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9

# Embodied Simulation: A Conduit for Converting Seeing into Perceiving

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Flipping through the content of Goldstein's (2007) *Sensation and Perception* popular textbook for undergraduate psychology courses, one finds nine chapters on visual perception. In them, one can read about the Nobel Prize winning discovery of orientation and ocular dominance columns (Hubel & Wiesel, 1959) and about the dorsal ("what") and ventral ("where") pathways in the brain (Ungerleider & Mishkin, 1982), as well as learn many detailed facts about basic shape, color, and motion processing. After reading this text, an undergraduate student may conclude that they now know all there is to know about visual perception. However, this undergraduate would mistakenly equated seeing with perceiving. In fact, in an often-repeated anecdote, Francis Crick jokingly complained that modern researchers are so focused on the lower vision that they stopped caring about what people actually perceive.

There is a famous philosophical puzzle that speaks to the dissociation of pure seeing (arguably an end result of the well-studied visual pathways originating in the retina and culminating in the inferior temporal and posterior parietal cortices) and perceiving (arguably an end result of more complex processing involving systems spread throughout the entire brain). The question is this. Imagine Mary, who is a color-blind. But Mary is a color-vision specialist. She is an expert on all aspects of color vision: the physics of light waves; the absorption and reflectance properties of surfaces; the physiology of the eyeball; the function of the rods and cones, optic nerve, and color processing areas of the brain. However, Mary herself has never experienced color. So, does she really know what it is like to see red? Jackson (1986) proposed that the theory–experience gap would preclude Mary from understanding the internal qualia, or mental content, of the experience of seeing red.

This theoretical scenario highlights the importance of an individual's own experiences in visual perception of even the most basic property. This is the main tenet of embodied perception, which claims that the process of perceiving an object, person, or scene relies on the same neural systems that process the

experience of what is observed. Though embodied perception can be demonstrated with elementary quale (e.g., color) that may require at least an implicit representation of an embodied "self" to experience the perception, it's perhaps more intuitive to consider its uses in social perception – the visual perception of another person. It is here that the insufficiency of Goldstein's portrayal of visual perception is most clearly demonstrated.

Thus, despite its mysterious absence from basic textbooks on perception, we will suggest herein that our own embodied knowledge critically contributes to that visual perception of social stimuli. Further, we will suggest that perception is more than simply seeing; it is understanding the meaning of what is seen. Though some stimuli such as inanimate objects can be, and are likely, processed in a disembodied fashion, embodied processing most clearly contributes to the perception of social stimuli. Whereas disembodied processes, for example, tell you that the man in front of you just tripped and now his face is turning red, it is embodied processing that allows you to understand his embarrassment. And although the visual system will tell you, for example, that the woman at the bar is moving her hand through her hair and moving her mouth in an upward direction, it is embodied processing that allows you to understand that she is flirting with you.

Clearly this type of perception (social perception) goes well beyond the capacity of basic visual processing. In this chapter we will discuss what is meant by embodied processing. We will also discuss behavioral, electrophysiological, and neuroimaging evidence for embodied perception. We will conclude by discussing why simulation and mirroring processes are critical for social perception and what deficits arise when embodied perception goes awry.

## EMBODIED AND DISEMBODIED THEORIES OF PERCEPTION

A thorough review of the history and debates between embodied (often referred to as modal) and disembodied (often referred to as amodal) approaches to perception is beyond the scope of this chapter. Still, it is helpful to briefly introduce some basic ideas and conceptual distinctions. The ideas of embodied cognition have a long history in philosophy (Heidegger, 1962; Merleau-Ponty, 1963). Yet, until recently, psychological theories of perception have been largely disembodied. The proponents of disembodied perception argue that the goal of vision is to create a detailed model of the world in front of the perceiver (Marr, 1982). The creation of this final model occurs via a set of fairly encapsulated, modular, hierarchical, mostly bottom-up processes (for a critique, see Churchland, Ramachandran, & Sejnowski, 1994). Further, to interact with higher cognitive processes, such as thought and language, the visual representation must be "transduced" into amodal (digital-like) symbols that are separate from its sensory origins and bear no analogical relationship to the experienced event (for a review see Fodor, 1975).

The embodiment theories arose as an alternative to such symbolic, hierarchical accounts of information processing. Their proponents argue that visual processing, language, thought, and behavior are intrinsically intertwined (for a review

see Barsalou, 1999, 2008). Gibson, an early embodied theorist, writes: "we must perceive in order to move, but we must also move in order to perceive" (Gibson, 1979, p. 223). Thus, low-order as well as high-order processing relies on modalities – perceptual, somatosensory, introceptive, and motor resources (Barsalou, 1999, 2008; Glenberg & Robinson, 2000; Prinz, 2002; Wilson, 2002). In this account, modalities are a critical part of "online" cognition (perceiving and understanding the present stimulus) as well as "offline" cognition (thinking about the absent stimulus). A notion shared by many embodiment theories is that recruitment of somatosensory resources often involves "embodied simulation" (Gallese, 2003). "Simulation" can be thought of as the offline projection of a perceived stimulus back onto the observer's own motor, cognitive, and emotional representations. Thus, the mechanisms by which we understand states of others overlap with mechanisms by which we experience those states ourselves.

It is now accepted by most that the typically developing human brain is capable of both embodied and disembodied perception. We will argue that specific properties of stimuli determine whether it will be processed in an embodied or disembodied fashion. Specifically, objects that offer an opportunity for interaction (either social or physical) will likely be processed in an embodied way, whereas those that do not offer an opportunity for interaction will be processed in a disembodied fashion. The concept of "opportunity for interaction" is most aptly described in the writings of Gibson in his *The Ecological Approach to Visual Perception* (1979). Gibson writes: "Each thing says what it is . . . a fruit says Eat me; water says Drink me; and woman says Love me . . . the postbox invites the mailing of a letter, the handle wants to be grasped, all things tell us what to do with them" (Gibson, 1979, p. 138). Gibson's concept of "affordances" or the concept of the perception of what a stimulus offers for interaction set the stage for embodied theories of perception. However, how can one perceive things that do not offer any opportunity for interaction?

Though this review highlights the benefits of embodied perception, especially as it pertains to social stimuli, it is clear that the perception of certain stimuli is inherently disembodied. Specifically, certain stimuli, such as sunsets, do not offer any opportunity for physical interaction and thus are unlikely to involve embodied processes at the stage of construing a visual percept, though perhaps not an emotional response that makes the red colors of sunsets "impressive", or "haunting" (Slater, 1997). Additionally, certain inanimate objects (such as components of a complex machine), which do not afford direct interaction, are thought to be processed in a disembodied fashion (Martin & Weisberg, 2003). Thus, in this chapter, we do not claim that *all* perception is embodied, but rather that embodiment provides a strategy for perception of socially relevant animate stimuli that allows the observer to go beyond just a representation of basic physical attributes of the stimulus.

Embodied cognition is thought to be most involved in processing of two classes of stimuli: inanimate objects that are associated with specific actions by the perceiver, and, more importantly, animate stimuli. Note that the actions of mechanical objects can be successfully predicted based on their physical characteristics and physical laws – using processing sometimes termed "systemizing"

(Baron-Cohen, 2002). However, this processing is not sufficient for understanding animate stimuli, and especially human behaviors. After all, those behaviors are motivated by internal states that typically do not follow mechanistically predictable patterns – requiring processing sometimes called "empathizing" (Baron-Cohen, 2002). Thus, many researchers have proposed an embodied account of human perception (Barsalou, 1999; Gallagher & Meltzoff, 1996; Gallese, 2001; Gallese & Goldman, 1998; Meltzoff & Moore, 1995). Though each researcher uses his or her own terminology, all generally claim that the understanding of human actions and internal states relies on both the capacity of the observer to perceive other humans as "like me" and the capacity to simulate the observed actions and internal states of other humans within the observer's own motor, cognitive, and emotional representations.

This embodied account proposes that when typically developing individuals perceive another person in a certain situation, they will automatically and unconsciously project that perception back onto their own motor, cognitive, and emotional representations in order to run an offline simulation (Gallese, 2003). This offline simulation, in turn, allows individuals to create an embodied understanding of the observed person's behaviors, thoughts, and feelings.

To understand why certain inanimate objects also result in embodied processing, we return to Gibson's pioneering work where he writes: "The observer who does not move, but only stands and looks is not behaving at the moment, it is true, but he cannot help seeing the affordances for behavior in whatever he looks at" (Gibson, 1979, p. 223). Through embodied perception, certain objects that the observer is capable of interacting with will automatically activate the motor representation associated with that interaction, thus facilitating the appropriate behavioral response to the perceived object. Indeed, there is direct neurophysiological evidence for this. A certain class of neurons, "canonical neurons" (see below), will fire not only when a monkey or a person reaches out to grasp an object, but also on the visual perception of that object.

In summary, we suggest that the world is perceived through two complementary mechanisms. Disembodied perception is used when observing inanimate objects and scenes that do not allow direct interaction, while embodied perception is utilized for perceiving animate stimuli and objects that are associated with specific actions. Thus, as it pertains to social stimuli, the embodied account proposes that when observers perceive a social scene, they will automatically and largely unconsciously project that perception back onto their own motor, cognitive, and emotional representations in order to run a simulation (Gallese, 2003). This simulation, in turn, allows the observer to create an embodied understanding of the observed person's behaviors, thoughts, and feelings (Barsalou, 1999, 2008).

## EVIDENCE FOR EMBODIED PERCEPTION

Thus far, this chapter has presented theoretical and philosophical considerations motivating the embodied account of social perception. In this section we will describe some empirical evidence for embodied processing. The embodied

account's claim that perception and experience share underlying representations makes two related predictions. First, perception and action should share an underlying neural circuitry. Second, perception should result in matching responses in the observer.

Behavioral investigations, as early as the informal observations performed by Darwin, indicate that when individuals are in the presence of others, the observer tends to synchronize his or her movements to match those of the others (Condon & Ogston, 1967; Darwin, 1872/1965; Kendon, 1970). Early behavioral studies show that mothers tend to open their mouths when their infant is feeding (O'Toole and Dubin, 1968) and infants mimic some mouth movements of the adults around them (Meltzoff and Moore, 1977). Imitation, however, is not limited to mouth movements. Specifically, people tend to mimic others' gestures and body postures (Chartrand & Bargh, 1999) and emotional facial expressions (Dimberg, 1982; Dimberg, Thunberg, & Elmehed, 2000; Wallbott, 1991).

In addition to behavioral studies, the existence of embodied processes during visual perception is substantiated by electrophysiological and neuroimaging studies that have recorded neural responses during visual perception and found activations in motor and somatosensory regions during visual perception of human actions and sensations. These studies have extended the knowledge beyond what behavioral studies are capable of and have given insight into the brain basis of embodied perception.

Electroencephalography (EEG) studies from as early as 1954 demonstrated neural activity in the region of sensorimotor cortex when nonmoving subjects watched other individuals performing specific actions. To investigate changes in brain activity, French researchers Gastaut and Bert (1954) recorded EEG activity while subjects performed actions as well as while they were presented with visual stimuli. Gastaut (1951) had previously reported that oscillations recorded over the sensorimotor region of the brain were reduced in amplitude when subjects performed an action or simply shifted their posture. Just 3 years later, Gastaut and Bert (1954) found that these same oscillations were also reduced when subjects identified themselves with an active person represented on a screen; for example, when they viewed a film of a boxing match. It is currently thought that suppression of this rhythm represents increased activity in the neural networks located in the sensorimotor region (Andrew & Pfurtscheller, 1997). Thus, as early as 1954, there was neurological evidence that the visual observation of actions in others activates neural systems in the observers' sensorimotor systems even when the observer himself is sitting completely still (Gastaut & Bert, 1954).

Over the past several years, other techniques have also been successful in identifying activity in the area of the sensorimotor cortex during action observation. Hari and colleagues have successfully used magnetoencephalography (MEG – an imaging technique measuring the magnetic fields produced by electrical activity in the brain) to measure the activity of the motor cortex following stimulation of the median nerve in the forearm (Avikainen, Forss, & Hari, 2002; Hari et al., 1998). As predicted by the shared system idea, MEG oscillations over sensorimotor cortex (an index of activity) showed a significant reduction during both action execution and action observation.

Additional support for the shared system for execution and observation comes from findings that readiness potential (marker of motor preparation recorded over the sensorimotor cortex) occurs prior to the actual movement as well as during observed actions (Kilner, Vargas, Duval, Blakemore, & Sirigu, 2004). Furthermore, when the nature and onset of action is predictable, the occurrence of the readiness potential precedes the observed movement's onset. Kilner et al. (2004) proposed that this type of timing might allow the observer not only to react to others' actions but also to anticipate actions that will be performed in the near future.

Though temporarily precise electrophysiological recordings from the scalp give us broad estimates of neural systems involved in certain behaviors, their spatial resolution is limited for exact localization of neural mechanisms. The ideal technique for such research is to record directly from individual neurons in awake human volunteers. However, such an opportunity is rarely available to researchers (though a recently published study that did just that will be discussed later in this section). Alternatively, animal studies on closely related species can be quite informative for such an investigation. The macaque monkey has been the prime subject for investigation of the mechanisms underlying action observation and execution.

The most relevant and well-known discovery in macaque single-unit electrophysiology research was made by Giacomo Rizzolatti and his colleagues (Di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Fogassi, Gallese, Fadiga, & Rizzolatti, 1998; Gallese, Fogassi, Fadiga, & Rizzolatti, 2002). While studying the premotor cortex (a motor planning region of the brain) in the macaque, they came across a system of neurons that responded not only when the monkey performed an action but also when the monkey watched the researcher perform a similar action (Di Pellegrino et al., 1992). The team named this system of neurons the *mirror neuron system (MNS)* because it appeared that the observed action was mirrored or simulated within the monkey's own motor system. In addition to the original mirror neurons found in the macaque's premotor cortex, neurons in the inferior portion of the parietal cortex have also been found to have mirror properties (Fogassi et al., 1998; Gallese et al., 2002).

The first attempt to localize the human MNS was a study by Fadiga, Fogassi, Pavesi, and Rizzolati (1995). Using transcranial magnetic stimulation (TMS – a noninvasive method to excite neurons in the brain), these researchers investigated whether the premotor cortex in humans responded when the participants watched others' actions. It was determined, on the basis of anatomical cytoarchitecture, that the human homolog to the region where mirror neurons were identified in the macaque is Brodmann's area 44/45, also known as Broca's area. Fadiga and colleagues found that TMS applied over Broca's area (temporarily activating this region) resulted in greater muscle activity in the observer's fingers when the subject observed another person moving, as compared with a baseline rest condition.

Subsequent to this neuromagnetic study work, several researchers conducted similar studies using positron emission tomography (PET, which measures glucose absorption in the brain) and functional magnetic resonance imaging (fMRI, which measures blood flow in the brain). Essentially, these studies showed selective activity in Broca's area and the inferior portion of the parietal cortex when subjects watched human actions (Decety et al., 1997; Iacoboni et al., 1999). Further, this

activity, similar to the macaque correlate, was somatotopically distributed (corresponding to specific body parts) in both premotor and parietal regions (Buccino et al., 2001).

Consistent with the proposals from embodied cognition, human mirror neurons appear to be selective to actions within the observer's motor repertoire (actions the observer is able to perform). In other words, if the observer is unable to match the observed action to a motor representation within his or her own system, the mirror neurons will not respond (Buccino et al., 2004; Stevens, Fonlupt, Shiffrar, & Decety, 2000). Interestingly, the individual need not be familiar or skilled at the action but only physically capable of performing it. For example, actions such as grasping and biting, which humans share with other primates, will activate the human MNS whether the observed action is performed by a human or a macaque. However, observing a dog barking, which is not part of the human motor repertoire, does not activate this system but rather is processed in lower level perceptual systems (Buccino et al., 2004).

Furthermore, actions that are part of the human motor repertoire but are not familiar will activate the MNS less than actions that are familiar to the observer. This property was demonstrated in a study conducted by Calvo-Merino, Glaser, Grezes, Passingham, and Haggard (2005). These researchers recorded fMRI data from expert dancers and found increased activity to the observation of others performing familiar styles of dance movements, as compared with unfamiliar styles matched for low-level visuomotor properties.

Though the majority of studies on the MNS in humans have utilized imaging technology, a recent study took advantage of a rare opportunity to record from individual neurons directly from the cortex in patients undergoing surgery for intractable epilepsy. Mukamel, Ekstrom, Kaplan, Iacobini, and Fried (2007) recorded the activity of 286 neurons in the central region of the frontal lobe while patients were instructed either to observe short video clips depicting a hand grasping a cup (precision grip or whole-hand prehension) or to actually grasp a cup in front of them. Patients were also instructed to either view still images of facial gestures (smiling or frowning) or to perform these facial gestures themselves. Out of the 286 neurons recorded, 12% responded during both the observation and execution conditions. This study suggests that a portion of neurons in motor cortices are active during the observation of human actions. A limitation of this study is that these patients had epilepsy, and thus it is unclear whether the findings can be generalized to healthy brains. Additionally, the specific regions that the team was able to record from were dictated by the neurosurgeon based on the specific patient's epilepsy. Thus, the researchers did not have control over which of the neurons provided recordings.

## PURPOSE OF EMBODIED PERCEPTION

The previous section explored the behavioral, electrophysiological, and neuroimaging data supporting the existence of embodied processes during visual perception. Though we would argue that the occurrence of spontaneous behavioral

mimicry and activations of motor and sensory regions of cortex during visual perception of others suggests that embodied processes play a critical role in perception, other theories may also account for this mirroring response. The earliest explanation for spontaneous mimicry was proposed by William James (1890), who suggested that "Every representation of movement awakens in some degree the actual movement which is its object" (p. 526). He believed that spontaneous mimicry was a result of automatic activation of previously learned stimulus–response relationships, similar to associative priming in which the presence of the stimulus increases the probability of a response. Another view suggests that the tendency toward mimicry can be accounted for by contagion, similar to contagious yawns or laughter, in which others first induce a similar emotional response, which then induces a similar action (Hatfield, Cacioppo, & Rapson, 1994; Laird et al., 1994). Neither of these accounts necessarily suggests that embodied processes play an active, constitutive role in perception.

The embodied perspective, however, suggests that the mimicry response can be the behavioral manifestation of the embodied perceptual process that contributes meaningful information toward the understanding of the visual stimulus. Thus, people smile when they observe a smile in someone else because the activation of one's own facial muscles helps them perceive the happiness of the other person. Similarly, people make slight movements of their arms while watching a sword fight because it is through the activation of the arm muscles that the observer is able to understand the action. Though these behaviors could be a result of the reflexive response that James speaks of, we humans are also able to mimic novel and nonevolutionarily relevant actions. Thus, a stimulus–response loop cannot fully account for the total range of mimicry responses.

A study conducted by Reed and Farah (1995) speaks to the causal contribution of embodiment in perception of action. Participants were asked to either move the same limb (arm or leg) as the observed action or the opposite limb. Results suggest that recognition of others' actions was significantly improved when the observer moved the same limb. In other words, if the observer was moving his own arm, he was more likely to recognize that the confederate moved her arm than her leg. This finding held up even when selective attention and conscious mimicry were controlled. Reed and Farah concluded that the participants used their own body schema to process the others' movements.

Embodied processes might also play a role in the perception of objects that are capable of being manipulated. Behavioral studies find that if subjects are asked to state whether a cup is upside-down or right-side-up, their response is facilitated if the cup's handle is on the same side as the response hand (Tucker & Ellis, 1998). This facilitation could be mediated by "canonical neurons" (located in the same brain regions that contain mirror neurons), which respond to graspable objects.

Perception of others' actions, as expressed in movements, and producing the appropriate behavioral response is critical to social interaction. However, of even greater importance for social perception is understanding the thoughts, intentions, and emotions that produced the observed behavior. The following studies demonstrate that embodied cognition serves the purpose for understanding not only the

surface perception, but also the underlying mental states that motivated the perceived behavior (for a review, see Niedenthal et al., 2005).

Let us start with the simple case of mental state attribution – emotion recognition. One early behavioral study that supports the role of embodied processes in social perception was conducted by Wallbott (1991). In this study, participants were videotaped while they performed an emotional facial recognition task. Each participant was then brought back to the laboratory for a subsequent session and asked to guess, on the basis of the videotape of his or her own face, what facial expression was presented on the previous session. The participants' judgments of their own facial expressions matched those of the presented stimulus at above chance levels, suggesting that the participants were imitating the facial expressions of the people they were judging. Additionally, the recognition rate from the original study correlated with individuals' recognition rate of their own (videotaped) facial expressions.

Niedenthal, Brauer, Halberstadt, and Innes-Ker (2001) examined the possibility that mimicry is causally involved in the perception of the facial expression of emotion. Participants were asked to identify the point at which a morphed face changed from happy to sad and vice versa. During this task, some participants were free to move their faces naturally, whereas others were holding a pen sideways in their mouths, between their teeth and lips This manipulation prevents facial mimicry and thus reduces somatic feedback that supports the detection of change in the observed expressions. Participants whose facial movements were blocked by the pen detected the change in expression later in both directions (happy to sad and sad to happy) than those who were able to move their face freely, supporting the role of facial mimicry in the recognition of facial expressions.

Oberman, Winkielman, and Ramachandran (2007) extended this study by adding several controls and, more importantly, examining the specificity of the mimicry-blocking effect. Note that the embodiment account predicts that recognition of a specific type of facial expression should be impaired by blocking mimicry in the group of facial muscles used in the production of this type of expression. The authors tested this hypothesis using four expressions (happy, disgust, fear, and sad) and four manipulations of facial mimicry: holding a pen sideways between the teeth, chewing gum, holding the pen just with the lips, and no task. The study found that the pen-in-the-teeth manipulation (which selectively activates the muscles involved in producing expressions of happiness) selectively impaired the recognition of happiness, but had no effect on the recognition accuracy for disgust, fear, and sad expressions. This finding suggests that recognition of a specific type of facial expression involves the selective recruitment of muscles used to produce that expression, as predicted by embodiment accounts.

## NECESSITY OF EMBODIED PROCESSES FOR SOCIAL PERCEPTION

The previous sections of this chapter provided evidence for the existence and possible benefit of embodied processes in typical social perception. In this section

we will propose that without embodied processes, social perception can be rather severely impaired. This conclusion is suggested by studies of clinical populations in which deficits in embodied processes are associated with deficits in social perception.

A study conducted by Ramachandran and Rogers-Ramachandran (1996) found that patients with anosognosia (denial of illness) that was due to damage to the right parietal and frontal cortices denied not only their own paralysis, but also the paralysis of another individual. The authors conclude that damage to an individual's own body schema may lead to deficits in making judgments about another individual's actions, again suggesting that having an embodied model to compare a perception to is necessary for accurate social perception.

Adolphs, Damasio, Tranel, Cooper, and Damasio (2000) provided evidence for the necessity of embodied processes in perception with another patient group. One hundred and eight focal brain lesion patients and 30 healthy control participants participated in three visual emotion recognition tasks. In the first task, participants were asked to rate the intensity of basic emotional facial expressions. In the second task, participants were asked to match a facial expression with the name of the emotion it is meant to convey. The final task required participants to sort facial expressions into emotional categories. Though each task identified a slightly different group of regions, damage to primary and secondary sensorimotor cortices impaired performance in all three tasks, supporting the critical role of sensory and motor cortices in the perception of emotion conveyed in visually presented faces.

The dependence of facial expression recognition on somatosensory cortices was also illustrated in a recent study by Pitcher Garrido, Walsh, and Duchaine (2008). In this study, healthy participants were given TMS that is capable of creating a "virtual" reversible lesion (or suppression of activity) in specific brain regions. Specifically, researchers targeted both the right occipital face area (rOFA) and right somatosensory cortex while participants discriminated facial expressions. TMS to either region, in the crucial time between 100 and 200 ms after presentation of expression, impaired discrimination of facial expressions but had no effect on a facial identity task.

These findings are contrasted with a study conducted by Calder, Keane, Cole, Campbell, and Young (2000) in which three patients with Mobius syndrome (a congenital condition that causes facial paralysis) were able to appropriately categorize faces from the Ekman and Friesen (1976) Face Stimulus set. Thus, it is important to note that though embodied processes likely are involved in emotion recognition, this ability can also be subserved through disembodied mechanisms, and an impairment in recognition may be recognizable only with very specific task conditions.

# DISORDERS OF EMBODIMENT

Certain populations provide organic insight into the role of embodiment in perception. These include disorders on the autism spectrum and schizophrenia as well as rarer conditions such as Capgras syndrome, phantom limb pain, somatoparaphrenia, apotemnophilia, and hypermimicry (echopraxia) in patients with frontal lobe lesions.

## Autism Spectrum Disorders

Autism is characterized by severe deficits in comprehending the behaviors of other people (social perception). Recent studies suggest that impairments in embodied processing may contribute to the deficit in social perception (for review, see Winkielman, McIntosh, & Oberman, 2009).

In one study, McIntosh, Reichmann-Decker, Winkielman, and Wilbarger (2006) showed pictures of happy and angry facial expressions to adults with autism spectrum disorders (ASD) and matched controls. In one condition, participants were simply asked to "watch the pictures as they appear on the screen." In another condition, participants were asked to "make an expression just like this one." Mimicry was measured by electromyography (EMG), with electrodes placed over the cheek (smiling) and brow (frowning) regions. In the voluntary condition there were no group differences, with ASD participants showing a normal pattern of voluntary mimicry (smile to a smile, frown to a frown). However, in the spontaneous condition only typical participants mimicked, with ASD participants showing no differential responses.

Interestingly, a recent study showed that under some conditions ASD participants will show spontaneous facial mimicry when, for example, they are focused on the task of recognizing emotions from the screen (Oberman, Winkielman, & Ramachandran, 2009). However, even then the mimicry is temporarily delayed, by about 200 ms, which could be critical for the ability of the somatic feedback to facilitate face recognition processes (Pitcher et al., 2008).

Indeed, this absence or delay of spontaneous mimicry may explain why participants with ASD have difficulties recognizing facial expressions under brief presentation conditions. Clark, Winkielman, and McIntosh (2008) compared ASD and control individuals on extraction of emotional and non-emotional information from stimuli presented briefly, in the range of micro expressions (15 and 30 ms), or for a long time (3 s). Participants' task was to detect if (i) emotional faces were happy or angry, (ii) neutral faces were male or female, and (iii) neutral images were animals or objects. ASD individuals performed selectively worse on emotion extraction from faces (60% versus about 75% for control groups). There were no group differences on gender or animal–object tasks, with groups all performing around 65%–70%. Importantly, there were no group differences in accuracy, which was perfect (100%) on any type of stimulus when pictures were presented at long stimulus duration (3 s). These findings suggest that participants with ASD can perform emotion detection under favorable presentation conditions, where presumably they use "disembodied" strategies, but have difficulties under brief condition where presumably they utilize their own facial feedback. Future studies should directly test the role of various embodiment mechanisms in perception of facial emotions among ASD individuals.

It has also been proposed that the social deficits in individuals with ASD result

from impairments in the MNS (Oberman & Ramachandran, 2007) and their inability to spontaneously map the mental representation of the self to the representation of the other (Williams, Whiten, & Singh, 2004). Evidence consistent with these proposals has been obtained by several research groups using different techniques. First, there are reports of anatomical differences in the MNS. For example, Hadjikhani, Joseph, Snyder, and Tager-Flusberg (2006) found that ASD individuals have local decreases of brain matter in the MNS areas, which correlated with severity of ASD symptoms. Similarly, Villalobos, Mitsuro, Dahl, Kemmotsu, and Muller (2005) found that individuals with ASD have reduced functional connectivity between the primary visual cortex and the premotor mirror neuron area. Second, several studies observed functional differences in the activity of the MNS during social perception.

Electroencephalogram (EEG) studies asked typical and ASD individuals to view videos of a person executing simple actions, or to perform the same actions. Similar to the findings of Gastaut and Bert (1954), the typically developing individuals showed suppression in the oscillations over sensorimotor cortex during both the execution and observation of action. However, individuals with ASD only showed suppression when performing their own actual movement but not when observing movement, indicating reduced mirror neuron activity (Altschuler et al., 2000; Oberman, Hubbard, McCleery, Ramachandran, & Pineda, 2005).

Interestingly, there is evidence that autistic impairment in spontaneous mirroring might relate to a deficit in mapping the representation of the observed action to the self. Theoret et al. (2005) asked typical and ASD groups to view videos of index finger and thumb movements that were directed either toward or away from the participants. During these tasks, the experimenters recorded muscle activity in the index finger induced by TMS. In the typical group, both participant-directed and other-directed actions increased muscle activity, suggesting spontaneous mirroring. However, the ASD group showed spontaneous mirroring when viewing actions directed toward the participant, but not when viewing actions directed away from the participant.

An fMRI study investigated the role of mirror neurons in the perception of emotion stimuli in individuals with ASD and controls (Dapretto et al., 2005). Participants were asked to both imitate and observe emotional facial expressions. As compared to controls, ASD participants showed lower activation in a wide variety of regions, including visual cortices, primary motor, limbic, cerebellum, and Broca's area. Though the group differences in brain activations were fairly broad, one intriguing finding is a negative correlation of the activity in Broca's area with the severity of autism symptoms, measured by the Autism Diagnostic Observation Schedule (ADOS) and the Autism Diagnostic Interview (ADI). Again, these findings suggest that deficits in social and emotional understanding in autism could be due to a reduction in brain regions involved in embodied cognition.

## Other Disorders of Embodiment

There are several other disorders that researchers have linked to embodiment. As embodiment involves a complex series of neural computations, it can be disordered in several ways. This section will explore several different psychological and neurological conditions in which disordered embodiment manifests itself.

If the role of embodiment is to simulate what is perceived "as if" the observer is actually performing the action, then an obvious question arises as to how the observer knows if it is really him actually performing the action, or if he is simply simulating it. This distinction is critical to embodied cognition and requires additional brain systems that are activated only during execution or only during perception. The ability to know that it is you (and not simply an embodied simulation of another person) performing an action is commonly referred to as agency, and its absence is one of the primary features of schizophrenia. Schizophrenia is characterized by auditory verbal hallucinations and delusions that other people are influencing their actions and thoughts (American Psychiatric Association, 1994). Patients with schizophrenia also often have difficulty in recognizing other people's actions and with expressing emotions through facial expressions and verbal communications. They also have difficulty in recognizing emotions on other people's faces (Penn & Combs, 2000).

The role of embodied cognition in schizophrenia has not been as well studied as it has in ASD. However, recently, Buccino and Amore (2008) argued that some behavioral symptoms of schizophrenia can be attributed to a dysfunction in embodied perception. This claim is supported by two behavioral studies where patients with schizophrenia were asked to perform simple hand movements without visual control. During the experiment the patients had to judge whether a hand presented on a screen was theirs or someone else's. These patients were not able to discriminate their own hand and sometimes attributed an alien hand to themselves (Daprati et al., 1997; Franck et al., 2001). These studies elegantly support the proposals that the lack of agency in patients with schizophrenia may lead to unconstrained embodiment. More generally, these results suggest that to assure successful processing, embodied systems of perception must be paired with other systems that provide a sense of agency to dissociate embodied perception from true experience.

Two rare conditions, somatoparaphrenia and apotemnophilia, also speak to the importance of agency in perception. In somatoparaphrenia the patient vehemently denies ownership of his left arm or leg, often attributing it to the examining physician or a spouse or sibling who may not even be in the vicinity. In these cases the patient sometimes develops an actual aversion to the limb. Likewise in apotemnophilia, otherwise sane and rational individuals express a strong and specific desire for the amputation of a healthy limb or limbs and suggest that it is not part of them. These disorders suggest that embodiment is relevant not only for the perception of others, but also the perception of one's own body.

It has previously been suggested by Brang, McGeoch, and Ramachandran (2008) that apotemnophilia results in representation of a specific body part (e.g., arm) being congenitally absent from their body image representation. However, the sensory input from the arm to primary and secondary somatosensory cortices is intact (because the limb itself is intact). It was suggested that this discrepancy between somatosensory cortices and body image representations in the parietal lobe leads to the characteristic alienation and aversion to the limb expressed by

individuals with apotemnophilia. Mere loss of sensory input to primary somatosensory cortex (e.g., brachial plexus avulsion, leading to complete denervation of an arm) does not lead to the aversion or desire for amputation because the signal does not reach secondary somatosensory cortex and fails to be relayed to the body representation so there is no discrepancy. Brang and colleagues (2008) tested this conjecture and found abnormal skin conductance response (SCR – a measure of autonomic arousal) when the affected limb was touched, but not when the other (unaffected) arm was touched. Since SCR is an automatic response, this finding provides compelling evidence for the disconnection between somatosensory cortices and body image representation.

In somatoparaphrenia the lesion affects both primary and secondary somatosensory cortices as well as body image representations in the parietal lobe. Consequently there is disownership, but no actual aversion since there is no discrepancy. However, if there is only partial rather than complete damage to either secondary somatosensory cortex or the parietal cortex, this creates some level of discrepancy, and sometimes aversion to the body part can be observed.

Interestingly, the abovementioned syndromes suggest that one's body image is intimately linked to emotions. Another condition in which a failure in embodied perception leads to delusions and sometimes aversion is Capgras syndrome. Capgras syndrome is characterized by the belief that an acquaintance, usually a spouse or other close family member, has been replaced by an identical looking impostor. Hirstein and Ramachandran (1997) argue that this delusion is a result of a disconnection between visual areas (especially fusiform gyrus) and the limbic (emotional) system. This leads to the inability to evoke relevant emotions on seeing a familiar individual. When these feelings are not evoked, the response is not simply recognition without emotions, but rather a delusion that it is a different person. This argument further suggests that the perception of a familiar person goes beyond their visual appearance to include also the embodied experience (including evoked emotions) of seeing that person. Two groups (Ellis, Young, Quayle, & De Pauw 1997; Hirstein & Ramachandran, 1997) tested the role of embodiment in perception of familiar individuals by using SCR. They found a reduced autonomic response to the person about whom the patient was delusional (usually the patient's mother), despite intact general ability to produce SCR responses. Thus, in addition to the two standard visual pathways (dorsal stream for action and ventral stream for object and face recognition), there appears to be a third pathway that lies ensconced between them and projects via a cortical area just below the inferior parietal cortex to the limbic structures. Capgras syndrome may be a result of damage to this "emotional–visual" pathway that, not coincidentally perhaps, overlaps with mirror neuron regions. These speculations await further testing.

In all of the above examples, the patients had access to their own physiological body feedback, but that feedback was somehow misinterpreted. But what happens if you lose that sensory feedback completely? Do you lose your ability to use embodied processes? The answer to this question comes in a recent study conducted by Ramachandran and Rogers-Ramachandran (2008). In this study, researchers asked two patients who experienced phantom sensations in their amputated arm to watch someone else being touched. The results were astonishing. Although a typical individual might activate his or her sensory representation in response to the perception of someone being touched, he or she wouldn't literally experience the other's touch. This is presumably because the lack of sensory input from the observer's intact limb overrides the embodied mechanisms. If the sensory input, however, is removed by amputating the limb, the override is also removed. As a result of the loss of the limb, phantom limb patients literally experience their own phantom hand being touched. In one of the patients, merely watching another subject's intact arm being massaged reduced the pain in the phantom. Ramachandran and Rogers-Ramachandran (2008) attribute this finding to a lack of sensory feedback leading to a corresponding lack of inhibition of complete embodiment of the perception. Further studies are necessary to confirm this finding.

The abovementioned examples all illustrate how embodied cognition allows us to peek into the elusive interface between body and mind and self and other. Disturbances in this interface can lead to a dissolution of self/other barriers, resulting in various psychological conditions. Additionally, there does appear to be one neurological condition that leads to hyperembodiment, which can be as disabling as no embodiment at all. In a study conducted by Lhermitte, Pillon, and Serdaru (1986) the researchers observed imitation behaviors in patients with lesions to the frontal lobe. Imitation behavior was defined as the persistence of imitation of the gestures and behavior of the examiner when the patient has not been asked to do so, and the continued imitation after being asked to stop. For these patients, the authors write "The sight of a movement is perceived in the patient's mind as an order to imitate; the sight of an object implies the order to use it." Of the patients with this behavior, 96% (28/29) had damage to the frontal lobe and of those 28 patients, 26 (93%) had damage to the inferior half of the anterior part of one or both frontal cortices. Thus, for embodied perception to work effectively, we not only need to be able to access our own body representations and interpret them appropriately, leading to mimicry. We also need to have some inhibitory mechanisms present to stop us from fully representing the perception of someone else in our own motor system, leading to mimicry that is uncontrolled.

## CONCLUSIONS AND FUTURE DIRECTIONS

In this chapter, we have argued that theories of embodied cognition offer a fruitful theoretical approach to investigating visual perception. We began by suggesting that the brain regions traditionally thought of as visual cortex in the occipital, inferior temporal, and posterior parietal lobes are not sufficient for visual perception. Though clearly they play a critical role in "seeing," "perceiving" is a much more complex process that involves the entire brain and arguably the extended nervous system. We then provided behavioral, electrophysiological, and neuroimaging evidence for the existence and benefit of embodied processes in visual perception. Finally, in the last section, we summarized several studies that speak to the necessity of embodied processes for social perception. Specifically, we

suggested that dysfunction of embodied processes due to lesions or mental disorders can lead to specific impairments in social perception.

Of course, there are open questions that still need to be explored. For one, how does one develop embodied processes? Are they hardwired and present from birth or are they acquired through learning, or a combination of both? The presence of behavioral spontaneous mimicry at birth as demonstrated by Meltzoff and Moore (1977) has been interpreted as evidence that some embodied processes do not have to be learned. However, there have been criticisms of these studies suggesting that the specific movements were a result of an innate releasing mechanism to feed, as the movements were limited to mouth opening, tongue protrusion, and hand opening, and the researchers suggest that the pattern of imitation is not likely the result of conditioning or innate releasing mechanisms. They argue that this early imitation implies that human neonates have an innate ability to equate their own unseen behaviors with gestures they see others perform.

However, it is possible that the actions investigated by Meltzoff and Moore (1977) were not, as suggested, based on an innate shared circuit, but rather could have been a reflex in response to a smile – like a sneeze in response to pepper. One way to find out would be to test whether infants can mimic an asymmetrical smile or another uncommon action. This would eliminate the "reflex" explanation and implicate a more sophisticated hardwired mechanism based on preexisting rules of translating visual appearance of the body into motor output, leading to accurate imitation.

If one assumes that most embodied processes are not innate, but rather learned, this opens up a bigger question. Namely, how are they learned? Is it an active process, or just a result of Hebbian association? For example, if every time a child reaches for something a motor command neuron fires and the child also sees his hand reaching, thus activating visual neurons, the two neurons (motor and visual) may become linked through Hebbian association. Over time, the motor neuron itself can be activated by the visual image of a reaching movement, even if the visual image is of another person's hand.

To answer these questions, one could record from the mirror neuron regions in a newborn macaque and expose the monkey to several actions, including actions that he will likely be exposed to early in life (e.g., peanut breaking, grasping), as well as novel actions that are unlikely to be based on preexisting hardwired mechanisms. If mirror neurons respond to both the familiar and novel actions the first time they are presented, that would argue for an innate system that does not depend on Hebbian association mechanisms. If mirror neurons respond only to the familiar actions, then the same argument could be made for these findings as was made for the findings by Meltzoff and Moore, that the brain is hardwired to respond to certain evolutionarily relevant actions. Finally, if no mirror neurons respond to the observation of any actions in newborn monkeys, this would argue against mirroring being innate. There are currently several possible mechanisms for the development of embodied processes. It is our prediction that, like other systems in the brain, these types of "shared circuits" are neither purely learned nor purely innate, but a result of both hardwired and learned processes.

Though challenges remain, it is clear that the embodiment approach offers,

has inspired, and is continuing to generate research that advances the understanding of how we perceive our world. We hope this review captures some of this excitement and points to some useful directions for future research.

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