Chapter 5

Social Perception: Understanding Other People's Intentions and Emotions through their Actions

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Since most of the natural behavior of higher primates takes place within the context of social interactions, it is of interest to study the neural encoding of high-level social features, such as the emotional states or intention of another individuals. (Brothers, Ring, & Kling, 1990, p. 199)

Perceiving Other People's Actions and Motor Resonance

Humans are adapted to living in social groups with complex patterns of social interactions. Understanding the meaning of other people's behavior is an essential aspect of human communication, and a large amount of our daily life is spent watching and interpreting the actions of others (Barresi & Moore, 1996). The neural mechanism underlying our ability to represent others' goals by the mere observation of their motor actions has been the target of considerable research. Behavioral experiments had suggested that the system for generating and representing actions is also used in the perception of actions (Knoblich & Prinz, 2001). This approach was strengthened by the discovery of "mirror" neurons in the macaque monkey brain, a class of neurons found in the parietal and the premotor cortex. They were seen to discharge not only when the monkey performed an action but also when the monkey was observing an experimenter or another monkey performing the same action (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992). Similarly, neuroimaging studies in humans have revealed parietal (PAR) and premotor (PM) activations both during execution and action observation, suggesting that action observation automatically triggers action representations (Grèzes, Armony, Rowe, & Passingham, 2003). The superior temporal sulcus (STS), involved in the perception of biological movements and in the observation of actions made by different body parts, was also active (Allison, Puce, & McCarthy, 2000). Finally, the correspondence between perception and action was shown to be somatotopically

organized (Aziz-Zadeh, Wilson, Rizzolatti, & Iacoboni, 2006; Buccino et al., 2001; Gazzola, Aziz-Zadeh, & Keysers, 2006). Taken together these results provide support for the notion that, when one observes the action of another, the motor program of the observed action is activated in the observer's brain, thereby suggesting that the observer uses his or her own motor system to perceive the action of others.

Influence of the observer's motor abilities and of social relevance

Motor resonance seems to exist only for movements that respect the biomechanical constraints of our body, imposed by our skeleton and articulations, and that we are able to produce ourselves. Shiffrar and Freyd (1993) showed that it was possible to influence the subject's perception by varying the time of presentation between pictures of body positions. For instance, the first picture showed a person whose right forearm was over the left, while in the second picture the left was over the right. Under appropriate time conditions, observers reported seeing indirect trajectories that respected biomechanical constraints (for example, the left forearm turned around the right forearm), whereas, under shorter inter-stimulus intervals, subjects perceived direct and therefore biomechanically impossible trajectories (for example, the left forearm crossed the right forearm). Using positron emission tomography (PET), Stevens et al. (2000) investigated whether a change in brain activity accompanies this perceptual shift and demonstrated that premotor and parietal cortex were involved only during the perception of a biomechanically possible movement. Along similar lines, Buccino et al. (2001) observed less motor resonance when participants viewed images of actions by non-conspecifics. These findings suggest that the brain system for action representations is selectively tuned to process actions that conform to the biomechanical and the joint constraints of normal human movement.

A person's motor repertoire is constrained not only by human musculoskeletal anatomy but also by the skills that have been acquired and honed over time. For example, the motor simulation process is influenced by the individual motor abilities of each observer. During the first recordings in monkeys, mirror neurons discharged when the monkey observed a grasping action performed by the hand of an experimenter, but were silent if the same action was performed with a tool (Rizzolatti, Fogassi, & Gallese, 2001), an action that is not present in the motor repertoire of the monkey. This result suggests that action representations cannot strictly be based on observation alone, without concomitant motor action. To test this hypothesis, Grammont et al. (2006) trained their monkeys to grasp an object with a tool. They showed that the mirror neurons discharged to this type of action only after motor training, and that the responses were specific to the trained action and did not generalize to other tools. In humans, Reid, Belsky, & Johnson (2005) investigated individual differences in the development of the ability to perceive human action in 8-month-old infants. Their results clearly show that only young infants with relatively well-developed motor skills perceive the differences between possible versus impossible human movements. As for adults, functional magnetic resonance

imaging (fMRI) was used to study differences in brain activity between watching an action that one has learned to do and an action that one has not (Calvo-Merino, Glaser, Grèzes, Passingham, & Haggard, 2005). Greater activations in STS, PAR, and PM where observed when expert dancers viewed movements that they had been trained to perform compared to movements that they had not. This effect could not be explained by visual familiarity (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006). To conclude, during action observation, there is activity in the parietal and premotor cortex as the subject internally simulates perceived movements, but the extent and level of activity within those regions will be constrained by the observer's motor abilities.

Finally, a recent paper by Kilner, Marchant, & Frith (2006) elegantly demonstrated that the activity during action observation is also modulated by social relevance – that is, by the degree of interaction between the actor and the observer. There is a modulation of activity only when the actor is facing the observer, and not when the actor is facing away.

Functions and possible limitations of motor resonance

This mechanism of shared motor representations was proposed as the basis of action understanding (Gallese, Keysers, & Rizzolatti, 2004; Grèzes & Decety, 2001; Iacaboni, 2005; Jeannerod, Decety, & Michel, 1994; Rizzolatti et al., 2001), and more recently it was suggested that it plays a role in action prediction (Csibra, 2007; Flanagan & Johansson, 2003; Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004; Knoblich, Seigerschmidt, Flach, & Prinz, 2002). Fogassi et al. (2005), for example, demonstrated that the discharge of mirror neurons in monkeys during the observation of an act (grasping an object) is influenced by the type of act that follows it (for example, eating the food or putting it aside). Thus, these neurons not only code observed actions but also allow prediction of the next step of an action. In humans, the higher motor facilitation when subjects perceived the still picture of a hand caught in an ongoing but as yet incomplete grasping action pleads in favor of a role of motor simulation in anticipating the actions of others (Urgesi, Candidi, Ionta, & Aglioti, 2006). According to Gallese (2006), the mechanism of motor simulation could participate in interpreting the simple intentions of others.

Indeed, social interactions are less simple and less predictable than interactions between physical objects. Using transcranial magnetic stimulation, Gangitano, Mottaghy, & Pascual-Leone (2004) studied the observation of predictable and unpredictable grasping movements in human subjects. The profile of cortical excitability suggested that a motor representation of the perceived action was activated as soon as the action started. However, once it had been activated, it tended to proceed toward its completion, regardless of whether the end of the action was the same or not – that is, was predictable or unpredictable. Furthermore, using fMRI, we scanned subjects while they watched alternate videos of themselves and of others lifting a box, and judged whether the actors had a correct (predictable action) or false expectation (unpredictable and accidental action) about the weight of the box.

A parietal-premotor circuit, which reflects motor simulation, was activated during action perception. Still, the activity within this circuit did not dissociate unpredictable from predictable actions (Grèzes, Frith, & Passingham, 2004a. These results support the idea that the internal simulation of a perceived action plays a crucial role in predicting how the perceived movement will continue. But they also suggest that the motor simulation process does not dissociate intended from unintended actions or predictable from unpredictable ones and therefore may not be sufficient to understand the complex intentions of other people during social interactions. Still, it is suggested that the mirror neuron system, originally found in motor-related areas, could play an important role in social cognition (Gallese, 2006; but see Sommerville & Decety, 2006, for a discussion).

Understanding Other People's Intentions and Emotions from their Actions

The term "social cognition" proposed by Brothers (1990) is defined as "the processing of any information which culminates in the accurate perception of the disposition and intentions of other individuals." Premack (1978) coined the notion of "theory of mind," thereby referring to a hypothetical mental mechanism whereby social agents attribute mental states to each other. Since the mid-1990s, developmental psychology, social psychology, and neuroscience have investigated this ability (see reviews by Frith & Frith, 2003; Frith & Frith, 2006), using mostly verbal and static stimuli. Brain regions involved in the ability to infer mental states to others that have come to the foreground are the STS, the amygdala (AMG), the medial prefrontal cortex (MPFC), the anterior cingulate cortex (ACC), and the orbitofrontal cortex (OFC) (see review by Gallagher & Frith, 2003). These regions figure prominently as components of the social brain (Brothers 1990). The research on theory of mind has developed in parallel and independently from the research on action understanding. None of the experiments had explored the ability to understand mental states through the observation of dynamic human behavior, and therefore the question whether motor simulation sustains mental states attribution remains.

Violation of expectations

Subjects were scanned while watching videos of actors lifting a box. They were asked to judge whether the action reflected a correct or a false expectation of the weight of the box (Grèzes, Frith, & Passingham, 2004a or the intent to deceive about the weight of the box (Grèzes, Berthoz, & Passingham, 2006; Grèzes, Frith, & Passingham, 2004b). We found activations in the parietal and premotor cortex, suggesting that motor simulation was involved. However, when the subjects judged that the actors had a false expectation or an intent to deceive, there was also activity bilaterally in the STS, lateral orbitofrontal, and cingulate cortex. The inference that the

actor was trying to deceive or had a false expectation was the difference between a prediction made by the observer and the action as perceived. People have a bias to judge other people's behavior as truthful (Levine, Park, & McCornack, 1999) and of attributing true beliefs to others' understanding of information (Bartsch & Wellman, 1995) that influence their predictions. The same biases were observed in our studies. Thus, the activations listed above may relate to the violation of the subject's prediction. In the STS, it was demonstrated that, when an observer's prediction was violated, the activity was higher compared with the situation in which the observer's predictions were met (Pelphrey, Singerman, Allison, & McCarthy, 2003; Saxe, Xiao, Kovacs, Perrett, & Kanwisher, 2004). The cerebellum may play a key role in signalling sensory discrepancy between predicted and actual consequences of movements (Blakemore, Frith, & Wolpert, 2001). Finally, activity in the orbital frontal cortex, as well as in the STS, has been reported when subjects perceived a mismatch between what they expected and what actually happened (Downar, Crawley, Mikulis, & Davis, 2001). We conclude that activations in the STS, cerebellum, and orbitofrontal cortex are best explained as reflecting the violation of the predictions made by the observer. When predictions are violated, the observer must update his or her representation of the mental state of the actor.

Communicative intent and personal involvement

Action observation can produce a strong emotional response, and can potentially induce or modify an observer's behavior, particularly when the content of the perceived action is directed at the observer him or herself. For example, it is particularly important to be able to distinguish whether a person is being honest or deceitful. Investigating this issue, we observed that communicative intent (deceit versus false expectation) and personal involvement influence the neural responses associated with the detection of deceit. Activations in the MPFC and AMG were found only for communicative intent as compared to non-communicative actions (Grèzes, Frith, & Passingham, 2004b. In the second study (Grèzes, Berthoz, & Passingham, 2006), subjects judged whether actors had been deceived about the real weight of a box. Personal involvement was manipulated by having the participants themselves among the actors. The STS and anterior cingulate cortex were activated irrespective of whether the participants detected that they themselves had been deceived by the experimenter or whether the other person had been misled. In contrast, the crucial factor determining AMG activation is subjective involvement, as there was activity in the AMG only in the condition in which participants observed themselves being deceived. The amygdala is said to play a key role in fast and automatic evaluation of the social significance of an event – for example, when the event constitutes a potential threat (Adolphs, 2003; Dolan, 2002). More importantly, Gloor (1972) reported that AMG stimulation induces subjective experiences of behavioral attitudes of others that the patients perceive as being directed at them (Gloor, 1972, cited by Brothers, 1990). However, Berthoz, Grèzes, Armony, Passingham, & Dolan (2006) contained judgments that were about social deception. We interpret the

activation of the AMG in this situation as reflecting the greater emotional reaction elicited when the deceived one is oneself. In the same vein, we found more activity in the AMG when participants read stories narrating their own as opposed to others' intentional transgression of social norms (Berthoz et al., 2006).

These results suggest that, while simulation can be a predictive mechanism playing a role in the implicit understanding of other people's dispositions, mental states attribution also involves other brain areas that are part of a neural system underpinning the social brain. Prominent among these are the brain areas that process the type of action, its social context, and the observers' personal involvement.

Emotional contagion and motor simulation

If we grant that simulation may play a role in social cognition, it is also likely to be involved in perceiving actions that have a strong emotional component. It was demonstrated that a mechanism of shared representations, originally found in the motor-related areas, applies to emotions and sensations. The same brain areas (for example, the insula and anterior cingulate cortex) are involved when subjects experience disgust (Wicker et al., 2003) or pain (Jackson, Meltzoff, & Decety, 2005; Singer et al., 2004), and when they observe someone else experiencing the same emotion. Also, observing someone being touched elicits activity in the same area of the somatosensory cortex as being touched oneself (Blakemore, Bristow, Bird, Frith, & Ward, 2005; Keysers & Perrett, 2004). Thus, a direct and implicit form of understanding others is achieved by embodied simulation (Gallese, 2006). This ability to share other people's emotions facilitates social communication and social coherence, and may be at the origin of altruistic behavior and cooperation (see the review by de Vignemont & Singer, 2006).

But there is also support in the literature for a second mechanism involving both the action and the emotion circuits. Recent neuroimaging data show that perceiving emotional facial and body expressions presented as video films elicits activations both in the regions underlying motor representations (the premotor cortex) and also in the regions involved in emotional processing (the AMG) (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003; Decety & Chaminade, 2003; de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Grèzes, Pichon, & de Gelder, 2007; Grosbras & Paus, 2006; Sato, Kochiyama, Yoshikawa, Naito, & Matsumura, 2004). It is, however, an open question whether the critical factor for understanding actions with an emotional component is the activity within motor-related areas as such (the mirror system) or the interaction between the emotion-processing areas and an action-related network. One explanation for enhanced activation in the premotor cortex for dynamic expression of emotion is that, when dynamic fear bodies are being viewed, an important priority for the brain is to represent the perceived emotional action. This would be in line with the findings of Adolphs, Tranel, and Damasio (2003) that patient B with extensive lesion of the ventral pathway, which includes the AMG, is able to recognize emotions from a dynamic facial expression

but not from a static one. A second possible explanation takes into account that emotions are adaptive in the sense that they prepare the organism for a behavioral response to the current environment (Darwin, 1872; Lazarus, 1991; LeDoux, 2000; Panksepp, 1998). The enhanced activation in the premotor cortex could be due to the fact that the perception, for example, of a fear stimulus (whether this is a sound, face, or body) triggers a fear reaction in the observer that is based on activation of a fear motor program encoded in subcortical and cortical circuitry (Tomkins, 1963) and does not involve mirror neurons. Further investigations are needed to disentangle whether the activations detected in motor-related areas during the perception of emotional action reveal either the motor simulation of the action perceived or the preparation of the motor response that would be appropriate to the situation.

To conclude this section, starting from the postulate that the resonance phenomenon plays a role in social cognition, it is probably just a step in the chain of components necessary for adaptive behavior to the physical and social environment. Moreover, for this contagion mechanism to have explanatory value, its relationships with the other components must be clarified. This issue is *a fortiori* important to explain whether a dysfunction of the mirror system can influence the problems of communication and social interaction observed in autistic syndromes.

Implication for Autism and Conclusion

Autism is a complex disorder that is heterogeneous in its phenotypic expression and its etiology. Nonetheless, it is usually defined on the basis of common symptoms, and its core deficit is in poor social communication, a lack of imagination, the inability to understand others as intentional agents, a lack of empathy, imitation deficits, and stereotypical behaviors. These socio-cognitive deficits may be related to structural and functional abnormalities of many brain areas of the social brain: the STS, the AMG, the OFC, and the ACC (e.g. Abell et al., 1999; Baron-Cohen et al., 2000; Boddaert & Zilbovicius, 2002), and more recently with the mirror system (Hadjikhani, Joseph, Snyder, & Tager-Flusberg, 2007; Williams, Whiten, Suddendorf, & Perrett, 2001). There are currently many lines of research on the possible causes of impaired social communication and of deficits in processing emotional cues. Briefly, some authors think the social deficit could be a consequence of an AMG dysfunction, leading to functional abnormalities that impair the ability to detect socially relevant visual cues (Baron-Cohen et al., 2000). Another model speculates that this impairment may be the consequence of a malfunctioning mirror system (Williams et al., 2001), generating a deficit in the ability to represent the actions of others, and impairing higher-level cognitive functions involved in building intersubjectivity (Gallese, 2001).

Three recent studies have shown, however, that, in high-functioning individuals with autism, the system matching observed actions onto representations of one's

own action is intact in the presence of persistent difficulties in higher-level processing of social information (Grèzes, Wicker, & de Gelder, forthcoming; Magnée, Stekelenburg, de Gelder, van Engeland, & Kemner, 2005; Sebanz, Knoblich, Stumpf, & Prinz, 2005). This raises doubts about the hypothesis that the motor contagion phenomenon – "mirror" system – plays a crucial role in the development of socio-cognitive abilities. One possibility is that this mirror mechanism, while functional, may be dissociated from socio-affective capabilities. In healthy subjects, a co-activation of those regions underlying motor resonance, on the one hand, and emotional processing (de Gelder, Snyder, Greve, Gerard, & Hadjikhani, 2004; Grèzes, Wicker, & de Geldre, forthcoming) or detection of intentions, on the other (Grèzes, Frith, & Passingham, 2004a, 2004b) is observed. A dissociation between these two mechanisms in autistic subjects seems plausible in the light of studies reporting problems in information processing at the level of the STS and the AMG (Boddaert et al., 2004; Castelli, Frith, Happé, & Frith, 2002) and problems in connectivity between these two regions. The superior temporal sulcus is, indeed, a brain region common to these three domains of motor and emotional contagion as well as intention detection. The data on the motor contagion for emotional expressions in autistic subjects do not address the issue of the feelings and emotional consciousness of these subjects, and the available results on the emotional contagion in autistic subjects are contradictory (Blair, 2003). Interactions between neural structures implied in intention and emotion recognition through action are an important topic for future research.

Finally, future studies also need to address the issue of variability between individuals, which is considerable (Frith, 2001) but is rarely taken into account in mind-reading tests or in neuroimaging studies using small samples. Correlation analyses between structure, function, and behavior will undoubtedly provide useful information for a better definition of neuro-cognitive phenotypes associated with inadequacy in everyday social relations that are the core deficit in autism, as well as for other psychiatric pathologies (for example, schizophrenia and personality disturbances) and degenerative neurological disorders (for example, fronto-temporal dementia). In the future a better characterization of these phenotypes will contribute significantly to more focused investigations into the genetic basis of these diseases (Leboyer Jamain, Betancur, Mouren-Siméoni, & Bourgeon, 2002) and for the development of therapeutic approaches (Baranek, 2002). More generally, an understanding of the cerebral mechanisms involved in the development of intersubjectivity in healthy subjects and of low-level mechanisms of social interactions is of great social relevance and promises new insights in these complex abilities.

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