), 229–239.

Wilson, M., & Wilson, T. P. (2005). An oscillator model of the timing of turn-taking. *Psychonomic Bulletin & Review*, *12*(6), 957–968.

Woolley, A. W., Chabris, C. F., Pentland, A., Hashmi, N., Malone, T. W. (2010). Evidence for a collective intelligence factor in the performance of human groups. *Science, 330,* 686. http://dx.doi.org/10.1126/science.1193147

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