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Bodily and Motor Contributions
to Action Perception

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Over the last 50 years, cognitive scientists have been on a hunt for a general architecture of cognition, initially with great enthusiasm (Newell, 1990; Newell, Shaw, & Simon, 1956; Newell & Simon, 1972), but facing an increasing number of problems later on. Although there are still attempts to define such general frameworks (Anderson et al., 2004; Kieras & Meyer, 1997; Wray & Jones, 2005), their impact on defining the research agenda for cognitive science seems to have dropped. What is the reason for this development? One of the main problems seems to be that most of these frameworks implicitly assume that cognition is detached from the world and from the body: Perception consists of translating physical stimulation into symbolic representations. Action consists in the manipulation of mental content or symbolic commands to the motor system, and it is frequently fully controlled by the cognitive system. Mechanisms for action execution are often underspecified.

At present, a countermovement has set in and *embodiment* is the new keyword. However, different researchers use this term in very different ways that can be traced back to James Gibson (1979), Maurice Merleau-Ponty (1945), Jean Piaget (1969), and William James (1890). Wilson (2002) distinguished six different, but related, theoretical assumptions for which the term *embodiment* has been used. These assumptions span from radical interactionism, the claim that

environment and cognitive system cannot be separated because of the dense information flow, to situated cognition, the claim that cognition is situated in particular perception-action contexts.

In this article I will focus on a particular brand of embodiment theory that stresses the close links between perception and action and assigns them an important role for cognition in general. The functional version of this theory is known as the common coding theory of perception and action (Hommel, Muesseler, Aschersleben, & Prinz, 2001; Prinz, 1997), and the neuronal version is known as mirror system theory (cf. Rizzolatti & Craighero, 2004). Intellectual precursors include William James's ideomotor principle (1890) and the motor theory of speech perception (Liberman & Whalen, 2000). Basically, the common coding theory generalizes James's ideomotor principle (James, 1890) and applies it to action perception (Greenwald, 1970; Hommel et al., 2001; Prinz, 2002).

Originally, the ideomotor principle was postulated to explain voluntary action. It states that imagining an action will create a tendency to carry it out. This tendency will automatically lead to the execution of the action when no antagonistic mental images are simultaneously present (James, 1890, vol. 2, p. 526). The common coding theory adds to this claim that the mental images (or representations in more modern terms) do not code actions per se (Prinz, 1997), but the distal perceptual events they produce. This creates a common medium for perception and action that leads to a functional equivalence of perceptual representations and action representations. As a consequence, action representations should become activated whenever one perceives an action that is similar to an action one is able to perform.

A growing body of neurophysiological evidence suggests that common coding of perception and action is implemented on a neuronal level (e.g., Blakemore & Decety, 2001; Decety & Grezes, 1999; Rizzolatti & Craighero, 2004). Rizzolatti and his colleagues provided evidence for "mirror neurons" in the premotor and parietal cortices of macaque monkeys (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996, Kohler et al., 2002; Umiltà et al., 2001). These neurons fire when the monkey carries out object-directed actions. The surprising finding is that these "motor" neurons also fire when the monkey observes the experimenter carrying out object-directed actions. Newer findings suggest that mirror neurons in the parietal cortex code action goals (Fogassi et al., 2005). Positron emission tomography (PET) and

functional magnetic resonance imaging (fMRI) studies suggest that humans possess a similar mirror system that involves premotor and parietal cortical areas (e.g., Iacoboni et al., 1999; Koski et al., 2002). Rizzolatti and Craighero (2004) provide a more elaborate description of findings about the mirror system in monkeys and humans and of the differences between the monkey mirror system and the human mirror system.

In which sense is this common coding/mirroring theory an embodied approach? It shares at least two of the six basic assumptions that Wilson (2002) identified as underlying different approaches to embodied cognition: First, it stresses that the ultimate function of the mind is to guide action, and that therefore, a better understanding of perception-links is necessary in order to better understand the mind. Second, it stresses that off-line cognition is body-based, and in particular, that action observation leads to the activation of structures that one uses to perform and execute the observed actions. This does not necessarily imply a focus on the particular anatomical structure of the body. Rather, any perceptual event that can potentially result from one's own actions leads to a resonance with the action system. For instance, hearing the sound of a hammer on wood will activate action representations involved in hammering (at least if one has performed hammering actions producing similar sounds earlier in one's life).

Furthermore, the common coding theory is sympathetic but not necessarily committed to three further embodiment claims that Wilson (2002) has identified: (1) cognition is situated in the real world and inherently involves perception and action; (2) acting in the real world involves time constraints; and (3) the environment is used to offload cognitive workload. Finally, the common coding theory is not easily reconciled with radical interactionist approaches of embodied cognition (e.g., newer versions of Gibson's ecological psychology), which claim that the information flow between organism and environment is too dense as to allow any meaningful characterization of cognition that does not include the environment at the same time. Common coding focuses on the goal-directed and intentional nature of human action (see Barresi & Moore, 1997, for related ideas), and postulates that internal states cause overt action. Thus it is a representational theory.

However, there is no compelling reason to assume that the representations involved are propositional or symbolic, as suggested in

some versions of the theory (e.g., Hommel et al., 2001). A weaker notion of representation, where representations are regarded as blueprints (A. Clark, 1997), as relational schemas (Barresi & Moore, 1997; Knoblich & Flach, 2001), or as regions in an attractor space (e.g., Spivey, Grosjean, & Knoblich, 2005), seems to be more appropriate. The notion of an attractor space fits nicely with the common coding theory's postulate of a similarity-based matching between perception and action. The assumption that perception and action use continuous, graded representations makes it easy to explain how perception and action can be matched in a multidimensional space, and provides a straightforward link between the functional principle of common coding and the rapidly growing empirical evidence obtained in the cognitive neurosciences. If one assumes propositional representations the similarity principle loses much of its power. For instance, if one categorizes continuous dimensions (left…right) into distinct propositions (e.g., far left, near left, near right, far right) a straightforward match occurs only if two events fall into exactly the same category (of course, this could be remedied by postulating additional processes).

Closely related are theories postulating that we internally simulate or emulate the actions we observe in others (Blakemore & Decety, 2001; Grush, 2004; Jeannerod, 2001; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). It is important not to confuse the meaning of "simulation" in this context of "action simulation" with the meaning of "simulation" in the context of the theory of mind debate (e.g., Dokic & Proust, 2002; Goldman, 2006; Harris, 1995). In the latter debate simulation refers to putting oneself into another person's shoes. In the context of research on action planning and action perception, simulation refers to predictive mechanisms or internal models that are used to plan and execute one's own actions. These models predict the sensory or perceptual consequences of actions. One of their main functions is to bridge timing delays between the issuing of motor commands and the arrival of reafferent information from the sensory organs in the central nervous system (Wolpert & Kawato, 1998). The basic idea behind action simulation theories is that matching perceived actions to our own action repertoire allows us to exploit such predictive mechanisms in our motor system in order to predict the future consequences of others' actions. The obvious functional advantage of this type of action simulation is that it is not necessary to have separate perceptual prediction mechanisms for predicting the outcomes of others' actions.

In the rest of this chapter I will provide an overview of empirical studies that provide converging evidence for the claims of the common coding theory and action simulation theories. The main claim of the common coding theory is that perceived actions are matched to one's own action repertoire. Theories of action simulation add that this match activates predictive motor mechanisms that allow one to predict the future outcome of others' actions. These predictions, in turn, might help to stabilize (Wilson & Knoblich, 2005) and to temporally structure (Thornton & Knoblich, 2006) perception.

There are several routes to testing these claims. I will focus on results from four different lines of empirical research. The first line of research shows that motor laws that hold in action execution also hold in action perception and motor imagery. The logic of this research is that if perception and action both rely on a common coding system one would expect that principles that govern action execution should also govern one's perception of others' actions and the way one imagines one's own actions. The second line of research demonstrates that acquiring expertise in a certain action domain profoundly affects the perception of the corresponding actions and their effects. The logic of this research is that acquiring new motor skills leads to the acquisition of new motor representations or to the modification of existing ones. According to the common coding principle, such changes in the motor repertoire should affect action perception. In particular, people should resonate more when they observe actions they can perform well than when they observe actions they cannot perform or not perform well. The third line of research suggests that one's own previous actions are a special object of perception, because they maximally activate common representations for perception and action. This leads to self-identification and more accurate predictions for self-produced actions. Finally, the fourth line of research provides evidence that the ability to sense the periphery of the body is one of the necessary conditions for some forms of action simulation.

Motor Laws and Action Perception

If perception and action both rely on a common coding system one would expect that the principles that constrain the production of one's own movements also constrain one's perception of others' movements and their effects. Research on the two-thirds power law

(Lacquaniti, Terzuolo, & Viviani, 1983), on the apparent motion of the human body (Shiffrar & Freyd, 1990; 1993), and on Fitt's law (Fitts, 1954) provides strong evidence in support of this claim.

Two-Thirds Power Law

The two-thirds power law (Viviani, 2002; Viviani, Baud-Bovy, & Redolfi, 1997; Viviani & Stucchi, 1989, 1992) describes a lawful relationship between the velocity of a movement and the curvature of a trajectory. I will illustrate the underlying principle in a simple example. Imagine repeatedly drawing a horizontally elongated ellipse on a piece of paper, as fast as possible. In the middle of the ellipse the curvature is low (almost a straight line) but at both ends the curvature increases until a direction change occurs (from left to right or from right to left). The two-thirds power law states that, as the curvature increases, one needs to systematically decelerate one's movement. Conversely, to the extent that the curvature decreases, one is able to systematically speed up again. The amount of deceleration or acceleration is directly proportional to the change in curvature. The two-thirds power law holds for most types of human movement. For instance, tracking studies show that people cannot accurately track the movement of a target when it deviates from the two-thirds power law. This is true for manual tracking (Viviani, Campadelli, & Mounoud, 1987; Viviani & Mounoud, 1990) as well as for tracking a target with one's eyes (DeSperati & Viviani, 1997).

Most important in the present context is the finding that this motor law also constrains the way we perceive motion. Viviani and Stucchi (1989) asked participants to estimate the eccentricity of ellipsoidal movements they observed. These estimates were biased towards the velocity profile predicted by the two-thirds power law. In another study, Viviani and Stucchi (1992) asked participants to adjust a randomly moving dot's (scribbles') velocity to be constant. Surprisingly, participants perceived the point as moving with constant velocity when it actually accelerated and decelerated according to the two-thirds power law. Thus perception was clearly shifted towards perceiving a dot that moved according to constraints of the human motor system, as moving with constant velocity. Similar effects have been observed in the kinesthetic modality, where a robot moved the participants' arms on different elliptical trajectories (Viviani, Baud-Bovy, & Redolfi, 1997).

Further studies show that people's ability to predict the future course of a handwriting trajectory (Kandel, Orliaguet, & Boe, 2000) breaks down when the observed writing trajectory is manipulated so that it no longer corresponds to the two-thirds power law (Kandel, Orliaguet, & Viviani, 2000). Finally, Flach and colleagues (2004a) demonstrated that forward displacements in perceived movement direction (representational momentum, cf. Hubbard, 1995, 2005; Kerzel, Jordan, & Muesseler, 2001) are reduced when the movement follows the rules of the two-thirds power law. Thus it seems to be easier to anticipate the future course of a movement when its velocity profile changes according to "human" characteristics. Taken together, the findings on the two-thirds power law provide overwhelming evidence that motor constraints can profoundly affect movement perception.

Apparent Motion of the Human Body

Further support for the claim that bodily and motor constraints affect action perception comes from research on apparent body motion (Shiffrar, this volume; Shiffrar & Freyd, 1990, 1993; Shiffrar & Pinto, 2002; Stevens, Fonlupt, Shiffrar, & Decety, 2000). These findings show that one perceives an anatomically plausible movement path in an apparent motion display of body movements (e.g., hand going around the head), although according to the classical laws of apparent motion (Korte, 1915) one should perceive the shortest, but anatomically implausible path (e.g., hand going through head). However, this is only true for movement speeds that lie within a range a human actor could achieve. At fast movement speeds (short SOAs) the shortest path is perceived. For movements of nonhuman objects one always perceives the shortest path, regardless of whether physical constraints are violated and regardless of the perceived movement speed.

One important part of the explanation for this finding is that a multimodal body schema provides important contributions to human body perception (Funk, Shiffrar, & Brugger, 2005; cf. Knoblich, Thornton, Grosjean, & Shiffrar, 2006). However, this assumption does not fully explain why the anatomically possible path is only perceived within a time range that corresponds to movement speeds that is actually possible to achieve for humans. Thus it is possible that another part of the explanation is that perception of the

anatomically possible path is partly driven by contributions from the motor system. The observer might covertly simulate performing the observed movement (Wilson & Knoblich, 2005). Such a simulation might be a precondition for perceiving the anatomically plausible movement path.

Fitts's Law

As a final example, a recent study by Grosjean, Shiffrar, and Knoblich (in press) provides direct evidence that Fitts's law (Fitts, 1954) holds in action perception. It could be argued that Fitts's law is the best-studied and most robust principle of human motor performance (Plamondon & Alimi, 1997). It states that the time it takes to move as fast as possible between two targets is determined by their width and the distance between them. As the target size increases one is able to move faster without missing the target. As the distance between the targets increases one needs longer to move between them without missing them. Thus there is a trade-off that is often referred to as speed-accuracy trade-off. Fitts's law describes this trade-off as:

$$MT = a + b \cdot ID,$$

where MT is movement time, ID is the index of difficulty of the movement, and a and b are empirical constants. The critical variable is the index of difficulty, which relates the amplitude (A) of the movement to the width (W) of the targets:

$$ID = \log_2(2 \cdot A/W).$$

Thus different combinations of amplitude and target width can yield the same index of difficulty, and accordingly, the same movement time. For instance, Fitts's law predicts the same movement times for targets that are 2 cm wide and 8 cm apart and for targets that are 8 cm wide and 32 cm apart (both have ID=3). It has been demonstrated that Fitts's law holds for different types of movement (discrete and cyclical), different effectors (finger, arm, and head), and different contexts (under a microscope and under water). Moreover, Fitts's law holds not only when one actually executes movements, but it also holds when one just imagines performing movements (Decety & Jeannerod, 1995).

In order to determine whether Fitts's law holds in action perception, Grosjean and colleagues (in press) asked participants to judge two alternating pictures of a person moving at various speeds between two targets. The targets varied in amplitude and width. There were three different amplitude/width combinations for each of the three IDs studied (2, 3, 4). Participants could watch these displays at leisure until they felt ready to report whether the observed person could perform such movements without missing the targets.

Alternating pictures were chosen instead of videos to avoid any influence of movement trajectory information, which is not addressed by Fitts's law. Perceived movement times were defined in terms of the speeds at which participants provided an equal proportion of "possible" and "impossible" judgments. The results showed a perfect linear relationship ($r2=.96$) between the index of difficulty and the movement time that was perceived as just possible for the observed person. This implies that the perceived movement time did not vary as a function of the target width or the movement amplitude (distance between targets) alone. Rather, the same speed-accuracy trade-off that is present in action production and motor imagery also governed action perception. Such a result is very hard to explain in purely perceptual terms. Rather, it provides strong evidence for motor contributions to action perception.

Expertise and Action Perception

The claim that action shapes perception implies that acquiring new motor skills should affect one's perception of others' actions that require the same skill to be performed. Thus as one makes progress in learning to play piano, one's perception of piano playing should become increasingly linked to the action representations that govern one's own piano playing. Likewise, learning new dance movements or becoming a ski expert should affect one's perception of dancing and skiing. Note that this does not necessarily imply that the action system remains silent when nonexperts observe the actions of highly skilled experts. Even hardboiled couch potatoes watching a soccer or basketball game will at times have been forced to carry out the general types of actions the observed players are performing (e.g., running, kicking, throwing, etc.), and should therefore resonate with the observed actions. However, experts in a certain domain who watch other experts should show a higher degree of resonance, because

the action knowledge they can apply to the observed actions will be more elaborate.

Several recent studies of musicians, dancers, and athletes, suggest that expertise with particular motor skills do indeed result in closer links between perception and action. In this section I will discuss studies that support two predictions arising from the claim that motor skills can affect perception: (1) watching actions that one is an expert in performing should, compared to nonexpert actions, lead to higher activation of brain areas that are related to action planning and motor performance, and (2) the increasing resonance of perceived actions with one's own action repertoire that result from the acquisition of new motor skills should alter the perception of actions which require these skills to be performed (Wilson & Knoblich, 2005).

Haueisen and Knoesche (2001; see also Bangert, Parlitz, & Altenmueller, 1999), using magnetoencephalography (MEG), found that pianists who listened to recordings of piano pieces showed much higher activation of areas in primary motor cortex than musically trained nonpianists (choir singers). This demonstrates that listening to the perceptual consequences of highly trained actions activates the corresponding motor programs in experts. In a recent functional brain imaging study, Haslinger and colleagues (2005) have shown that when an expert pianist observed another pianist performing finger movements related to piano playing, brain networks that support action planning and action execution were activated. This activation did not occur in novices and was not observed for finger movements that were unrelated to piano playing. Even when expert pianists watched silent piano playing, auditory sensory areas were activated. This suggests that the observation of finger movements led them to recover the auditory consequences of the visually observed actions. Highly skilled pianists seem to perceive melodies when observing others silently playing piano.

The role of expertise in action perception has been further addressed in an elegant brain imaging study on ballet dancers and capoeira dancers (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005). Capoeira is an Afro-Brazilian martial art dance that can be highly artistic and requires skills that are quite different from the ones that are required for ballet dancing. For instance, whereas ballet dancers often hardly touch the ground, extensive "groundwork" is key in capoeira dancing. The kinematics of the performed move-

ments differ between the two dance styles. Whereas ballet dancers most often perform elegant, swift, and airy movements, capoeira dancers prefer sweeps, kicks, and head-bangs.

Calvo-Merino and her colleagues asked whether the two groups of dance experts would show higher activation of action-related brain areas (the human mirror system) when observing their own dance style. Ballet dancers observed videos of ballet dancing and capoeira dancing and capoeira dancers observed videos of ballet dancing and capoeira dancing. As predicted, capoeira dancers showed higher activation of the mirror system (premotor cortex, interparietal sulcus, and superior temporal sulcus) when observing capoeira dancing as compared to ballet dancing. In contrast, ballet dancers showed a higher activation in the same areas when observing videos of ballet dancing. It should be noted that in both groups of dancers the mirror system was activated during the observation of both dance styles. Thus the dancers' mirror system also responded to some extent when they observed a different dancing style. Together, the results suggest that being an expert in a particular domain has very specific influences on action perception. The more similar the observed actions to the actions one is an expert in performing the higher the resonance of the action system with the observed movement.

One possible function of this higher resonance could be to better identify the intentions underlying observed actions. Testing this hypothesis, Sebanz, Zisa, and Shiffrar (2006) asked whether basketball experts are better able than novices at deriving deceptive intentions from the movements of their opponent. In particular, they investigated whether basketball players are better able to detect fakes (pretending to pass the ball to teammate, but actually keeping it) from pictures, videos, and dynamic movement displays. The static pictures depicted the exact moment at which the ball left or did not leave the observed player's hands. The videos and the dynamic movement displays ended exactly with the same frame that was displayed in the static picture condition. Sebanz and colleagues found that only experts could use the movement information provided in videos to detect whether the observed player was performing a pass or a fake. In this condition the experts performed significantly better than novices. When static pictures were displayed, experts and novices were hardly better than chance and there was no difference between the groups. A second experiment showed that only experts could identify fakes from dynamic movement displays of a

basketball player, whereas novices' identification did not differ from chance level. Thus basketball experts seem to have an improved ability to derive deceptive intentions from bodily actions.

Direct evidence for the assumption that the acquisition of new skills leads to a close coupling between certain actions and their perceivable effects comes from a single-cell study on monkeys (Kohler et al., 2002). Kohler and colleagues investigated whether mirror neurons respond to auditory stimuli. In addition to "noise-producing" actions that are already in the monkey's repertoire, such as cracking nuts, they also trained monkeys to perform a number of new actions that produced particular noises, such as ripping a paper. They found that premotor neurons generally fired in response to auditory stimuli that reflected the consequences of actions the monkey could perform, regardless of whether the actions belonged to monkey's natural repertoire or whether they were recently acquired.

Two recent studies have taken the next important step in exploring how action perception changes as a particular person acquires a particular new skill. Casile and Giese (2006) trained students to perform new gait patterns and investigated whether perceptual accuracy for identification of these gait patterns improved. Specifically, they trained their participants to perform "funny" arm movements with a 270° phase relationship while walking (e.g., left arm half-way between front and back, right arm in the back). During normal gait this phase relationship is approximately 180°; for example, left arm in the front and right arm in the back). Performing the funny arm movements with the 270° relationship is impossible without training, but training can lead to a quite steep improvement in performance, at least for some people. The participants were blindfolded during training. Only verbal and haptic feedback was provided. Casile and Giese (2006) performed the training in the dark to rule out any effects of visual familiarity and visual cues during learning.

Before and after the training the participants were asked to judge whether two consecutively presented point-light displays of human gait were the same or different. One of the displays depicted one of three different gait prototypes: A 180° phase relationship (normal gait), a 225° phase relationship (untrained funny gait), and a 270° phase relationship (to be trained/trained funny gait). The second display was either the same or slightly differed from the prototype that was presented first. The main dependent variable was the accuracy of the same-different judgments.

Before the training, participants were quite accurate for displays of normal gait (180° displays), less accurate for the 225° funny gait displays, and even less accurate for the 270° funny gait displays. After participants had received training in performing the 270° gait pattern in the dark, they selectively improved in their visual same-different judgments for the 270° displays, but not for the other types of displays. Thus there was a very specific effect of motor training on visual perception that was not mediated by visual cues. Moreover, the degree of improvement in the visual task was highly correlated with participants' improvement during training. The more successful participants had been in acquiring the funny gait pattern, the larger was their improvement in the visual task (after training compared to prior to training).

These results are quite surprising. Why should visual perception change through training during which visual cues are absent? Theories that postulate common coding of perception and action (Prinz, 1997) suggest that as one's action repertoire changes, perception should be affected in a reciprocal way. But how exactly could this work? Thornton and Knoblich (2006) suggested that timing might be the key to explaining why learning a new motor task can affect visual perception. Learning to perform the 270° arm movements in Casile and Giese's experiment mainly requires temporally coordinating familiar action components in a new manner. Each of these components would already be linked to its visual consequences. Thus, learning a new temporal coordination pattern between the action components most likely improved participants' ability to temporally parse the visual elements that were already linked to the action components. This would explain the higher sensitivity for slight temporal deviations when observing point light displays of the newly acquired 270° gait pattern.

A second study that directly addressed the establishment of close perception/action links during the acquisition of motor skills was recently performed by Cross, Hamilton, and Grafton (in press). They monitored changes of brain activation in expert dancers of a modern dance ensemble as they learned and rehearsed new dance sequences. The dancers practiced these sequences for about five hours per week for five weeks. During this five-week period each of the dancers was scanned with fMRI once per week. The dancers watched videos of sequences that they were currently practicing as well as videos of relatively similar dance sequences that they were currently not

practicing. After watching a video, they imagined themselves performing the observed movement and then rated their own ability to perform a particular movement.

As in many previous studies (e.g., Blakemore & Decety, 2001; Grezes & Decety, 2001; Jeannerod, 2001; Rizzolatti & Craighero, 2004), action observation and action imagery led to activation of the human mirror system including premotor cortex and inferior parietal sulcus. The first critical finding was that activation was stronger for action sequences the dancers were currently rehearsing than for the control sequences they were not currently rehearsing. The second critical finding was that activation in these areas was highly correlated with the dancers' judgments about how well they were able to perform the observed sequences. This is a clear demonstration that activation in the human mirror system flexibly changes when new motor skills are acquired.

Actor Identity, Action Prediction, and Action Coordination

The experiments described in the previous section suggest that the proficiency with which one is able to perform particular actions affects the perception of similar actions in others. However, there is a particular class of actions every single person is an expert in performing, the actions in one's own action repertoire (Knoblich & Flach, 2003). Accordingly, perceiving one's own actions, for instance, when watching a video of oneself dancing or listening to a recording of one's own clapping, should maximize the activation of common representations for perception and action. The reason is that there should be a high degree of similarity between performed and perceived actions in this case, if the same representations that generated a particular action become activated through observation. As a consequence, one should be able to identify one's own previous actions, to better predict the outcomes of such actions, and to better coordinate new actions with previous ones.

Action Identification

The first experimental psychologist who addressed the identification of self-generated actions was probably the German Gestalt psy-

chologist Werner Wolff (1931). He was interested in the question of whether people "involuntarily express themselves" through their movements. The participants in his experiment were filmed while they walked up and down in a room and carried out a number of actions. They were all dressed in the same loose clothing. This served to remove static anatomical cues. In addition, each film was manipulated to disguise the filmed person's face thus removing facial cues to recognition. This was an attempt to isolate movement kinematics. When the participants watched these films a few days later, they could recognize themselves much better than they could recognize the other persons whom they all knew well. Wolff concluded from these results that people are able to recognize their own "individual gait characteristics." However, there are many alternative explanations for this early result. For instance, it is unlikely that the loose clothing effectively removed all anatomical characteristics, such as the size of a person, the width of his or her shoulders, and so on.

More than 40 years later Cutting and Kozlowski (1977) came up with a modern version of Wolff's self-recognition of gait paradigm that used the point-light technique developed by Johansson (1973). This technique allows one to effectively isolate the movement (kinematic) information from form information. Light sources are attached to the main joints of a person. The person is completely dressed in black and filmed with a video camera in front of a black background. At high contrast the resulting displays show a number of moving dots that give a stunningly vivid impression of human movement that allows one to derive various attributes of the observed actor and the observed actions (for overviews see Casile & Giese, 2005; Thornton, 2006). These attributes include a person's gender (Cutting, Proffitt, & Kozlowski, 1978), emotions (Dittrich, Troscianko, Lea, & Morgan, 1996; Pollick, Paterson, Bruderlin, & Sanford, 2001), and expectations (Runeson & Frykholm, 1983). Furthermore, the properties of invisible target objects of actions, such as weight, can also be derived (Hamilton, Joyce, Flanagan, Frith, & Wolpert, 2005; Runeson & Frykholm, 1981).

Cutting and Kozlowski asked whether people would be able to recognize themselves and their friends from point-light displays of gait. In contrast to Wolff's earlier results, they found that their participants were not better able to recognize themselves than their friends. In a similar study Beardsworth and Buckner (1981) found a small advantage for self-recognition over friend-recognition from

point-light displays of gait. It should be noted, though, that the recognition rates for self and friends in both studies were hardly above chance. At first glance it seems as if these results would contradict the assumption of close perception/action links.

However, recent experiments that looked at self-recognition in different types of bodily motions have provided clear evidence that people are actually quite accurate in identifying themselves from point-light displays. In support of close perception/action links they also demonstrated that one is much more accurate at identifying oneself than identifying one's friends (Loula, Prasad, Harber, & Shiffrar 2005; see also Shiffar, this volume). A further interesting aspect of these findings is that, whereas people were quite accurate in identifying themselves from point-light displays of dancing or boxing, the recognition rates were hardly above chance for actions like walking and running, just as in previous studies.

This suggests that walking was the wrong place to start looking for self-identification effects. But why is it hardly possible to identify one's own walking and running? In hindsight the explanation seems simple. Walking and running are motion patterns that are highly biomechanically constrained. Thus there are hardly any movement cues that would allow one to distinguish one's own walking pattern from a stranger's walking pattern or a friend's walking pattern from a stranger's walking pattern. Movements like dancing or boxing allow for more individualistic styles and thus provide rich kinematic cues for self-recognition.

All of the studies reviewed so far used bodily movements of human actors as stimuli. However, the common coding theory (Prinz, 1997; 2002) and recent findings on the mirror system (Kohler et al., 2002) suggest that any perceivable effect of an action can result in resonance or activation of representations that are used to produce the action. Thus people should not only be able to identify bodily movements as self-generated, but also the visual and auditory effects of different types of actions. Take handwriting as an example. The visual effects of writing and drawing can be described as a simple trajectory of a moving dot with two spatial dimensions and one temporal dimension. Nevertheless, writing and drawing are complex skills that everybody is familiar with (Van Sommers, 1984). Can people identify point-light displays of their writing and drawing?

Knoblich and Prinz (2001) addressed this question in a series of experiments. Although it seems quite obvious that people are able

to identify their writing when they are confronted with a finished product (e.g., a page from their diary), it is less clear whether they can identify their writing from a point-light display that provides only movement information (think of writing with a laser pointer on a white wall). The participants came for two individual sessions that were at least one week apart. During the first session, they produced writing samples of a number of familiar symbols (numbers and letters from the Latin script) and unfamiliar symbols (e.g., letters from Thai and Mongolian scripts) on a writing pad. The kinematics of their writing was recorded (sampling rate was 100 Hz). During the whole recording session the participants' writing hand was screened from view. No visual feedback about the emerging trajectory was provided. In addition, the participants were required to follow a certain stroke sequence and stroke direction for each letter. For instance, in order to produce the letter "P" they were required to start with a down-stroke, lift the pen, and produce the bended stroke from top to bottom. This was required because otherwise stroke sequence could have been used as a further potential cue to self-recognition (Flores d' Arcais, 1994).

In the second session, participants were asked to identify their own writing. They observed two point-light displays of the production of the same symbol. One display reflected the kinematics of the participant's own writing and the other display reflected another participant's writing. Self- and other-produced displays appeared in random order. The task was simply to decide whether the first or second display was self-produced. The participants received no feedback about whether their judgments were correct in order to avoid effects of perceptual learning during the experiment.

The result of a first experiment demonstrated that participants could indeed recognize their own writing based on the minimal information provided by a single moving dot. The same results were observed when self- and other-produced displays were scaled to have the same size and overall duration. Thus, these two potential cues were not crucial for self-identification. However, in an experiment where the dot moved with constant velocity, participants were not able to identify their own writing. The result that particular changes in velocity were crucial for self-identification was further supported by a post-hoc analysis of the characters that led to the highest self-identification rates. It turned out that self-identification was more accurate for characters that required large velocity changes during

production (e.g., characters having corners that lead to a pattern of rapid deceleration followed by rapid acceleration). Interestingly, the accuracy of self–other judgments was not higher for writing samples reproducing familiar symbols.

Taken together, these results show that one is able to discriminate one's own handwriting from someone else's on the basis of a single moving dot. Importantly, velocity changes seemed to be crucial for identifying one's own handwriting, whereas the familiarity of the symbol produced did not affect self-identification. This supports the assumption that self-identification is informed by one's own action system. Velocity changes are clearly an action-related parameter, whereas effects of familiarity would have suggested that identification might be based on mere visual experience. In a sense what participants seem to have recognized is the "rhythm" of their writing (technically speaking, the invariant relative timing of their writing).

This seems to suggest that a similar self-identification advantage for the effects of one's own actions should be present in the auditory domain. Thus, Flach, Knoblich, and Prinz (2004a) conducted another series of studies that explored the identification of one's own clapping. In contrast to trajectories of handwriting, it is possible to remove all spatial information from the sounds of clapping. What remains is pure temporal and acoustic information. Repp (1987) reported some evidence that musically trained participants were able to identify their own clapping from a recording. He suggested that his participants used systematic differences in the acoustical patterns to derive information about their individual hand configurations.

Flach and colleagues' study aimed to determine whether action-related timing information also provides a cue to self-identification. Again, there were two experimental sessions separated by a week. In the first session, participants were recorded while they clapped rhythmic patterns of varying complexity. In the second session, participants listened to a recording of clapping and were asked to indicate whether it reflected their own clapping or somebody else's clapping. In this study, pairs of two participants were formed for the recognition session. The two participants in each pair provided judgments for exactly the same recordings. Half of the recordings reflected a participant's own clapping and the other half of the recordings reflected the other participant's clapping. The same recording that needed to be judged as self-produced by one participant, needed to be judged

as other-produced by the other participant. Thus in this design self-identification cannot be explained by stimulus differences.

The results of a first experiment provided clear evidence that participants were able to identify original recordings of their own clapping. Self-identification was not affected by the rhythmic complexity of the clapping pattern. A second experiment assessed whether self-identification was still possible when one listens to a sequence of simple tones (beeps) that reproduce the temporal intervals between the maximum amplitudes of two consecutive clapping sounds. Although the beep sequences retained the general tempo and the relative timing of the original recording, all other acoustic differences were removed. Thus these sequences did not allow the participants to derive their relative hand orientations using acoustical cues (different hand orientations during clapping systematically produce different sounds; Repp, 1987). Surprisingly, participants were almost as accurate in identifying their own clapping from such beep sequences as from the original recordings. Tempo and rhythmic information provided sufficient cues for self-identification.

A further experiment assessed the contributions of overall tempo and rhythmic information (relative timing) to self-identification. The participants listened to beep sequences that retained the original relative timing of consecutive intervals between claps, but were replayed in the tempo the other participant had chosen for the same rhythmic sequence. In this experiment, participants were not able to identify their own clapping. This result shows that general tempo as well as relative timing information was used for self-identification. If participants had only used general tempo they should have mistaken the other participant's clapping for their own. If they had only used relative timing information they should have been as accurate as for the beep sequences that retained their own tempo.

Taken together, the results show that one can identify one's own actions based on timing information. As in the earlier handwriting study, it is likely that the main cue for self-recognition was a higher activation of participants' own action knowledge when they listened to recordings of their own clapping. Other explanations seem implausible. No cues about the relative hand orientation can be derived from beep sequences. The recognition session took place one or two weeks after the recording session, making it highly unlikely that recognition was based on episodic memories of the production session.

Also, if episodic memory was crucial the original recordings of clapping should have been easier to identify than the beep sequences.

If nonmusicians are able to recognize their own clapping based on rhythmic cues, one would expect that musicians excel at identifying their own performances. And, indeed, most expert musicians are convinced that they are able to tell apart their own performance of a particular piece from somebody else's. But exactly which cues allow, say, an expert pianist to identify her or his own performance? An experiment by Repp and Knoblich (2004) addressed this question. In a first session, 12 expert pianists who were either graduates at the Yale School of Music or took lessons with its piano faculty performed 12 excerpts selected from the standard classical piano literature (Bach, Mozart, and Beethoven). The excerpts had durations of 15 to 20 s. A practice session that included a metronome made sure that the performances had roughly the same tempo and that they were largely error-free. Each pianist received auditory feedback for half of the pieces and no auditory feedback for the other half of the pieces. In addition, the pianists indicated for each piece how familiar it was to them (whether they had heard or played it before).

The recognition session took place approximately two months after the recording session. The pianists listened to 12 performances of each piece, 11 performed by other pianists and one self-performed. For each piece they indicated on a 5-point scale the likelihood that it was their own performance. The pianists knew that only one out of 12 performances was their own. The results showed that the pianists were very good in identifying their own performances. In fact, their average rating for their own performances was higher than the highest rating for any of the remaining 11 pianists.

Interestingly, self-identification was equally good for pieces that were played with and without auditory feedback in the recording session. In addition, self-identification was equally good for familiar and unfamiliar pieces. This suggests that expert pianists were able to identify their style of playing even if they were not familiar with a piece and had actually never heard themselves perform it! So what allows them to identify their own playing? To address this question an additional recognition session was performed (roughly two to three months after the first recognition session). In this session participants listened to recordings from which all dynamic nuances (expressive dynamics) had been removed, leaving only articulation and expressive timing as cues for self-identification. The pianists rec-

ognized these edited recordings as well as the original recordings. Thus, expressive timing and articulation seem to be the main cues for self-identification in expert pianists. Again, the results suggest that self-identification is based on a stronger resonance of the action system with self-generated auditory effects of actions.

Prediction

The previously described studies on action identification show that people can explicitly judge from a recording whether the observed action reflects their previous performance. It was suggested that this ability reflects a more extensive involvement of the motor system in action perception when people observe their own actions. But what is the underlying mechanism? One possibility is that people can "sense" the higher activation of common representations for perception and action that result from the high similarity between perceived actions and the underlying action knowledge (Knoblich & Prinz, 2001). Another possibility is that the higher activation of common representation results in better predictions of the perceptual consequences of actions. As a consequence, observing others' actions leads to larger discrepancies between what is predicted and what is observed (Repp & Knoblich, 2004; Wilson & Knoblich, 2005). One way to test the latter assumption is to test whether people are able to make more accurate predictions when they observe recordings of their own actions than when they observe recordings of somebody else's actions.

To address this issue we investigated whether people are better able to predict the landing position of a dart on a target board when they observe a video of their own throwing movement (Knoblich & Flach, 2001). In the recording session participants were asked to throw darts at the upper, middle, and lower third of a target board until 10 video samples had been collected where the participant intended to hit and actually did hit the upper, middle, and lower third, respectively. After a week, participants returned for a second session where they watched video clips of themselves or somebody else throwing darts. Two participants formed a pair and watched exactly the same stimuli. Each clip showed a side view of a person throwing a dart and ended at the video frame at which the dart had just left the person's hand (the target board was also visible). Participants were asked to predict where on the target board the dart would land.

Participants could predict the landing position of the dart quite well. In initial trials, the predictions were equally accurate for self and other. Only in later trials did the predictions become significantly more accurate for self, although no feedback was provided. Presumably, it took participants some time to adjust to the unfamiliar situation of watching themselves from a third-person perspective. Further experiments varied the amount of information provided about the throwing person. In one of these experiments only the upper body and the throwing arm were visible (the head was hidden behind an occluder to remove cues of gaze direction). In another experiment the whole body of the person except the throwing arm was occluded. Although these manipulations successively decreased the overall accuracy of the predictions, the same pattern of results as in the first experiment was observed for the self-other manipulation. The predictions were equally accurate during the initial trials and the accuracy selectively increased for self-generated throws in later trials. A possible reason for the initial lack of a self-other difference is that a certain time is needed to adjust the predictions to an unfamiliar perspective. After this adjustment, particular aspects of individual throwing seem to have informed and increased the accuracy of the prediction of the outcome of self-generated dart throwing movements.

For a further test of the hypothesis that people are able to more accurately predict the consequences of their own actions we turned again to the domain of handwriting (Knoblich, Seigerschmidt, Flach, & Prinz, 2002). Participants were asked to write different versions of the digit "2" on a writing pad. In addition, they also produced the first stroke of the digit "2" in isolation (two strokes are needed to produce the digit "2"; a bended one that ends at the lower left corner and a consecutive straight one). The kinematics of their writing was recorded. The writing hand was screened from view, so that no visual feedback about the emerging trace was provided.

After a week, participants returned for a second session. They observed kinematic displays of bended strokes. These strokes were either produced in isolation or they were produced in the context of writing the complete digit "2." The latter strokes were obtained by separating the bended stroke from the straight stroke in the kinematic trace. (This was easy to achieve because there is a clear velocity minimum at the transition from the bended stroke to the straight stroke.) A single moving dot reproduced the movement of

the pen tip without painting a static form trace on the monitor. Half of the strokes reflected the participant's own writing and the other half reflected another participant's writing. The task was to decide whether the stroke had been produced as a part of the digit "2" (or in isolation). Thus participants needed to predict whether the observed stroke was followed by another stroke in the original recording.

The results showed that the predictions were at chance for other-produced strokes, but clearly above chance for self-produced strokes. In a further experiment participants were asked to fit their writing within horizontal and vertical auxiliary lines during the production session. The reasoning behind this manipulation was that it should constrain interindividual differences in production (this is why exercise books for first graders use auxiliary lines). Because these laws govern everybody's performance, predictions should be equally accurate for self and other. And indeed, the results showed that participants' predictions were above chance and equally accurate for self-generated and other-generated strokes. Thus, when production was unconstrained, there was a large variability in production between different persons' actions, and predictions were only accurate if participants observed their own productions. When production was highly constrained, all productions reflected general invariants of human performance (Kandel, Orliaguet, & Boe, 2000), leading to accurate predictions for self and other.

Coordination

The finding that people are better able to predict future outcomes of their own actions suggests that the higher resonance between perception and action during the observation of self-generated actions also supports predictive mechanisms. Most likely, these mechanisms are similar to the ones that predict the perceptual consequences of one's own actions when one is currently performing them. This raises the question whether such predictive mechanisms can also help to temporally coordinate one's own actions with those of other people. In order to achieve this one would often have to synchronize the predicted consequences of one's own action with the predicted consequences of a partner's action. Is such coordination more successful when one is coordinating one's current actions with one's own previous actions? In case you are a good dancer, would you be your

best dance partner? More realistically, do expert pianists duet better when they play with themselves?

We investigated this question in a recent study (Keller, Knoblich, & Repp, in press). In a first session we recorded nine expert pianists performing parts of three duet pieces (upper part or lower part, also know as primo and secondo) that were unknown to all pianists (two duets by Carl Maria von Weber and one by Edvard Grieg). Their playing was recorded in MIDI format. In the second session that took place a couple of months later the pianist were asked to perform the duet with a recording of their own playing or somebody else's playing (performing the secundo with a recorded primo or vice versa).

The variable of interest in this study was the accuracy of synchronization with the recording. We predicted that the temporal synchronization error for notes that are nominally simultaneous in the score would be lower when pianists duet with their own recordings. This is what we found. Furthermore, the pianists were able to identify their own performances after they had performed the duet. In fact, there was a high correlation between self-identification and synchronization error. The lower the synchronization error, the more confident the pianists were that they had performed with their own recording. This suggests that the pianists might have used accuracy of synchronization as a cue to self-identification. Note, however, that the previously discussed study on piano experts (Repp & Knoblich, 2004) showed that pianists can recognize their own playing when they just listen to their own performance. Thus, it is unlikely that accuracy of synchronization was the main cue for self-reconizion.

A further study of nonexperts explored whether one can synchronize one's finger taps more accurately to visual events that correspond to one's own writing (Flach, Knoblich, & Prinz, 2004b): In a first session, participants were asked to draw zigzag line patterns with constant or alternating amplitudes on a writing pad. In a second session, participants observed a moving point light display reproducing their own or somebody else's writing patterns. They were instructed to press a button at the exact moment in time at which the dot changed its direction at corners. In order to perform well in this task one needs to time one's own action based on a temporal prediction of the next turning point in the trajectory.

Initially, the task was not easy for the participants, but they learned to perform well in later parts of the experiment. Timing errors between the time of their tap and the time of the turning points in

the visual movement trajectory decreased. After participants had reached an asymptote in their general task performance, differences in timing error were observed between self- and other-generated trajectories. If the trajectories were irregular (changing amplitudes) this error was lower when participants synchronized with a self-produced trajectory. For regular trajectories no self-other differences in timing error were observed. In other words, participants could better coordinate the timing of their actions with self-generated visual trajectories, when they had sufficient practice with the synchronization task and when the production of the trajectories was relatively unconstrained.

Action Perception and Body Sense

So far, the discussion has focused on how the ability to perform certain actions influences how one perceives others (or one's earlier self) performing these actions. The results demonstrate that perception and recognition of others' actions involves a direct, similarity-based matching of perceptual representation of observed actions onto action representations in the observer. Furthermore, the results on prediction and coordination suggest that this match can result in a simulation of the future consequences of the observed action that is based on internal models capturing contingencies between certain movements and the perceptual consequences they produce in the world, given a particular context (cf. Hamilton, Wolpert, & Frith, 2004). However, it is not clear whether peripheral sensation of one's own body is a prerequisite for being able to run such simulations. Do we need continuous input from our tactile and proprioceptive sensors in order to engage in action simulation? In other words, do we need to sense our body in order to fully understand others' actions?

This question was addressed in a study that addressed action perception and action understanding in two individuals who live with the extremely rare condition of selective and complete haptic deafferentation due to a sensory neuronopathy (Bosbach, Cole, Prinz, & Knoblich, 2005). These individuals have completely lost their senses of cutaneous touch and proprioception. Thus they don't have any peripheral information from their bodies below the neck (IW, see Cole, 1995) or below the nose (GL, see Cole & Paillard, 1995). Bosbach and colleagues hypothesized that these patients should have

deficits in action understanding if peripheral sensory information about one's body is required for action simulation.

They tested this hypothesis using Runeson and Frykholm's (1981; see also Grezes, Frith, & Passingham, 2004) box lifting task. In one condition the two deafferented individuals and age-matched controls observed videos of healthy actors lifting boxes having different weights. The actors had been informed about the true weight of the box before they lifted it. The task was to estimate the weight of the box lifted by the actor. In a second condition, the deafferented individuals and the controls watched videos of healthy actors who had been either told the true weight of the box to be lifted or had been deceived about the true weight of the box (e.g., they were told the box was heavy when it was actually light).

Replicating earlier findings (Cole & Sedgwick, 1992; Fleury et al., 1995), the results showed that, for weight judgments, there were no differences in accuracy between the two deafferented patients and controls. However, whereas controls performed quite well in inferring the observed actor's expectation about the weight (correct or deceived?) the two deafferented individuals were hardly able to perform this task (their judgments were close to chance). In fact, both patients' judgments were clearly less accurate than that of the least accurate person in an age-matched control group of 12. A follow-up study showed that neither IW himself nor control participants were able to derive expectations about weight when they observed IW lifting the box.

How can these results be explained? Both, the weight task and the expectation task require deriving a hidden state from the kinematics of an observed action (Runeson & Frykholm, 1981). However, deriving the weight of the box does not seem to require simulating the observed action. In fact, the duration of the lifting phase provided a simple kinematic cue to derive the weight of the box. However, deriving the actor's expectation from the observed action seems to require action simulation that depends on peripheral sensory information about one's body. This seems to be a prerequisite for being able to make use of the more complex kinematic cues that underlie judgments of an actor's expectation (the relative duration of the lift phase relative to the overall duration of the movement). These results imply that the internal models that are used in action simulation are not fully functional when peripheral information about one's own body is missing.

Conclusions

Converging evidence supports the view that the perception of others' actions is constrained and informed by perceivers' body schema and their ability to perform the perceived actions: The same laws that govern performance constrain what is perceived as doable in others. Becoming an expert in a particular action domain sharpens perception of corresponding actions. Perception of one's previous actions informs self-identification and leads to more accurate predictions. The lack of peripheral sensory information updating one's body schema can result in difficulties with using complex cues in action perception.

All of these results suggest close links between perception and action. These links are governed by two functional principles. First, representations of perceptual events that can be caused by one's actions ("common codes") provide a medium in which perception and action are commensurable (Prinz, 1997). This assumption allows one to define similarity relations between perception and action. Second, when common codes are activated, simulation mechanisms in the motor system will predict which events are likely to be perceived next. Such simulations use internal models capturing the contingencies between one's body, one's movements, and the environment. In this way "motor knowledge" is used to provide a context for the perception of future events (cf. Wilson & Knoblich, 2005).
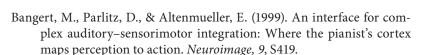
Acknowledging the intricate bounds between perception and action does not leave the study of "higher" cognitive processes unaffected (Pecher & Zwaan, 2005). Language researchers discuss how language is grounded in perception and action (Barsalou et al., 2003; Glenberg & Kaschak, 2002; MacWhinney, this volume). Research in social cognition explores how perception-action links serve to align interacting individuals (cf. Sebanz, Bekkering, & Knoblich, 2006). Thus new research on perception and action will likely lead to a new understanding of how people make sense of the world and of how they interact with their conspecifics.

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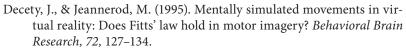
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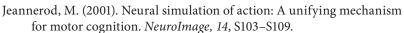
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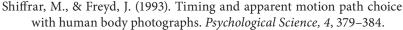
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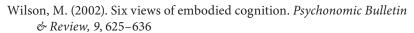
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