The Case for Motor Involvement in Perceiving Conspecifics

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Perceiving other people's behaviors activates imitative motor plans in the perceiver, but there is disagreement as to the function of this activation. In contrast to other recent proposals (e.g., that it subserves overt imitation, identification and understanding of actions, or working memory), here it is argued that imitative motor activation feeds back into the perceptual processing of conspecifics' behaviors, generating top-down expectations and predictions of the unfolding action. Furthermore, this account incorporates recent ideas about *emulators* in the brain—mental simulations that run in parallel to the external events they simulate—to provide a mechanism by which motoric involvement could contribute to perception. Evidence from a variety of literatures is brought to bear to support this account of perceiving human body movement.

Keywords: imitation, mirror neurons, prediction, emulator, representational momentum

Among the vast diversity of stimuli we encounter in our daily lives—trees, buildings, machines, animals, household objects, food, printed words—there are some that can be mapped isomorphically onto our own bodies. This special category of stimuli consists primarily of other humans and the movements they make with their arms, legs, facial muscles, and vocal tracts. These are stimuli that can be imitated, and there is growing reason to believe that the property of *imitability* in a stimulus has important cognitive and neurological sequelae (M. Wilson, 2001b).

A recent but impressive range of evidence shows that perceiving the body movements of other people activates imitative motoric representations in the brain—that is, representations of how our own bodies would perform those same movements (for reviews, see, e.g., Buccino, Binkofski, & Riggio, 2004; Rizzolatti, Craighero, & Fadiga, 2002). However, in most everyday situations, imitation is not an especially common response to watching other people. Indeed, there is evidence that structures in the spinal cord specifically inhibit undesired imitative action (Baldissera, Cavallari, Craighero, & Fadiga, 2001). That is, in most cases, perceiving human action generates a motor plan that goes nowhere. What is the purpose of this apparent neurological extravagance?

A number of proposals have been put forward in the literature, variously suggesting that covert imitation in the brain is used for understanding others' actions, for facilitating overt imitation, or for rehearsing materials in working memory (e.g., Iacoboni et al., 1999; Rizzolatti, Fogassi, & Gallese, 2002; M. Wilson, 2001b). This article examines the case for an alternative proposal: Motor

activation contributes to the perception of the behavior of conspecifics (cf. Knoblich & Flach, 2001; Liberman, Cooper, Shankweiler, & Studdert-Kennedy, 1967; Liberman & Mattingly, 1985; Loula, Prasad, Harber, & Shiffrar, 2005; Stetson, 1905a, 1905b). More specifically, the proposal advanced here is that covert imitation functions as an *emulator*, tracking the behavior of conspecifics in real time to generate perceptual predictions.

Covert Imitation Is a Routine Cognitive Event

The body postures and actions of conspecifics have two special properties. First, they preferentially attract visual attention, calling processing resources to themselves automatically (e.g., Downing, Bray, Rogers, & Childs, 2004; Ro, Russell, & Lavie, 2001). Second, their structure is such that they can be covertly imitated with the observer's own body representation. A large weight of recent evidence shows that, in fact, such stimuli *are* covertly imitated, routinely and automatically. The evidence for this comes from a variety of literatures, including social, cognitive, developmental, and neuropsychology.

The Chameleon Effect

One of the most obvious indications of imitative motor activation is the unconscious tendency for people to actually mimic others' behavior. This is known as the *chameleon effect* (Chartrand & Bargh, 1999), or, in the context of emotion-related behaviors, *emotional contagion* (Hatfield, Cacioppo, & Rapson, 1994). For example, people tend to mimic one another's facial expressions (Bavelas, Black, Lemery, & Mullett, 1986; Dimberg, Thunberg, & Elmehed, 2000; Surakka & Hietanen, 1998; Wallbott, 1991; Zajonc, Pietromonaco, & Bargh, 1982), gestures, postures and body sway (Bernieri, 1988; Boker & Rotondo, 2002; Chartrand & Bargh, 1999; Rotondo & Boker, 2002; Shockley, Santana, & Fowler, 2003), tone of voice and pronunciation patterns (Goldinger, 1998; Neumann & Strack, 2000), and breathing patterns (McFarland, 2001; Paccalin & Jeannerod, 2000).

Automaticity of Imitation

Imitation of others seems to be a fast and automatic process (see Prinz, 2002, for a review). In this respect, imitation can be thought of as the extreme case of stimulus–response compatibility, in which people are faster to produce responses when the triggering stimulus shares features with the response (Greenwald, 1970). Thus, people are faster to perform a finger movement in response to seeing a video of that same finger movement (i.e., to imitate) than they are to perform the finger movement in response to an arbitrary cue (Brass, Bekkering, Wohlschläger, & Prinz, 2000). Similarly, people are faster to pronounce a syllable (/pa/, /ta/, or /ka/) in response to hearing that same syllable than in response to hearing a high, medium, or low tone; and indeed, the imitative responses are very nearly as fast as simple response times to pronounce a prechosen syllable, suggesting that extremely minimal processing is necessary to engage the correct motor programs to imitate (Fowler, Brown, Sabadini, & Weihing, 2003; Porter & Castellanos, 1980; Porter & Lubker, 1980).

In addition, imitation shows the Simon effect, which is stimulus–response compatibility for a task-irrelevant stimulus. Thus, Brass, Bekkering, and Prinz (2001) found that people are faster to make a finger movement to an arbitrary cue when an irrelevant but response-compatible visual finger movement is also shown and are slower to respond when an incompatible finger movement is shown (Brass et al., 2000; see also Stürmer, Aschersleben, & Prinz, 2000). Note that this differs from the above in that the imitable stimulus is not used to signal to the subject what the response should be—yet it still affects the speed of the response. Similarly, people's attempts to perform an arm movement become more variable when watching an incompatible arm movement (Kilner, Paulignan, & Blakemore, 2003). Similar results occur for imitable auditory stimuli. People are faster to pronounce a printed syllable when they see a mouth pronouncing the same syllable than when they see a mouth pronouncing a different syllable (Kerzel & Bekkering, 2000). And expert pianists and guitarists are slower to perform a chord when the cue to produce the chord is accompanied by an incompatible chord—but only when the incompatible chord is played on their own instrument (i.e., piano or guitar; Drost, Rieger, Brass, Gunter, & Prinz, 2003). Also relevant to the Simon effect for imitable stimuli is the finding that people are faster to make a preplanned movement in a go/no-go paradigm when the "go" signal is a compatible hand posture and slower when the "go" signal is an incompatible hand posture (Brass et al., 2001; Craighero, Bello, Fadiga, & Rizzolatti, 2002; Vogt, Taylor, & Hopkins, 2003). In this case, although the stimulus is not precisely task irrelevant, the *form* of the stimulus is irrelevant yet still has an effect. In sum, intentional imitation is faster than other stimulus–response mappings, and even nonimitative mappings can be speeded by task-irrelevant perception of the response movement.

Imitation in Neonates

The automaticity of mapping from perceived actions to performed actions is also supported by evidence of spontaneous imitation in infants. Neonates show imitation of simple facial gestures such as mouth opening and tongue protrusion (Meltzoff & Moore, 1977). The original finding has been criticized, in part, on the grounds that the data could be explained by innate releasing mechanisms (see Heyes, 2001, for a review). For example, babies show a similar tongue protrusion response to any object approaching the face, such as a ball or a felt-tip pen (e.g., Jacobson, 1979). However, subsequent studies have shown imitation in neonates for a range of behaviors, including emotional facial expressions (Field, Woodson, Greenberg, & Cohen, 1982), blinking (Kugiumutzakis, 1999), specific vowel sounds (Kuhl & Meltzoff, 1982), and the lip movement for the consonant /m/ (Chen, Striano, & Rakoczy, 2004). In addition, slightly older babies, with their greater neuromuscular control, can imitate more specific behaviors such as tongue protrusion to one side (Meltzoff & Moore, 1995) and additional consonant sounds (Kugiumutzakis, 1999). This wider range of behaviors makes an explanation based on innate releasing mechanisms less likely, as a separate mechanism would need to be posited for each behavior (cf. Chen et al., 2004). The study by Chen et al. (2004) makes the further point that neonates produce lip movements that correspond to the spoken phonemes /a/ and /m/ whether or not the baby's eyes are open. That is, even babies who received no visual signal of the adult's mouth shape produced differential mouth movements in response to these two speech sounds. This indicates that a connection between heard speech and corresponding motor representation is hard-wired.

Frontal Lobe Damage

One of the hallmarks of frontal lobe damage is loss of inhibitory control over one's actions. Thus, frontal lobe patients may show perseveration on a single behavior, difficulty inhibiting automatized responses as shown by excessive Stroop interference, and utilization behavior with common objects that offer strong action affordances (see Brass, Derrfuss, Matthes-von Cramon, & von Cramon, 2003, for a review). If covert imitation is automatically generated by imitable stimuli, but overt execution is actively inhibited, then we would expect frontal lobe patients to show a reduced ability to inhibit imitation. Indeed, patients with frontal lobe damage have been reported to show an automatic and uncontrollable tendency to imitate (De Renzi, Cavalleri, & Facchini, 1996; Lhermitte, Pillon, & Serdaru, 1986; Luria, 1966). More recently, it has been shown that a difficulty in inhibiting imitation can be elicited under experimental conditions even in frontal lobe patients who do not show spontaneous uncontrollable imitation (Brass et al., 2003). In that study, frontal lobe patients asked to execute a finger movement showed greater interference from an irrelevant finger movement (i.e., a stronger Simon effect) than did posterior lesion patients or normal controls.

Mirror Neurons

The above lines of evidence deal with cases in which overt imitation results from perceiving body movement. Recent research using various neurological techniques has highlighted the existence of imitative motor activation even when overt behavior does not result. The line of evidence that has gained the most attention in recent years has been the discovery of *mirror neurons* in area F5 of monkey premotor cortex. These neurons fire both when the monkey is executing a movement, as one would expect in a motor-related area, and when the monkey is merely watching the same movement being performed by another (di Pellegrino, Fa-

diga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; for a review, see Fogassi & Gallese, 2002). Neurons with similar properties have also been reported in area PF of monkey parietal cortex (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002). Furthermore, mirror neurons have been reported that respond to auditory stimuli that accompany actions, such as the sound of tearing paper (Kohler et al., 2002).

Although these data represent a groundbreaking discovery, it is important to be careful in extrapolating to the human case. It is worth noting, for example, that mirror neurons are primarily restricted to object-directed hand and mouth movements (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003; Fogassi & Gallese, 2002), particularly grasping movements, and thus, the field is still far from having identified neurons that code for whole body imitation and for imitation of numerous, possibly novel, actions. In addition, the *strictly congruent* mirror neurons of interest here which code for the same action, whether produced or perceived, are a minority of neurons in a system that also includes *broadly congruent* mirror neurons, which respond to logically related actions (e.g., perceived placing of an object and performed grasping of that object), and *cannonical* neurons, which respond when the monkey sees an object and when the monkey performs an appropriate action with that object. Finally, there is little or no evidence that the macaque monkey, in which mirror neurons have been observed, engages in imitative behavior. Nevertheless, the existence of mirror neurons in monkeys suggests an evolutionary precursor to the neurological systems that subserve imitation in humans.

Activation of Motor Planning Areas in Humans

Fortunately, neurological research with humans has extended the evidence for covert imitation. Functional MRI (functional magnetic resonance imaging) shows that observing finger, hand, arm, mouth, or foot movement leads to activation of motor-related areas of cortex (Buccino et al., 2001; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Iacoboni et al., 1999; Manthey, Shubotz, & von Cramon, 2003; Rizzolatti et al., 1996; Stevens, Fonlupt, Shiffrar, & Decety, 2000). However, the activation is restricted to movements that are biologically possible—that is, imitable—and does not occur for impossible body movements such as an arm passing through a leg or an arm rotating past its possible range (Stevens et al., 2000). In addition to simple limb movements, motor activation also occurs for complex, skilled whole-body movements, such as ballet or the martial art capoeira, and the activation is greater for subjects who are experts in performing that type of movement (Calvo, Glaser, Grèzes, Passingham, & Haggard, 2003). Another important category of movement for which this effect has been found is speech. Subjects who listen to speech sounds show brain activation in premotor areas that largely overlap with those of speech production (S. M. Wilson, Saygin, Sereno, & Iacoboni, 2004). Furthermore, using magnetoencephalography, heard piano melodies activate hand-related motor cortex in expert pianists (Haueisen & Knösche, 2001) and even in recent learners after as little as 20 minutes of practice with a keyboard (Bangert & Altenmüller, 2003). In the experts, differential areas of activation can even be identified on the basis of whether a note would typically be played by the thumb or by the little finger (Haueisen & Knösche, 2001). These findings (together with the findings of Drost et al., 2003, on pianists and guitarists, discussed earlier)

make two important points. First, new imitative mappings can be learned. Whereas the link between seeing a hand movement and planning a hand movement might plausibly be hard-wired, the link between hearing a diminished seventh chord and planning a hand movement is clearly not. Second, the sensory modality of the proximal stimulus is not critical, so long as the distal stimulus (as understood by the perceiver) is movement of a human body. Thus, the proximal stimulus is the acoustic pattern of a piano chord, but the distal stimulus is a human hand manipulating a keyboard. The purpose of all perceptual systems is to recover information about the distal stimulus in the world, and this is apparently what happens in expert piano players hearing piano music. That is, an auditory stimulus can be "heard as" human movement, just as a visual stimulus can be "seen as" human movement (cf. M. Wilson, 2001b).

Facilitated Muscle Activity

Further evidence comes from transcranial magnetic stimulation of motor cortex together with recording motor evoked potentials from relevant muscles. Using these techniques, increases in muscle potentiation in the subject's own hand have been observed when the subject watches a hand performing gestures, grasping, or manipulating an object (Clark, Tremblay, & Ste-Marie, 2003; Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Hari et al., 1998; Maeda, Kleiner-Fisman, & Pascual-Leone, 2002). Likewise, increases in muscle potentiation of the subject's own mouth occur when the subject listens to or watches speech (Fadiga, Craighero, Buccino, & Rizzolatti, 2002; Watkins, Strafella, & Paus, 2003). This latter finding (together with imitation of simple speech sounds in neonates) is particularly interesting given the beleaguered history of the motor theory of speech perception. Note, however, that these findings only show that perceived speech can result in outflow into the motor system, and do not, by themselves, indicate that such outflow feeds back and affects the perceptual processing itself.

Motor-Related Brain Rhythms

Yet another line of evidence concerns electroencephalogram or magnetoencephalogram rhythms that are characteristic of certain brain activities. Of particular interest is a rhythm originating in central cortex that is present at rest but disappears during motor activity. Various studies have shown that this rhythm is also blocked by merely observing human activity such as finger movement or leg movement (see Rizzolatti et al., 2002, for a review). Similarly, a rebound effect in motor cortex following stimulation of the median nerve of the wrist is inhibited by the subject manipulating an object during the nerve stimulation and is also inhibited by the subject merely watching someone else manipulate an object (Salenius, Schnitzler, Salmelin, Jousmaki, & Hari, 1997). These findings suggest an equivalency between perceived and performed actions, as far as certain brain systems are concerned.

Why Do We Covertly Imitate?

A variety of proposals have been made regarding the purpose of covert imitation. One is that covert imitation actually facilitates *overt* imitation for those times when copying others is indeed

appropriate (e.g., Iacoboni et al., 1999; Rizzolatti, Fogassi, & Gallese, 2001). Among humans, imitation is important for a variety of social purposes. The most obvious case is observational learning, in which children and even adults pick up culturally appropriate behaviors from those around them without active teaching (e.g., Blandin, Lhuisset, & Proteau, 1999). That is, the observer is able to map the observed person's body and bodily actions onto a mental representation of their own body and to reproduce those actions either immediately or at a later time. In addition, imitation of body postures and gestures may play a role in interpersonal bonding by signaling affiliation, liking, and empathy (e.g., Bavelas et al., 1986; Chartrand & Bargh, 1999; Lakin & Chartrand, 2003) and by generally encouraging a prosocial orientation in the observer (van Baaren, Holland, Kawakami, & van Knippenberg, 2004). Thus, the importance of the ability to imitate when needed may justify the automatic activation of neural resources. On this account, watching a particular behavior primes that same behavior in the observer, making its execution more probable and more easily initiated (cf. Byrne & Russon, 1998; Dijksterhuis & Bargh, 2001; Jeannerod, 2001). In support of this account, the mirror system in humans does indeed seem to be active during action imitation (Buccino, Vogt, et al., 2004).

Alternatively, it has been suggested that covert imitation plays a role in our ability to understand other people's actions, and the intentions and goals behind those actions, perhaps leading ultimately to theory of mind (Arbib & Rizzolatti, 1996; Buccino, Binkofski, & Riggio, 2004; Gallese & Goldman, 1998; Kohler et al., 2002; Meltzoff & Decety, 2003; Rizzolatti et al., 2001, 2002; Rizzolatti & Luppino, 2001). Thus, a conspecific's hand moving through the air while the fingers close is not just seen as a visual movement sequence but is understood to be an act of grasping and furthermore may be interpreted as an intention to steal food.

We can distinguish at least three versions of this proposal, in order of increasing strength. The first is that *action understanding* refers essentially to recognizing or categorizing—understanding various individual acts to be instances of "grasping," for example. The second is that action understanding involves a teleological component (cf. Gergely & Csibra, 2003) regarding the goals or reasons for which a motor movement is being performed—understanding a grasping hand as being directed at taking a piece of food, for example. The third is that action understanding supports a more full-blown representation of the other's mental state that drives the action—for example, understanding the desire for food that lies behind the action.

One route by which such inferences might occur, particularly in the stronger versions of the proposal, is if the observer's brain not only reproduces the motoric patterns of an action but also reproduces the sensory consequences that normally accompany the performance of those motoric patterns (e.g., Blakemore & Decety, 2001; Hesslow, 2002; Rizzolatti et al., 2002; cf. Hommel, Müsseler, Aschersleben, & Prinz, 2001). By reinstating the sensory consequences of a particular action, such as the kinesthetic and tactile feelings of the hand wrapping around a desirable piece of food, the observer may be able to access the reasons for performing that action, in other words, the intention of the actor.

A third proposal is that a major function of covert imitation is to subserve working memory (M. Wilson, 2001a, 2001b). According to this account, working memory is a fundamentally sensorimotor process, recruiting perceptual resources and articulatory resources to temporarily code information in a relatively peripheral format and thus free up more central processing resources. The extremely effective strategy of articulatory rehearsal in working memory, exemplified by mentally repeating a phone number or a shopping list to oneself, is crucially dependent on a greased path between input and output forms of the same representation, that is, on the automaticity of translation between a perceptual representation and a corresponding motor representation, and back again.

Finally, it has been proposed that the mirror neuron system for covert imitation played a role in the evolutionary development of language (Arbib, in press; Bråten, 2002; Corballis, 2004; McCune, 2002; Rizzolatti & Arbib, 1998; Studdart-Kennedy, 2002; but see Deacon, 2004, for a critique). The argument for this rests, in part, on the physical homology between area F5 in the macaque, where mirror neurons reside, and Broca's area in the human, which plays a role in language processing (Binkofski & Buccino, 2004). The second leg of the same argument is that, for language to be successful, users must be attuned to the functional equivalence between perceived and produced speech forms. This recognition of equivalence between certain perceptual events and corresponding motor events is similar in spirit to the function of mirror neurons. Thus, the neural hardware of the mirror system may have been a prerequisite for the development of language in human evolution.

These various proposals are not mutually exclusive, and it is possible—perhaps even likely—that covert imitation plays a role in each of these cognitive activities. Once the neurological infrastructure for covert imitation was in place, it may well have been co-opted for a variety of purposes.

Here, though, we examine the case for another proposal, which has received relatively less attention in the literature: Covert imitation of perceived human action may contribute, in a top-down fashion, to the ongoing perceptual processing of that same human action (e.g., Knoblich, Seigerschmidt, Flach, & Prinz, 2002). The fact that perceiving others' bodies activates representations of moving one's own body indicates that the two types of representation are commensurable, arguably consisting of a three-dimensional structured representation of the limb relations of the body and (possibly) various biomechanical constraints on their movement abilities. Given such commensurability, it is possible that the influence feeds back in the other direction as well, with the activated motor representations mapping back onto and influencing the representation of perceived bodies.

More specifically, we propose here that covert imitation functions as part of a *perceptual emulator*, using implicit knowledge of one's own body mechanics as a mental model to track another person's actions in real time. This emulation serves a top-down function of helping to fill in missing or ambiguous information and projecting the likely course of an ongoing action a short way into the future, even when the actor becomes temporarily hidden.

Note that this goes beyond a theory on which motor representations themselves serve a predictive or "filling-in" function without feeding back into the perceptual system. One could imagine, for example, a system in which imitative motor programs predict the consequences of an observed action by projecting what would happen if the observer's own body were performing the action. (This is lent plausibility by the fact that motor imagery can project forward in time for the person's own actions; e.g., Jeannerod, 1994; Johnson, 2000; Johnson-Frey, McCarty, & Keen, 2004). However, such a theory would not predict any specifically visual

(or other perceptual) consequences of motor activation. The present proposal differs from such a motor-only proposal in that the information from the motor system is hypothesized to "leak out" and influence incoming perceptual information.

We must also consider how this proposal differs from the action-understanding proposal described above—particularly the stronger versions, in which intentions are inferred by reinstating the sensory consequences of an action. Because both that proposal and the present one posit a role of sensory or perceptual representations, and both also posit the drawing of inferences about the actor, it is worth considering in detail how these proposals differ from each other.

The most important difference is that the action-understanding proposal does not posit any impact on ongoing perceptual processing of the external event. Instead, the activated sensory representations that it posits are of quite a different kind. They are stored representations of sensory consequences of one's own actions (e.g., kinesthetic feedback) and bear no necessary connection to the current perceptual processing of the other person's action. Although they are perceptual in format, their function is not a perceptual one. The result is, broadly speaking, an enhanced mental representation of the external action but not an ongoing influence on concurrent processing in the visual system. Rather, their function is to draw inferences about the motives and purposes of actions.

In this respect, the function of these activated sensory representations is essentially *postdictive*. They allow the perceiver to project backward in time to recover the intentions that caused the initiation of the action in the first place. In contrast, the present proposal is fundamentally *predictive*, positing that the perceptual system projects the probable future course of an ongoing event. (We should note that there is also a predictive element to the action-understanding proposal, in the sense that actions may be categorized before they are completed. Thus, the perceiver may realize that grasping is going to happen before the fingers actually contact the object. However, this sort of prediction is categorical, not perceptual. In contrast, the present proposal involves *perceptual* prediction, which is modality specific and models particular movement trajectories unfolding over time in a continuous fashion.)

A second important difference is that the present proposal requires a structural representation of the human body that is *allocentric* (not tied to the observer's viewpoint). Such a representation can be used to model information about the body from either a first-person or a third-person perspective and can therefore be mapped isomorphically onto external information about another person's body. A similar proposal has been made in the speech perception literature. According to gestural theories of speech perception (a class of theories modified from the older and more radical motor theory), the phonemes of perceived speech are represented in terms of articulatory gestures. That is, they are represented in terms of the movements of the vocal apparatus that produced them (or more precisely, equivalence classes of movements defined by common target state) and thus are commensurable with representations of phoneme production (e.g., Browman & Goldstein, 1992; Fowler, 1986; Liberman & Whalen, 2000; Studdart-Kennedy, 2002).

In contrast, the action-understanding proposal is not committed to such a claim. For example, the idea that there is activation of

associative links between a particular action and its particular sensory effects, based on past experience (e.g., Blakemore & Decety, 2001; Buccino et al., 2004; Hesslow, 2002), suggests that the activated sensory representations will be from a first-person point of view: kinesthetic, proprioceptive, tactile, and (possibly) visual feedback from performing the action. Indeed, we know that watching others does result in first-person sensory activation, as shown, for example, by activation of secondary somatosensory cortex when watching another person being touched (Keysers et al., 2004). One advantage of a first-person representation is that it is ideally suited for what the action-understanding proposal claims it is for, which is to put oneself in the shoes of the actor and understand what that person is doing. In contrast, a viewpoint-independent representation is perhaps less suited for making inferences about intentions and goals but better suited for interfacing with incoming sensory input, as claimed in the present proposal.

In short, one proposal is about action understanding, while the other is about action perception. There is no reason, we should note, why these two proposals could not be hybridized into a single, more complex model, but this is beyond the scope of the present article. Here we consider simply the proposal that covert imitation feeds back onto the perceptual processing that gave rise to it, a proposal that is logically separable from the action-understanding proposal. As discussed in later sections, the present proposal gives rise to unique predictions that do not emerge from the action-understanding proposal.

Perception Is a Predictive Activity

Before directly addressing the main proposal, however, we first consider the general phenomenon of perceptual prediction. Perceptual prediction is in fact extremely common, not limited to perceiving conspecifics. A familiar example occurs when listening to a favorite CD: As each song comes to a close, one finds oneself anticipating the opening bars of the next tune. This anticipation is not driven by abstract knowledge, such as recalling an ordered list of the songs. Instead, one almost literally "hears" the next song coming.

Perceptual anticipation of this kind has been demonstrated experimentally in the visual domain. In the phenomenon of *representational momentum*, originally reported by Freyd and Finke (1984; Finke & Freyd, 1985), movement or implied movement results in mental extrapolation of a trajectory beyond what was actually perceived. In a typical experiment, an object is shown in three successive positions, implying movement in a particular direction. Subjects are probed immediately after, with a fourth presentation of the object, and are asked whether the probe is in the same position as the last of the three inducing stimuli. These probes may in fact show a position further along the trajectory, or less far along the trajectory, than the true final position. Subjects are more likely to say "different" when the probe is shifted backward than when it is shifted forward. To put it conversely, it is hard for subjects to reject a forward-shifted probe as being different from what they actually saw. This suggests that the subjects' perceptual representations of the inducing stimuli incorporated an extrapolation into the immediate future.

This forward projection occurs for real motion, apparent motion, and motion that is merely implied by presentation in successive positions. With the exception of the case of smooth real motion

(Kerzel, 2002a; Kerzel, Jordan, & Müsseler, 2001), the effect still occurs when eye movements are eliminated and therefore is not an artifact of gaze position (Kerzel, 2003). The effect can even be found for stimuli that imply motion without showing any change of position, such as a rocket (Reed & Vinson, 1996), an object from which support is removed (Freyd, Pantzer, & Cheng, 1988), a spring released from compression (Freyd et al., 1988), or a photograph of a person jumping off of a wall (Freyd, 1983). Representational momentum occurs for a variety of predictable motion trajectories, including object rotation (Freyd & Finke, 1984), circular paths (Hubbard, 1996), spiral paths (Freyd & Jones, 1994), and optic flow generated by observer motion (Thornton & Hayes, 2004). It is sensitive to velocity (Freyd & Finke, 1985), acceleration and deceleration (Finke, Freyd, & Shyi, 1986), and predictable changes in direction, such as oscillatory motion (Verfaillie & D'Ydewalle, 1991) and rebound after collision (Hubbard & Bharucha, 1988).

Although representational momentum can be penetrated by conceptual knowledge (as in the rocket example), a number of findings indicate that the effect itself is perceptual in nature: The effect is strongest at retention intervals of up to a few hundred milliseconds and decays thereafter (Bertamini, 1993; Freyd & Johnson, 1987); the effect occurs, and indeed is stronger, under divided executive resources (Hayes & Freyd, 2002) but is weakened when specifically visual attention is diverted (Kerzel, 2003); and when the trajectory of the effect is in conflict with classical mechanics, as in the case of an object emerging from a spiral-shaped tube, expert physicists show the effect just as novices do (Kozhevnikov & Hegarty, 2001). All of these findings suggest that the effect is not due to explicit, nonperceptual expectations. Perhaps most convincing is that stimuli that imply motion and moving stimuli that become occluded activate areas of the brain that process real motion, such as area MT (Kourtzi & Kanwisher, 2000; Olson, Gatenby, Leung, Skudlarski, & Gore, 2003; Senior et al., 2000), and furthermore, disruption of these brain areas by transcranial magnetic stimulation eliminates representational momentum (Senior, Ward, & David, 2002). In short, the findings of representational momentum suggest that the perceptual system extrapolates movement beyond what is actually perceived.

Perceptual extrapolation has also been suggested by a variety of misalignment illusions that have come to be known collectively as the *flash lag effect*. When a predictably moving stimulus (such as a rotating line or a drifting sine-wave grating) is paired with an unpredictable stationary stimulus (such as a flashed line or a flashed sine-wave grating), the spatial relationship between the two stimuli is misperceived. In general, the predictably moving stimulus is perceived as being further along on its trajectory, relative to the stationary stimulus, than it actually is at the moment that the two stimuli co-occur (de Valois & de Valois, 1991; Khurana & Nijhawan, 1995; MacKay, 1958; Nijhawan, 1994, 1997; Ramachandran & Anstis, 1990; see also Emerson & Pesta, 1992). Nijhawan, Watanabe, Khurana, and Shimojo (2004) have demonstrated that this is not due to faster neural processing of moving objects than stationary objects (as proposed by Purushothaman, Patel, Bedell, & Ogmen, 1998). Instead, in accordance with the findings on representational momentum, these findings suggest that the visual system extrapolates predictable movement a short way into the future. Indeed, a recent study combining the flash lag effect and representational momentum into

a single experimental paradigm suggests that the two phenomena have a common basis (Munger & Owens, 2004). (We should note, though, that there is disagreement regarding the extrapolation account of the flash lag effect. An alternative proposed by Eagleman & Sejnowski, 2000, is that the effect is actually postdictive, being reconstructed in the 80 ms following the flash.)

A further line of evidence for perceptual extrapolation comes from perceivers' judgments of when a falling object will hit the ground, in a situation where the object becomes hidden part way through its trajectory. Judgments are most accurate when subjects' eye movements spontaneously track the (hidden) object's path, suggesting that subjects are mentally tracking the extrapolated path in real time (Huber & Krist, 2004).

Perceptual extrapolation is akin to a constellation of other phenomena in perception, that of filling-in or completion effects. Some of these completion effects happen with static patterns. Examples include illusory contours, where stimuli that strongly imply a missing edge result in a compelling perception of that edge; amodal completion, where a partially occluded object looks like a whole object that is only partly visible, rather than like a truncated object; and boundary extension, where objects and scenes are remembered immediately after as being wider angle shots than they really were, containing regions that were not actually seen (Intraub & Richardson, 1989).

Other completion effects involve patterns across time, where the perceptual system fills in missing information after the fact. These include apparent motion, where two static, alternating stimuli are perceived as a single object hopping back and forth, and the phonemic restoration effect, where a word with a phoneme deleted and replaced with noise is heard as the complete word.

In all of these cases, incomplete perceptual patterns are perceived as more complete than they really are. That is, the missing information seems to be filled in or supplied for us, either on the basis of prior experience with similar patterns or on the basis of principles such as geometric simplicity (cf. Shepard, 1994). These phenomena involve the generating of an expectation or assumption on the part of the perceptual system as to the nature of the missing information. The only difference between these phenomena and perceptual prediction is that the former involve completion of patterns that are static or already finished, whereas the latter involves completion of patterns that have not yet finished unfolding over time.

The cases of perceptual prediction discussed above generally involve geometrically simple movement trajectories. However, it has also been shown that perceptual prediction occurs for the considerably more complex movement patterns involved in actions of the body. For example, in a study by Verfaillie, De Troy, and Van Rensbergen (1994), subjects watched a point-light walker (a moving human figure indicated only by small lights at the joints, in an otherwise dark field) and tried to detect changes that occurred between eye fixations. The eye is temporarily blind during these jumps, or *saccades*, so a change that is timed, through eye-tracking technology, to occur during a saccade can only be detected by comparing presaccade and postsaccade information. The authors found that some kinds of changes (e.g., rotation of the figure in depth) were easy to detect, and others (e.g., translation of the entire figure sideways) were hard to detect. This might seem to suggest that changes in configuration of the point lights are more noticeable than changes in absolute position of the whole figure. In

contrast, though, a configural change that showed an upcoming moment in the walker's stride was difficult for subjects to detect as a change. Just as in the representational momentum experiments, the difficulty in "rejecting" the changed display implies that the subjects' perceptual representations had already been updated on the basis of a prediction of how the movement will proceed.

A further study used computer-generated human figures (Verfaillie & Daems, 2002). Subjects were shown sequences of static body postures that implied continuous movement. Later, subjects were asked to judge whether single body postures were "possible" or "impossible" (e.g., head facing backward). The purpose of this judgment was simply to provide a task for which reaction time could be collected. Of the "possible" postures, some were postures that would have immediately followed the sequences shown previously. Others were postures that would have immediately preceded those sequences, and still others were novel. Relative to the novel postures, subjects showed priming for the immediate-future postures but not the immediate-past postures. In other words, subjects generated a representation of the body movement sequence that went forward in time beyond what was shown (see also Kourtzi & Shiffrar, 1999).

Perceptual Prediction and Emulation

How is perceptual prediction accomplished? One possibility is that the visual system (and other perceptual systems) engages in a kind of rote memorization, learning regularly experienced temporal patterns as temporally extended templates (cf. Beintema & van den Berg, 1998; Perrone, 1992). An alternative and more plausible theory is that the perceptual system develops a structured internal model of the system to be predicted, a model that is isomorphic on a part-by-part basis to that external system, and contains information about the mechanics of its movement properties. The perceptual system could then generate predictions by running simulations using the model. One major advantage of this solution is that each new real-world occurrence need not be memorized as a unique event. Instead, whole classes of events that share structural properties can be represented by a single model.

A growing body of evidence indicates that the brain makes use of this second solution in a variety of ways. Clearly, simulation of various sorts plays an important role in cognition, including imagery, counterfactualizing, spatial reasoning, and pretend play; but one special category of simulation is simulation that is actually time locked to a currently ongoing real event. Such simulation can be described as occurring "online" or "in real time." As the external event unfolds, the simulated event likewise unfolds in the same way and at the same pace. For example, in the motor control literature, theorists have proposed that motor commands are fed into a simulation device, called a *forward model*, that runs in parallel with the actually executed movement (Desmurget & Grafton, 2000; Miall & Reckless, 2002; Wolpert & Flanagan, 2001). Using information about the movement properties of muscles and limbs, the forward model simulates the unfolding course of the movement, in parallel with the actual movement occurring in the external world. Any discrepancy between the forward model's simulated movement and the desired movement results in corrective commands being issued. The advantage of this arrangement is that the forward model can produce its simulated feedback well before real feedback from the world arrives at the relevant

parts of the brain, and thus, corrective commands can be issued in a timely fashion. (Proponents of the action-understanding theory of covert imitation, discussed earlier, have proposed that exactly this kind of motor control forward model is co-opted for generating the predicted sensory consequences of others' actions as if they were one's own; e.g., Blakemore & Decety, 2001.)

More generally, Grush (in press) has discussed a class of simulations or models that he terms *emulators*. An emulator is any model of an external system that runs simulations of that system in real time—that is, in parallel with the external system itself. In general, emulators are a way of circumventing transmission delays to and from the external system. If the emulator is well calibrated, and is running its simulation accurately, information about the current state of the external world can be achieved before actual sensory input arrives. This allows the organism to form a veridical, rather than a temporally delayed, representation of the current state of the world and to interact with it in an appropriately time-locked fashion. Recently Nijhawan, Watanabe, Khurana, and Shimojo (2004), as well as Grush (in press), have suggested that this kind of mechanism exists not just in the motor system (as mentioned above) but in the visual system as well.

In the case of visual perception, the predictions generated by an emulator of the perceived event would act as top-down information to help with interpretation of the incoming visual signal. Just as in other cases of top-down influence, the output of an emulator would act as a hypothesis of what is going on, to be verified by the incoming signal and to help disambiguate in cases of uncertainty. If a stimulus were to disappear, temporarily or permanently, the emulator would provide information about its motion slightly beyond the point where it ceased to be visible. Emulation may also be responsible for the sense of fluency and ease one's experiences in perceiving familiar movement patterns. Rather than having to encode all aspects of the movement in real time, one can generate an expectation and then perform the computationally easier task of verifying that the expectation is being met (cf. Koch & Poggio, 1999; Rao & Ballard, 1999).

But how would a perceptual emulator achieve its results? To be successful, an emulator must internalize principles or regularities of the external system that allow predictability. This suggests that emulating perceptual events is sharply limited in certain ways. Two types of cases clearly lend themselves to emulation. The first is movement trajectories that follow simple geometric principles, such as linear translation, rotation, smooth arcs, simple collisions, and so on. The second case is movement patterns that are stereotypic and highly familiar, such as a tennis serve, a wave breaking, dynamic advertising logos, or (to take an auditory example) songs on a CD. Together, these two categories of movement buy us a lot. However, there still remain a large number of events in the real world that do not lend themselves to perceptual prediction: flying insects, rocks bouncing down a hillside, a kite blown on the wind. Indeed, a study by Kerzel (2002b) has shown that when both direction and final position of the inducing stimuli are varied randomly across trials to disrupt predictability, representational momentum is absent. (In fact, a small degree of predictability remains within each trial even in Kerzel's paradigm, as a result of the successive presentations along a particular path, but this may not be sufficiently robust to trigger reliable output by the emulator. This interpretation is supported by the literature on the flash lag effect, in which the "stationary" stimulus that does not evoke

extrapolation is often in fact presented stroboscopically in successive positions. This kind of presentation is apparently not enough to trigger strong extrapolation in the visual system.) By and large, any event that is nonuniform and nonstereotypic is not a good candidate for emulation.

The jointed structure of the human body means that human movement is not uniform, in any simple geometric sense, and the diversity and creativity of human activity means that human movement is often nonstereotypic. How, then, would an emulator accomplish perceptual prediction of human actions?

Motor Involvement in Perceptual Prediction

An emulator, as we have argued, needs to internalize regularities of the world in order to build up a model that is isomorphic, in certain relevant properties, to the system being modeled. In the case of human movement, this would arguably need to be a model of the biomechanics of the human body, including muscle response properties, the hierarchical jointed structure of the limbs, range of motion of various joints, and so on.

Notice that this type of model would be commensurable with motoric and somatosensory representations of one's own body (cf. Prinz, 1997, on the "common coding principle"). This opens the door to the possibility that perceptual emulators for human movement are not created de novo within the perceptual system (see Jacobs, Pinto, & Shiffrar, 2004; Loula et al., 2005, for reviews of this perceptual learning viewpoint) but instead employ preexisting resources for representing the human body. In the case of human movements, the knowledge needed to predict trajectories is already built in. In virtue of possessing a human body, the perceiver has an insider's perspective on how bodies run, reach, grasp, scowl, laugh, kick, push, dance, and wiggle their fingers.

We now come to the crux of the argument: Is there evidence to support the contention that covert imitation plays a role in perceptual prediction of imitable stimuli, particularly the behavior of conspecifics? In fact, a number of lines of evidence converge to support this account.

Motor Activation That Precedes the Related Perceptual Event

This possibility of motor involvement is lent credibility by findings that appropriate motor-related brain areas can be activated before a perceived behavior occurs, in cases where the behavior is predictable. The study of expert pianists, described earlier, found that activation of finger-related motor cortex in response to a particular note in a familiar sequence occurred in the 300 ms before the note's onset (Haueisen & Knösche, 2001). That is, not only do pianists generate motor imagery in response to hearing familiar pieces, but this motor imagery actually anticipates and precedes the unfolding melodic event. (A similar conclusion is suggested, though somewhat more indirectly, in work by Schubotz & von Cramon, 2002.)

Predictive Capabilities of Mirror Neurons

Furthermore, there is evidence that mirror neurons, described earlier, are capable of projecting the immediate future of an observed action. Umiltà et al. (2001) reported that mirror neurons that usually respond to seeing a hand grasp an object will also respond to seeing a hand make a grasping motion as it disappears behind a screen—but only if the monkey knows that there is an object behind the screen. When the monkey knows that there is no object, these neurons do not respond to the grasping movement. These results suggest that perceptual prediction can engage motor representations, although they do not tell us what functional role is played by those motor representations.

Influence of Self-Action on Perceptual Judgments of Other-Action

Suggestive evidence that motor resources may be involved in perception of conspecifics comes from studies that show an influence of concurrent action on making judgments about another person's movement or posture. Reed and Farah (1995) found that unconstrained motion of relevant body parts by the subject facilitated an immediate-memory same–different judgment on body postures. Conversely, Hamilton, Wolpert, and Frith (2004) found that constraining subjects to perform a particular motor task (lifting a light or heavy box) produced an interference effect on a perceptual judgment (judging a box someone else was lifting to be light or heavy). Some caution is due in interpreting these results because it is not certain that the influence occurred at a perceptual level. For example, in the Hamilton et al. study, lifting a heavy box could have activated general conceptual knowledge about heaviness, which could then have created a cognitive, nonperceptual contrast effect. Nevertheless, these findings are compatible with, and strongly suggestive of, the account being advanced here.

Influence of Motor Learning on Perception

Further plausibility for the present claim comes from evidence that motor representations can indeed feed back and have an impact on perception. Some of this evidence involves the perception of abstract nonhuman stimuli but still makes the point that motor learning can influence perception. Hecht, Vogt, and Prinz (2001) trained subjects to make arm movements with a sinusoidal temporal pattern, without visual feedback. These subjects were subsequently better at recognizing a visual movement with the same sinusoidal timing than were subjects in a control group. In other words, motoric expertise improved performance on a perceptual task (see also Casile & Giese, 2004).

Activation of Visual Brain Areas by Motor Movement

In a further demonstration of motor-to-perceptual flow of information, subjects' own body movement results in activation of a body-perception area of the visual system (Astafiev, Stanley, Shulman, & Corbetta, 2004). The *extrastriate body area* (EBA), which lies in the lateral occipito-temporal area of cortex, responds selectively to human bodies and body parts (Downing, Jiang, Shuman, & Kanwisher, 2001). However, subjects also show activation in the EBA when performing movements with the hand or the foot, even when they cannot see their own limb (Astafiev et al., 2004). This shows that observer body movement can influence the visual system and furthermore suggests that the influence is directed particularly at mechanisms for representing others' bodies. As noted above, however, a direct influence on the perception of

others' bodies is still wanting. It is possible, for example, that the EBA is used for representing the observer's own body and does not always serve a directly visual function.

Superior Perceptual Prediction When Viewing Oneself

We now turn to more direct evidence for the present proposal. If an emulator uses motoric knowledge to simulate an external event, then the more closely the forces behind that event are matched by one's own motor programs, the better the prediction will be. At the limit, the best prediction will be had from observing a conspecific with motor programs identical to one's own. In ordinary life this of course never happens, but it can be accomplished by showing subjects videos of themselves, in effect showing them human actions driven by their own motor programs. This is the tactic taken by Knoblich and colleagues (Knoblich & Flach, 2001; Knoblich et al., 2002), who found that subjects are more accurate at predicting a trajectory when watching a video of themselves than when watching a video of another subject. This effect was found both for large-scale body movements, such as throwing a dart at a dartboard (Knoblich & Flach, 2001), and for small-scale movements, such as handwriting (Knoblich et al., 2002). Furthermore, Loula et al. (2005) report that subjects are better at identifying themselves as point-light figures in videos performing various actions than they are at identifying a friend or a stranger. (Previous studies yielded more ambiguous results on this issue; e.g., Beardsworth & Buckner, 1981; Cutting & Kozlowski, 1977.) Because people have greater visual experience with their friends' movements than with their own, the superior identification performance for the self indicates that motor experience contributes to perceptual recognition. The motor-based interpretation of these data is further supported by a recent functional magnetic resonance imaging study in which subjects watched videos of themselves or their friends lifting a box. The onset of activation in areas forming the human mirror system (left premotor and inferior-parietal) occurred significantly earlier when subjects observed themselves than when they observed their friends (Grèzes, Frith, & Passingham, 2004), suggesting that covert motoric imitation is indeed optimized when watching oneself. Together, these findings indicate that perceptual prediction of human movement is dependent on the specific qualities of one's motor programming: Predictive accuracy is better when the motor programs provide a truer representation of how the perceived movement unfolds.

Superior Visual Judgments for Possible Movements

Further evidence of a direct impact of the motor system on visual perception comes from Jacobs et al. (2004), who reported that the ability to discriminate point-light-walker speed varies according to whether the action is possible (forward walking) or impossible (forward walking played backward). This finding might be dismissed as a consequence of visual experience, except for the fact that other variables of visual familiarity (familiar vs. unusual gait, and familiar vs. unfamiliar actor) had no effect on speed discrimination. Provided that the action is biomechanically possible, observers are good at perceiving walker speed, but with biomechanically impossible movement, performance on this perceptual task suffers. A similar effect of biomechanically possible

movements was reported by Kourtzi and Shiffrar (1999). Like the study by Verfaillie and Daems (2002), this study showed priming for postures implied by a sequence of postures; however, the effect occurred only when the postures shown were biomechanically possible. This suggests that the perceptual prediction reported in both studies is influenced by motoric knowledge.

Note that the constellation of evidence reported in this section would not be predicted by the action-understanding account discussed earlier, in which motor involvement is used to categorize actions and perhaps infer intentions. On such an account, motor activation could help to form a mental representation that generally characterizes the action (e.g., grasping) and perhaps predicts its outcome (e.g., interpreting a hand's action as grasping before completion of the movement). However, this cannot account for the moment-by-moment perceptual sensitivity to, and prediction of, exact movement trajectories suggested by these various findings. This divergence of prediction is particularly clear for movements that do not have categorically defined end-states. For example, identifying an act of throwing as throwing provides no information about where exactly the thrown object will hit. This is not to say that these data contradict or disprove the proposal that motor activation subserves action understanding but merely that such a proposal is not sufficient to explain the perceptual data. For that purpose, an additional theoretical proposal, something like the present perceptual-emulation account, is needed.

Conclusion

Based on the various lines of evidence reviewed here, the following proposal emerges: The various brain areas involved in translating perceived human movement into corresponding motor programs collectively act as an emulator, internally simulating the ongoing perceived movement. This emulator bypasses the delay of sensory transmission to provide immediate information about the ongoing course of the observed action as well as its probable immediate future. Such internal modeling allows the perceiver to rapidly interpret the perceptual signal, to react quickly, to disambiguate in situations of uncertainty, and to perceptually complete movements that are not perceived in their entirety. A perceiver who can "see" where a movement is heading has enormous advantages, both physically and socially. Thus, what originally appeared to be a neurological extravagance—the activation of motor resources when no motor movement is intended—may instead be an elegant solution to a perceptual problem.

We should note that this proposal does not preclude other possible functions for the motoric representation of others' movements. If motoric representations act as an emulator, that emulation may then be used to drive other cognitive events, such as overt imitation, working memory, or understanding others' behaviors, but this need not be the emulator's primary or original purpose. One advantage of the present account is that it can accommodate the fact that mirror neurons are found in nonhuman primate species that do not imitate and do not seem to have a theory of mind.

Another point to be noted is that the strength of covert imitation may be mediated by task demands. For example, Kerzel (2003, p. 117) has suggested that the filling-in and extrapolating functions of perception may be more strongly activated with implied motion than with smooth motion. In the case of human movement, stimuli that require filling in may more strongly trigger the emulating

function of covert imitation than do stimuli that are more complete. Covert imitation may also be particularly strongly triggered in situations that require effortful cognitive transformations, such as mental rotation of body parts (e.g., Gentilucci, Benuzzi, Bertolani, Daprati, & Gangitano, 2000; Parsons & Fox, 1998; Parsons et al., 1995).

On the other hand, covert imitation may be inhibited in situations where the perceiver is simultaneously engaging in incompatible body movement or movement planning. Covert imitation may also be relatively weak in cases of highly complex physical skills for which the perceiver lacks the relevant expertise (Calvo et al., 2003). Thus, a dance performance or martial arts performance may literally look different to an expert than to a novice because the former will engage robust motoric emulation, and the latter will not. This further suggests that motoric expertise may have a practical role to play in learning difficult perceptual tasks. For example, learning to "read" the finger spelling that is part of American Sign Language is an extremely difficult, slow learning process for non-native signers, but one that may perhaps be speeded by motor practice in performing finger spelling oneself.

The present proposal that motoric representations can act as an emulator might also have important implications for the study of joint action. This area of research addresses the question of how people engage in rapid interactive activities such as playing basketball, rowing a canoe together, dancing a waltz, fighting a karate match, or taking turns in conversation. It has been suggested that such activities require that each member of the group represent the others' actions (Sebanz, Knoblich, & Prinz, 2003) and plan his or her actions in relation to what the others will do, in real time (Knoblich & Jordan, 2003; T. Wilson & Wilson, 2002). The present proposal suggests that, in tasks requiring fast action coordination, the emulator derives predictions about the future course of others' actions, which could be integrated with the actions one is currently planning. The ability of the emulator to project forward into the future would allow the rapid integration of self- and other-produced action in real time. Note that this account presupposes that motor knowledge is used simultaneously for emulating and planning. The highly parallel and modular architecture of current models of motor control (Wolpert & Kawato, 1998) makes such an assumption plausible. Such an account would predict that interference occurs only if emulating and planning access the same internal models of a given movement (cf. Hamilton et al., 2004).

Finally, to place the current proposal in a more general context, we should note that recruitment of motor resources for nonmotor tasks is not unique to the case of perceiving human action. Evidence is emerging in a variety of research domains to show that motoric resources serve a number of representational functions that do not involve the immediate execution of movement (cf. Jeannerod, 2001). These include perceiving objects and environments with strong action affordances (Grafton, Fadiga, Arbib, & Rizzolatti, 1997; Grèzes & Decety, 2002; Gross, Heinze, Seiler, & Stephan, 1999; Murata et al., 1997), predicting projectile motion (Hecht & Bertamini, 2000), and mentally transforming objects and spatial relationships (Wohlschläger, 2001). Given all this, it would seem odd if we did not use our motoric resources to model what they are best at modeling—that is, human bodies. The use of motor resources to simulate imitable action may be part of a larger principle of brain organization: Neural resources originally de-

signed to move the body may now be routinely recruited to help represent the world.

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