Action Perception From a Common Coding Perspective

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Traditional approaches within the field of cognitive science view the mind as a symbol manipulator. This view originated in developments in the computer sciences of the 1950s and led to the then popular analogy between the computer and the human mind (e.g. Newell, Shaw, & Simon, 1958). Characteristic for this mind-as-computer framework is the assumption that perception involves the translation of physical stimuli into symbolic representations (e.g. Anderson & Bower, 1973, Marr, 1982; Kladzky, 1975, Kieras & Meyer, 1997). Once stimuli are perceived, they can be stored in memory as symbolic codes, or these symbolic codes can be passed on to the motor system for action generation. Perception and action form two isolated processes, and action execution is merely a pair of hands (quite literally) that is put to service by higher-level cognitive processes. Perception and the mental operations performed on its products drive action, but action does not influence perception and cognition.

Recent developments cast doubt on the feasibility of this approach as a general framework for understanding human behavior. Researchers increasingly consider perception and action from an embodied perspective. The term embodiment has different meanings in different theoretical frameworks (see Knoblich, 2008; Wilson, 2002). For our purpose, 'embodied cognition' refers to the notion that perception and action are grounded in the physical properties of our bodies as well as the external world we interact with. Thus, perception is not a process that happens in isolation from other cognitive processes in this approach. Similarly, action execution is more than a pair of hands employed by our cognitive machinery. Instead, it is an integral and interactive aspect of cognition itself.

Considering cognition from an embodied perspective has important implications, as it raises a multitude of old and new research questions. It reintroduces the question of how perception and action are represented, how they shape one another, and how others' actions are perceived. For example, do the constraints we face during action execution also influence the way in which we perceive others' actions? Does expertise in a certain action domain influence the way in which we observe actions? What are some of the problems that arise when we consider perception and action from an embodied perspective?

In this chapter, we provide an overview of findings that point to the tight interplay of perception and action, and the implications that follow from it. The chapter is organized in three sections. We first outline a theory in which perception and action rely on similar mechanisms. We then articulate the several claims that follow from this perspective, and provide evidence for them. Finally, we address a paradox that the interplay between perception and action seems to create for the experience of agency.

Common Coding for Perception and Action

Several theories stress the close link between perception and action and their central role for cognition. One such theory is the common coding theory of perception and action (Hommel, Muesseler, Aschersleben, & Prinz, 2001; Prinz, 1997; for an alternative account, see Gibson, 1954). The core postulate of this theory is that perception and action rely on common codes. These codes do not represent actions per se, but instead reflect the perceptual events that actions produce. Because actions are coded in terms of their perceptual effects, perception and action occupy a common representational domain. Thus, perception and action use the same currency in this account. To illustrate what this means, consider two people sitting across from each other at a table. Now imagine that the table has a cup and a jar of coffee on it. If one of the people picked up the jar and poured coffee into the cup while the other person watches, both people would have a very similar representation of the action according to the common coding theory.

As this example indicates, to say that perception and action use a common representational domain implies that action representations may become activated when one observes an action that one is able to perform. This is reminiscent of William James's ideomotor principle (1890), which states that imagining an action (motor imagery) creates a tendency to carry out the action. It extends this principle to the domain of action perception (Greenwald, 1970; Prinz, 1997). A growing body of evidence indicates that perceiving and imagining actions relies on common mechanisms. The common coding theory accounts for the ideomotor principle and perception-action linkages by placing perception, motor imagery, and action in a common representational domain.

The common coding theory for perception and action is a functional theory that does not make particular predictions about neural implementation. It is important to note however that neurophysiological evidence consistent with the common coding theory is rapidly accumulating. The discovery of so-called mirror neurons (cf. Rizzolatti & Craighero, 2004) in macaque monkey first sparked this development. Mirror neurons in premotor and parietal cortex fire when an object-directed action is performed but also when such an action is perceived. Mirror neurons thus provide a possible neural instantiation of the use of a common code for perception and action (see Calvo-Merino, this volume, for a description of the brain areas that comprise the mirror neuron system). The finding that mirror neurons fire only during the observation of goal-directed actions provides evidence that actions may be represented with respect to more distal rather than proximal goals. Although mirror neurons have not been conclusively established in humans (see for example Dinstein et al., 2008), the brain regions underlying action observation overlap with the brain regions underlying action execution (e.g. Gallese & Metzinger, 2003; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Georgieff & Jeannerod, 1998). In addition, it has been claimed that the same mechanisms are involved during the imagery of a motor act and the actual execution of that motor act (e.g., Henrik Ehrsson, Geyer, & Naito, 2003; Jeannerod & Decety, 1995).

Because action perception, action imagery, and action execution occupy a common representational domain in the common coding theory, one would expect interactions between these processes. We will now review different kinds of evidence that suggest the existence of such interactions.

Actions Observation Induces Action Simulation

It has been proposed that common codes for perception and action can be used to simulate observed actions (Blakemore & Decety, 2001; Grush, 2004; Jeannerod, 2001; Wilson & Knoblich, 2005; Wolpert, Doya, & Kawato, 2003). This form of simulation is different from the type of simulation implicated in the debate about theory of mind (e.g. Dokic & Proust, 2002; Goldman, 2006; Harris, 1995), which concerns the simulation of mental states to understand the behaviors of other individuals (putting yourself in another person´s shoes as it were). The basic idea in action simulation is that predictive or internal models guiding performance of one's own actions can be applied to simulate others' actions. Such internal models predict the perceptual consequences of actions, allowing for a faster interaction with the environment and with other actors than would be possible based on feedback alone. If people use internal models to simulate others' actions, then how accurately an observer can predict the consequences of an observed action should depend on how closely the observed action maps onto the observer's own motor repertoire.

One way to address this hypothesis is to test whether people are better at predicting the consequences of observed actions when they perceive their own (earlier performed) actions than when they observe someone else's actions. When people perceive their own actions, such actions map fully onto their motor repertoire. In such a case, if people simulate the observed action then they should perform well when asked to predict the consequences of the observed actions. In contrast, when people observe the actions of another person, such actions map less well onto the observer's own motor repertoire. Thus, in that situation people should perform worse when asked to predict the consequences of such observed actions.

Two studies employed this logic, and provide evidence for it. A first study (Knoblich & Flach, 2001) used a dart throwing paradigm in which participants had to predict the landing position of dart throws when they observed recordings of their own earlier throws or another person's throws. Participants first completed a recording session in which they were asked to throw darts at either the upper, middle, or lower part of a dartboard. Ten successful performances for each of the three areas on the dartboard were recorded and used as stimuli for the second part of the experiment. Participants returned for the second part a week later to minimize the effect of recent experience with performing the throwing actions. In the second part, pairs of participants together watched the video recordings that displayed a side view of the dart throwing motion up until the point at which the dart left the thrower's hand (the dart board was also visible). The thrower in each recording was always one of the two participants in the pair. Thus, in different trials a participant observed either a recording of their own action or of the other participant's action. The participants' task was to predict in which of the areas on the dart board the dart would land. The question of interest was whether observers' ability to accurately predict the landing position of the dart depended on whether they saw themselves or the other.

[Figure 1 here]

The results indicated that participants initially predicted the landing position for their own throws as accurately as others' throws. In later trials, performance was more accurate for observing self than for observing others, regardless of the amount of visual information provided in the recordings. Perhaps the initial lack of a difference in the accuracy of prediction for self and other resulted from the fact that participants observed all throws from a third person perspective. Thus, participants may have had to overcome some initial difficulties with taking this perspective. The results suggest that once they did, prediction for self was better than for others. Thus, particular aspects of the individual's motor repertoire, in this case the way of throwing, seem to have improved the accuracy of prediction during the observation of self-generated dart throwing movements.

Another study on handwriting provides more evidence for this conclusion (Knoblich, Seigerschmidt, Flach & Prinz, 2002). Again, the prediction was tested that people should be better at predicting the consequences of their own earlier actions than at predicting the consequences of actions performed by others. However, this should only be true when the action context allows for sufficient inter-individual variability. In other words, when performed actions are highly constrained by the task context, different participants would necessarily produce very similar actions. As a result, the benefit in predicting the consequences of one's own versus others actions should be strongly reduced or absent in such a case. This is exactly what was found. Participants first completed a recording session in which they generated either the digit "2" or one of its subparts (a "2" requires two strokes; a bended one ending in the lower left corner, and a straight horizontal one) by writing on a digitizing tablet that recorded the pen strokes. The writing hand was not visible during writing to prevent any visual feedback of the pen strokes during production. In a second session conducted a week later, participants viewed kinematic displays of the bended strokes recorded in the first session. They could only see a moving dot that reproduced the recorded kinematic pattern, without leaving a static trace. The task for participants was to indicate whether they thought if the observed bended stroke was followed by another stroke that made it a "2" in the original recording or not. Importantly, the recording was either a participant's own previous performance or somebody else's. In addition, the recorded writing was either in a context where participants had to write between two lines (a highly constrained case in which there is not much room for interindividual variability), or they were spatially unconstrained (allowing for larger interindividual variability). The results revealed that the accuracy of predicting whether another stroke followed the bended stroke or not was higher during observation of self-generated versus other-generated actions, but only for recordings of unconstrained writing trajectories. Thus, the accuracy of prediction depended on how well the observed trajectories mapped onto the observers' own motor repertoire.

The results of the two studies just discussed are consistent with the claim that similar internal models are employed during action observation and action execution. Thus, action simulation appears to occur when one observes actions that one is able to perform. The better the match is between one's own action execution and the observed action, the better is the accuracy with which the consequences of observed actions can be predicted.

Action Expertise Influences Action Observation

If action perception and action execution rely on similar codes, one may expect an influence of one on the other. Thus, action perception may influence action execution, and vice versa. A common approach to examine the influence action has on perception is to take experts in certain domains and to compare their perceptual abilities to those of novices. The central claim here is that if action shapes perception, then what people perceive when they observe a particular action should depend on the extent to which people can perform the perceived action themselves. Thus, perception should be different for someone who does not have much experience with an observed action than for someone with a high level of expertise in performing the observed action. Of course, the question whether action expertise shapes action perception can be examined in different sensory domains. Here, we focus on studies in the auditory and visual domain.

To examine if action expertise shapes auditory perception, Repp and Knoblich (2007) employed a powerful auditory effect called the tritone paradox (Deutsch, Kuyper, & Fisher, 1987) and coupled it with the execution of one of two possible actions. The tritone paradox refers to existence of tone pairs that are perceptually bi-stable despite a change in pitch. Thus, when one tone in the pair is played before the other and participants need to indicate whether the pitch goes up or down from the first tone to the second tone, the perception of the pitch going up or down is equally likely. This is paradoxical because under most conditions an increase in pitch unambiguously leads to the perception of higher tones.

By coupling the two tones with two key presses and varying the direction in which the keys were pressed in succession, Repp and Knoblich (2007; 2009) studied the effect of movement direction on pitch perception. To be able to predict a directional effect of such a manipulation, these authors relied on the fact that for expert pianists rightward movements on the piano keyboard map onto pitch increases, and leftward movements on the piano keyboard correspond to pitch decreases. If action expertise influences auditory perception, then one would predict that expert pianists should be more likely to perceive the pair of tones to increase in pitch when they produce these tones by moving from left to right. Conversely, they should be more likely to perceive the pair of tones to decrease in pitch when they produce the tones by moving from right to left. For novices, this effect should be less strong. The results confirmed these predictions. Thus, action expertise shaped auditory perception.

Increasing evidence suggests that action expertise also shapes visual perception (e.g., Casile & Giese, 2006). For example, Hecht, Vogt, and Prinz (2001) showed that visual perception of movements with a sinusoidal pattern was better for participants that beforehand produced arm movements with a similar timing profile compared to participants that were not first trained to perform such arm movements. This finding was obtained despite the fact that participants did not get visual feedback of their arm movements during the training phase. Thus, the results suggest that visual perception can be modulated by a person's recent movement history.

More recently, several other sources have provided additional support for the notion that performing certain actions can shape visual perception. For example, Abernethy and colleagues (Abernethy, Zawi, & Jackson, 2008; Abernethy & Zawi, 2007) demonstrated that expert badminton players are better at predicting the direction and depth of a badminton stroke than novices based on the kinematics of the lower body and racquet before contact. This was true regardless of the level of detail of the perceptual information provided (i.e. full image versus point-light displays), although the effect of expertise was stronger when the perceptual displays contained linked segments whose motion followed biomechanical constraints that are present during action execution.

Similarly, Aglioti and colleagues (Aglioti, Cesari, Romani, & Urgesi, 2008) examined the relationship between action anticipation and expertise in basketball at a behavioral and neural level. In their study, participants belonging to either a group of novices, a group of coaches and sport journalists experienced with watching basketball (expert watchers), or a group of professional basketball players (expert players) individually watched clips of free throw shots with the task to predict whether the shot would go in the basket or not. The amount of visual information available in the video clips varied parametrically between conditions, such that participants sometimes only saw the very beginning of the throwing movements, sometimes they saw the complete throwing movements plus a part of the ball's trajectory towards the basket, and sometimes they saw something in between.

Overall, the results revealed that expert players were better able to predict the success of the basket shot based on shorter clips than expert watchers and novices. Expert watchers and novices did not differ significantly in their ability to predict the success of shots. Importantly, expert players outperformed expert watchers and novices most strongly when the shown clip ended before the basketball left the hand of the shooter. This result implies that expert players could read the body kinematics of the shooter and use this information effectively to make predictions about performance. Because expert watchers and novices did not show sensitivity to such body kinematics, the results exclude the possibility that the effect can be ascribed to an improved recognition of the actions, as expert watchers should have shown such an effect as well. Instead, the results are most easily accounted for by assuming that expert players ran a motor simulation during which they matched the observed actions with their own action repertoire when they watched the clips. Doing so allowed them to make better predictions about the outcome of the observed actions.

The results of a second experiment indicated that at a neural level both expert players and expert watchers showed an increase in motor-evoked potentials when they watched clips of basketball shots, but not when they watched clips of soccer kicks or static images of basketball. Novices did not show such action specific effects. The finding that both expert players and expert watchers showed an increase in motor-evoked potentials suggests that both visual and motor expertise may induce action simulation during action observation when the observed action maps onto the domain of visual or motor expertise. However, for expert watchers the action itself does not map onto the observer's motor repertoire, whereas for expert players it does. Thus, it is likely that both visual expertise and motor expertise induce motor simulation, but the nature of this simulation is probably more directly related to the observed actions for people with motor expertise than for people with visual expertise. The results of the Aglioti et al. (2008) study suggest that when an observed action maps onto one's own visuo-motor repertoire, this mapping provides a source of information that an observer uses to enhance the ability to predict the outcome of observed actions.

Besides predicting the outcome of observed actions, information based on perception-action coupling has also been shown to influence the ability to detect deceptive intentions of players in a variety of sports (e.g. Canal-Bruland & Schmidt, 2009; Jackson, Warren, & Abernethy, 2006; Sebanz & Shiffrar, 2009). In such studies, people who are experts in performing the observed actions systematically outperform novices in terms of their accuracy to detect deceptive intentions. For example, Sebanz and Shiffrar (2009) recently asked experts and novices in basketball to watch video clips or static images of a basketball player passing or faking to pass the ball to another player. During the recordings of the videos a defender tried to interrupt the pass to ensure that the fake passes were truly deceiving. Thus, the experimental videos that showed a fake pass only consisted of cases in which the defender had in reality been faked out. The defender was never visible in the videos however. The videos showed the player right up to the point when the ball was about to leave the player's hand. In the picture conditions, only the posture of the player right before passing was shown. Participants indicated whether they thought the player was about to pass or fake a pass.

The results indicated that participants who were experts in basketball outperformed novices in terms of the accuracy of their judgments, but only when they watched the full videos. Thus, when the judgment was based only on static information (the last image of the video), experts and novices did not differ in their accuracy. In a second experiment, participants again watched videos of real and fake passes but now they only saw videos showing point-light displays of the player's body movements. Again, experts outperformed novices. Experts performed better when they saw a front view of the player versus when they saw a half-profile view. Together, the results suggest that experts used kinematic information to infer the intentions of players they observed.

One problem for the interpretation of these results is that people who are expert watchers are often also expert players. Thus, it is unclear whether experts performed better than novices because of their perceptual expertise, their motor expertise, or both. Although perceptual expertise has been shown to influence the accuracy of perceptual judgments (e.g. Behrmann & Ewell, 2003; Jacobs, Pinto, & Shiffrar, 2004), the influence of motor expertise on such judgments may be even stronger (Loula, Prasad, Harber, & Shiffrar, 2005).

The observation that one's own action repertoire influences action observation raises the question of how early in life such effects arise. If action and perception develop hand in hand, one would expect to find evidence for an influence of action expertise on action observation in early infancy. Indeed, van Elk and colleagues (van Elk, van Schie, Hunnius, Vesper, & Bekkering, 2008) provided neural evidence for such effects for 14- to 16-month old infants. In their study, infants watched video clips of crawling or walking infants while recording their EEG, eye movements, and body kinematics. The results of this study revealed a stronger desynchronization in the mu- and beta-frequency bands of the EEG recordings for watching crawling versus walking. Stronger desynchronization in these frequency bands has been shown to relate to an increase in motor resonance. In addition, activity in the mu- and beta-frequency bands of the EEG recordings correlated with the infants' own crawling and walking abilities. Thus, infants showed stronger motor resonance for actions that they had more experience with (crawling versus walking), and the strength of such motor resonance depended on their action capabilities. These findings suggest that action production and action observation interact already at a very young age.

Functional imaging studies further corroborate how action expertise influences action observation. Calvo-Merino and colleagues (Calvo-Merino, Glaser, Grèzes, Passingham, &

Haggard, 2005) performed a study in which they asked novices and experts in either capoeira or classical ballet to observe video clips of either Capoeira or classical ballet movements. Capoeira is an Afro-Brazilian dance style that is distinctly different from classical ballet. Whereas classical ballet mostly involves producing elegant, swift and smooth movements, capoeira features aspects of martial arts such as sweeps, kicks, and head butts. Thus, Capoeira and classical ballet consist of a different set of motor actions. As a result, watching Capoeira mapped onto the motor repertoire of Capoeira dancers, but classical ballet did not. For classical ballet dancers, the opposite was true. For novices, neither of the two categories of dance mapped onto their own motor repertoire. The main hypothesis was that observing actions that one can perform would give rise to more activation in brain areas underlying action execution than actions that one cannot perform.

The results were in line with the hypothesis. Parts of the premotor cortex, the intraparietal sulcus, the right superior parietal lobe, and the left posterior superior temporal sulcus showed greater activation for actions that matched a person's own action expertise compared to actions that did not match a person's own action expertise. These results provide support for a simulation account of action observation, according to which observing an action results in a mental simulation of the action, as if the observer performed the action him or herself.

One problem for the interpretation of the results described above is that expert dancers not only have more experience with performing the dance movements, but also with watching them. Thus, it is unclear whether the dance-dependent brain activation is due to expertise in performing, observing, or both. To address this concern, Calvo-Merino and colleagues (Calvo-Merino, Grèzes, Glaser, Passingham, & Haggard, 2006) asked expert ballet dancers to watch movies of ballet dancers. Importantly, the gender of the observed dancer either matched or did not match the gender of the observer. This manipulation is powerful because in ballet many of the movements are gender-specific. Thus, although ballet dancers have visual expertise for ballet movements for both genders, they only have motor expertise for the ballet movements for their own gender. By comparing brain activation when observers watched movements for their own gender versus for the other gender, the authors showed an increase in brain activation in areas associated with action execution for movements that matched the observers' motor expertise. Thus, the strength of action simulation depends on how familiar the observed physical action is for the observer. It is important to note that this result does not imply that action simulation does not take place for observed actions that a person is less familiar with. Instead, it suggests that action simulation may be less strong in such cases.

Finding a difference in brain activation based on the level of familiarity with the physical execution of the observed action suggests that one should be able to establish changes in brain activation when people observe actions that they are learning to perform. Indeed, Cross and colleagues (Cross, Hamilton, & Grafton, 2006) reported exactly such changes in brain activation during action observation while experts in modern dance learned a new dance pattern. In their study, participants practiced a new dance pattern for five hours a week over a period of five weeks. From the second week of the study onwards, participants also completed a scanning session in which their brain activation was measured while they watched recordings of dance patterns. Half of the recordings matched the dance pattern that they were learning to perform, and half of the recordings were of a different dance pattern that they were not familiar with. After each recording, participants indicated to what extent they felt that they were capable of performing the observed action.

The results indicated that motor areas became active during the observation of the dance patterns. Importantly, the activity in the inferior parietal lobule and ventral premotor areas scaled with physical competency, such that activation in these areas was stronger for actions that participants felt they could perform themselves.

In a follow-up study, Cross and colleagues (Cross, Kraemer, Hamilton, Kelly, & Grafton, 2009) asked whether increased activation in motor areas of the brain could also emerge from increased perceptual expertise. This possibility is of particular importance for the common coding theory of perception and action. If action observation and action execution rely on common codes, and if increased motor expertise leads to increased activation in action-related brain areas, then perceptual expertise should do so as well. To test this claim, Cross and colleagues trained inexperienced participants on a computer dance game called Dance Dance Revolution. In this game, participants perform dance patterns by stepping on targets positioned in front or behind them, and to the left or to the right of them. Different patterns can be produced in this game. Before the study started, participants first completed a scanning session in which their brain activation was recorded while they watched videos of people performing eighteen different dance patterns. The participants then completed five consecutive days of training in which they practiced performing six of the dance patterns and also watched a person perform six of the other dance patterns. Thus, participants completed physical training for six dance patterns, and they completed observational training for six other dance patterns. After the training period, the participants again completed a scanning session in which they watched the six dance patterns they had practiced physically, the six patterns they had observed, and six untrained patterns. A general question was whether brain activation during observation of the trained dance patterns would differ from the untrained dance patterns. A more specific question was whether there would be a difference in brain activation during observation of dance patterns that participants physically practiced or observed repeatedly. The common coding theory predicts that no difference between these two cases should be observed because observation leads to similar activation of action representations as action performance.

The results confirmed that motor activation during observation differed for trained versus untrained dance patterns, but did not depend on the type of training. Thus, training through observation and physical training yielded similar changes in brain activation. This result suggests that when people gain expertise with certain actions, it changes their representation of those actions. Importantly, such expertise could be either visual expertise or motor expertise, thus suggesting that a common code underlies these two domains of expertise. These findings raise the question what visual and motor expertise share and how people manage to enhance one form of expertise on the basis of the other. One possibility is that people are highly sensitive to timing information. Such information forms an invariant that both visual and motor signals carry.

Constraints for Action Production in Action Observation

The previous two sections suggest that action production influences action perception and vice versa. Thus, the reviewed findings are consistent with the common coding framework. However, to strengthen the claim that action execution and action observation rely on a common code it would help to show that the principles that govern action execution also govern action observation. Support for this claim comes from studies on the two-thirds power law (Lacquaniti, Terzuolo, & Viviani, 1983) and on Fitts's law (Fitts, 1954; Fitts & Peterson, 1964).

Two-Thirds Power Law

The two-thirds power law (Viviani, 2002; Viviani, Baud-Bovy, & Redolfi, 1997; Viviani & Stucci, 1989, 1992) captures the relationship between the velocity and the amount of curvature of a movement. In particular, the law states that the velocity of a movement increases as the curvature of the movement trajectory decreases. It is intuitive to think of this relationship in the context of driving a car. When there is a turn in the road while driving, one needs to slow down to negotiate the turn. The amount of slowing down is related to the sharpness of the turn, such that drivers (at least those who live) slow down more for sharper turns. Interestingly, although the consequences of taking a turn with too high a speed are usually not as severe as for driving, people show a similar relationship when they move their body. Originally the two-thirds power law was established based on data from handwriting trajectories, and it has since been shown to hold for many other types of movements such as manual tracking (Viviani, Campadelli, & Mounoud, 1987; Viviani & Mounoud, 1990) and tracking of a target with one's eyes (de Sperati & Viviani, 1997). Thus, as curvature increases, velocity decreases.

If the two-thirds power law holds for action execution, then based on the common coding framework it should also constrain action observation. Indeed, several studies provide evidence that action observation also complies with the two-thirds power law. For example, Viviani and Stucci (1989) asked participants to watch ellipsoidal movements with the task to estimate the eccentricity of the observed movements. The results indicated that participants' estimates were biased towards the curvature that would be expected for the velocity of the observed movement based on the two-thirds power law. In another study, Viviani and Stucci (1992) showed that participants perceived a moving dot to move at a constant velocity when the velocity was not constant. Instead, participants perceived the velocity to be constant when the movements of the dot followed a velocity profile that was consistent with the two-thirds power law. Thus, perception of movement clearly followed the constraints of the human motor system. Such effects are not limited to the visual modality but also occur for kinesthetic perception, for example when a robot moves a participant’s arm along different elliptical trajectories (Viviani, Baud-Bovy, & Redolfi, 1997).

Finding that both action production and action observation follow the two-thirds power law raises the possibility that people use this law for predicting the future course of actions as well. Indeed, prediction of the future course of a handwriting trajectory is much better when the trajectory follows the two-thirds power law than when it does not (Kandel, Orliaguet, & Boe, 2000; Kandel, Orliaguet, & Viviani, 2000). Similarly, Flach and colleagues (Flach, Knoblich, & Prinz, 2004) demonstrated that people’s representational momentum, the tendency for a representation of perceived motion to precede the actual position of the perceived motion (Hubbard, 1995, 2005; Kerzel, Jordan, & Muesseler, 2001), is influenced by the extent to which the observed motion follows the two-thirds power law. Thus, people could better anticipate the future trajectory of a movement when its velocity profile changed in correspondence with characteristics of human movement. Together, demonstrating that the two-thirds power law constrains action observation provides strong evidence for common coding of perception and action, to the extent that motor constraints shape action observation.

Fitts's Law

Research on Fitts's law indicates that the influence of motor constraints on action observation extends beyond the two-thirds power law. Fitts's law relates to the time it takes people to move between two targets. It states that the width of the two targets and the distance between them determine the time it takes to move as fast as possible from one target to another target. In particular, movement time increases with increasing amplitude (the distance between the targets) and with decreasing target width according to the following equation:

$$MT = a + b*ID,$$

where MT is movement time and a and b are empirical constants. ID refers to the index of difficulty. The index of difficulty depends on the amplitude (A) and target width (W) in the following way:

$$ID = \log2(2*A/W)$$

Because the index of difficulty depends on both movement amplitude and target width, Fitts's law predicts that different combinations of the two result in similar movement times. Thus, moving between targets that are 16 cm apart and have a width of 4 cm should take as long as moving between targets that are 32 cm apart and have a width of 8 cm (both have ID = 3). Fitts's law is probably the most studied and replicated law in human motor control (Plamondon & Alimi, 1997), and has been shown to hold for different movement types (discrete and cyclical), for different effectors (finger, arm, leg, and head), and in different context. Importantly, Fitts's law does not require the execution of a movement, but also holds when people are asked to imagine moving between two targets (Decety & Jeannerod, 1995). This finding suggests that Fitts's law relates to a relatively abstract, representational level of action planning.

If motor constraints shape action observation, then one would expect Fitts's law to hold when people observe movements as well. To test this prediction, Grosjean, Shiffrar, and Knoblich (2007) asked participants to watch two alternating pictures of a person or a robot moving between two targets at different speeds. The target pair differed in amplitude and width. Participants watched pictures that created apparent motion between the targets instead of videos of full movements because Fitts's law does not make predictions about movement trajectories. Participants judged whether or not the actor could perform the observed action at the observed speed. The maximum perceived speed at which participants judged the observed movement to be possible was defined as the speed for which participants provided an equal proportion of "possible" and "impossible" judgments.

[Figure 2 here]

The results showed that Fitts's law holds for action perception, because the index of difficulty of the observed actions showed a very strong positive correlation ($r^2 = .96$ for human displays and $r^2 = .93$ for robot displays) with the perceived movement time that participants judged to be just possible. The finding that movement time correlated strongly with the index of difficulty and not just with target width or movement amplitude suggests that the same speed-accuracy tradeoff that exists for action execution and motor imagery also shapes action observation. This finding provides strong support for the use of common codes for action execution and action observation.

If action observation and action execution rely on common codes, then one would expect that deficits in one of these domains should also manifest themselves in the other domain. Thus, neurological impairments that result in deficits in action execution should be accompanied by deficits in action observation. Using the Fitts's law paradigm described above, this is exactly what Eskenazi and colleagues (Eskenazi, Grosjean, Humphreys, & Knoblich, in press) found. Patient DS, who suffered from a frontal brain lesion, displayed a deficit with ignoring target size during action execution. This deficit extended to action observation as well. Thus, when asked to judge whether observed movements at certain speeds were possible or not, patient DS systematically ignored information about the size of the targets. These results provide further support for the notion that perception and action rely on common codes.

Agency and Common Coding

Although common coding provides a parsimonious mechanism for action observation, it also raises a problem: How do people know whether they caused an action or observed one? In other words, given the overlap of codes for action observation and action execution, how do people distinguish between the two to determine agency? The term agency refers to the feeling of being the causal source of a behavior (Sato & Yasuda, 2005).

A minimum requirement for experiencing agency over an action may be that one has a representation of the performed or observed action. By the term representation we simply mean the availability of a code that in some way corresponds to the action. However, having an action representation may be a necessary condition but cannot be a sufficient one. Because action execution and action observation employ common codes, having an action representation does not signify whether the code corresponding to such a representation originated from action execution, action observation, or both.

How is agency over an action determined then? One proposed theory for the experience of agency is the theory of apparent mental causation (Wegner, 2002). According to this theory, actors may experience agency over an action when a thought about the action arises just before the action occurs, when the action is consistent with the thought, and when no clear other cause for the action is present. Central to Wegner's argument is the observation that illusions in the experience of agency can be elicited under certain conditions. For instance, people may feel that they switched on the lights even though someone else did a moment earlier. This raises the question to what extent our experience as being a causal agent is at all veridical.

However, focusing on the role of general principles of causality neglects the fact that perceptual and sensorimotor cues can be used to determine agency. Thus, a more comprehensive theory for the experience of agency requires identifying the cues that people use to determine agency, and specifying how such cues interact. Other proposals to explain agency focus on the role of different cues for determining whether one has caused perceived events. These proposals vary in the importance they ascribe to cues that are private to the actor (sensorimotor cues), and cues that are shared with others (perceptual cues). Whereas sensorimotor accounts do not predict difficulties in determining agency for self and other, accounts focusing on the role of perceptual cues do predict such difficulties.

The sensorimotor account states that when people perform an action they form a prediction or forward model about the sensory consequences of the action (e.g. Wolpert & Kawato, 1998). According to this account, when the sensory consequences match what is expected based on the forward model, people experience themselves to be the source of the action (e.g.

Blakemore, Wolpert, & Frith, 2002; Haggard, 2005; Tsakiris, Prabhu, & Haggard, 2006). For example, when you pick up a cup, you experience agency because the motor commands sent to the hand match the sensory feedback that arises from moving. Thus, the exact motor commands to generate the action provide a central cue for agency in this account. Whether perceptual cues resulting from one's own and others' actions play an additional role is not specified.

Perceptual accounts of agency emphasize that such perceptual cues are crucial for determining agency because actions are planned in terms of their perceptual consequences rather than in terms of motor commands. In this view, people are more likely to focus on perceivable action consequences rather than sensorimotor cues that are private and often not accessible to awareness. As perceptual cues may result from one's own or others' actions, perceptual accounts predict that it should be difficult for people to distinguish between self-generated and other-generated actions. In particular, Jeannerod and colleagues (e.g. Georgieff & Jeannerod, 1998) have stressed the overlap of mechanisms for action production and action observation, much like common coding. For example, they showed that people adjust their actions to perceived visual feedback without explicit awareness, while ignoring sensorimotor cues arising from their movements (Fourneret & Jeannerod, 1998). These findings confirm that perceptual cues play a central role in the experience of agency and demonstrate that misattributions can occur as a result of ambiguities in the perceptual domain. As the perceptual consequence of an action may stem from one's own or another's actions, it is easy to get confused about who did what. This may provide an alternative account for misattribution errors interpreted within the mental causation framework (Wegner, Fuller, & Sparrow, 2003; Wegner & Wheatley, 1999).

However, most of the time, people do infer agency correctly. How is this accomplished? Jeannerod and colleagues propose a who-system that tracks the source of actions. Whereas perceptual cues for action identification are processed relatively automatically, the who-system is thought to operate at a more conscious level. Patient studies and studies with healthy controls provide evidence (see Jeannerod, 2009) for the existence of two largely separate brain substrates underlying the processing of perceptual cues (cerebellum) and the operating of the who-system (posterior parietal cortex).

Although the who-system has been pinpointed in terms of its neural substrate, its functional properties are less clearly defined. One possibility is that the content representations obtained through perceptual cues are tagged by the who-system. In particular, the who-system could provide a time-tag that provides an agent with information about when they generated an action in time. If an action code becomes available that temporally matches the issuing of a time-tag provided by the who-system, then an agent experiences to be the causal source of the action. Thus, the time-tag would originate from a private mechanism, and be linked to the content representations or common codes that are shared with others. This could provide a way to integrate sensorimotor and perceptual accounts of agency, in that private -sensorimotor- cues would be matched up with shared perceptual cues, thus exploiting all available cues for agency.

If this account holds, then people should be quite sensitive to the timing of perceptual cues for inferring agency. The precise timing of perceptual events should be used to inform an agent about whether they are the source of an action or not. Several studies have investigated the timing of perceptual events as a cue for determining agency. Importantly, these studies focus on the detection of switches in agency (gaining or losing control over perceptual events) while people are listening to perceptual events. By eliminating action production in some conditions, the role of timing cues for determining agency can be studied in isolation.

Knoblich and Repp (2009; see also Repp & Knoblich, 2007) employed this method to study the relative contribution of perceptual cues and sensorimotor cues for the experience of agency. The authors asked participants to perform an agency detection task. Participants either only listened or actively tapped along with tone sequences that were either recordings of the participant's own tapping (self-control) or computer-generated with a fixed interval between taps (external control). The tones switched from one form of control to the other at some unpredictable point in the sequence. Participants had to indicate when they perceived such switches from one mode of control to the other. Importantly, active tapping versus passive listening created a comparison to evaluate the relative contribution of sensorimotor cues and perceptual cues for the ability to detect switches in agency. In the active conditions participants could use both sensorimotor cues and perceptual cues, whereas participants could only use perceptual cues in the passive conditions. If participants can detect switches in agency based on perceptual cues alone, then they should perform above chance in the passive conditions. In addition, if people make use of sensorimotor cues for the detection of agency, then performance should be better in the active conditions than in the passive conditions. Finally, the reliance on sensorimotor cues relative to perceptual cues may depend on action expertise. In particular, one may expect that having action expertise increases the reliance on sensorimotor cues for particular actions, as experts have more experience with such cues. The results confirmed each of these predictions. Importantly, the results suggest that the variability in the timing of perceptual events is used as a cue for determining agency, as evidenced by the finding that participants performed well above chance in the passive conditions in which they did not have sensorimotor cues at their disposal. Other studies further substantiate the observation that timing cues are central to the detection of agency (e.g. Flach, Knoblich, & Prinz, 2003; Daprati et al., 2007).

The above-described findings indicate that perceptual cues are used to determine agency. This observation raises the interesting possibility that people use such cues not only to determine agency for themselves, but also for determining agency in others. The use of common codes for action observation and action production may provide a representational ground to attribute agency to others in much the same way as people do for their own actions. One potential problem is that people would not have a time-tag issued by the who-system to temporally match the perceptual cues provided by the other's actions onto their own action system. However, this could be resolved by generating a time tag through simulating the other's action. Thus, when combined with a mechanism that allows one to simulate other's actions in real time, common coding not only provides a representational mechanism for integrating actions of self and other, but may also provide a common ground for inferring agency for self and others.

Conclusions

Our overview of findings on the interaction between perception and action suggests that viewing perception and action as independent processes in the service of higher-level cognition is outdated. Rather, action production and action perception rely on common representations, enabling and constraining the simulation of perceived actions as a function of the perceiver's own action system. Importantly, perceptual cues that are shared for self and other do not only provide a way of mapping the "what" of others' actions onto one's own repertoire, but also allow one to exploit timing mechanisms for predicting others' actions. Such mechanisms may also play a critical role in determining agency for self and others.

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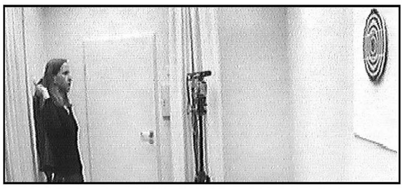
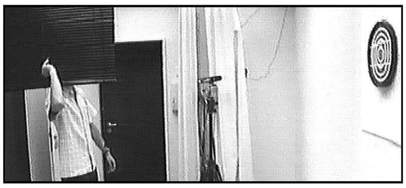
CAPTIONS

Figure 1. Manipulations (left panel) and results (right panel) from Knoblich and Flach (2001. Participants showed an increase in sensitivity (d') to motion cues for their own actions versus the actions of another person, as reflected in more accurate prediction of dart landing positions for self versus other in the second half of the experiment.

Figure 2. Stimuli and results taken from Grosjean, Shiffrar, and Knoblich (2007). The left panel shows the human and robot displays with variations in target width and movement amplitude. The right panel shows that Fitts's law holds for observation of apparent motion for human (a) and robot displays (b), as evidenced by the scaling of the perceived minimum possible movement time with the index of difficulty.

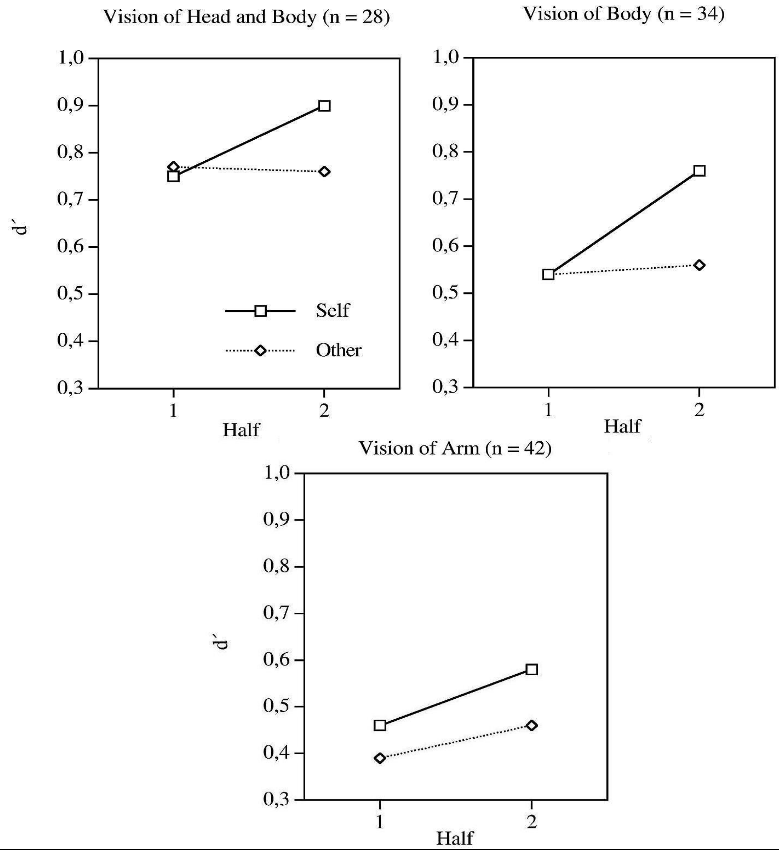


(a) Group 1: Vision of head and body



(b) Group 2: Vision of body

(c) Group 3: Vision of arm



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