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Perceptual resonance: action-induced modulation of perception

Simone Schütz-Bosbach and Wolfgang Prinz

Max Planck Institute for Human Cognitive and Brain Sciences, Department of Psychology, Leipzig, Germany

A direct relationship between perception and action implies bi-directionality, and predicts not only effects of perception on action but also effects of action on perception. Modern theories of social cognition have intensively examined the relation from perception to action and propose that mirroring the observed actions of others underlies action understanding. Here, we suggest that this view is incomplete, as it neglects the perspective of the actor. We will review empirical evidence showing the effects of self-generated action on perceptual judgments. We propose that producing action might prime perception in a way that observers are selectively sensitive to related or similar actions of conspecifics. Therefore, perceptual resonance, not motor resonance, might be decisive for grounding sympathy and empathy and, thus, successful social interactions.

Introduction

If you have never played tennis in your life, you will probably never think of buying a ticket to watch a game at Wimbledon. You probably cannot feel the same joy in watching a match as somebody who played tennis from early childhood on. The motoric knowledge of the tennis fan acquired through personal experience might help to 'relive' the observed moves of the players, thereby leading to a more intensive experience and fun when watching their game.

Indeed, over the past decade, cognitive and neuroscientific research has boosted the idea of the existence of a mirror system in our mind and brain. This system simulates the actions we observe [1] by mapping an observed action onto a motoric representation of the same action in the observer, thus activating specific cortical networks [2]. Such a mirror mechanism implies that, at some level, action must be intrinsically linked to perception. This modern motor theory of (action) perception has its roots in the early work of Lotze [3]. Following Lotze, James [4] stated that the mere imagination of an action is sufficient to excite the motor programs used for executing this action. Later, Greenwald [5] put a similar thought forward by claiming that action can be induced automatically by externally perceived information. This so-called ideomotor principle of action control stresses that actions are represented not only in terms of body movement but also in terms of the distal perceptual effects they aim to generate. In this way, action and perception are commensurate (i.e. they share the distal reference) and are coded in a common representational medium [6]. When a certain movement is performed, an association is created between the motor pattern it is generated by and the sensory effects it leads to. This association can then also be used in the reverse direction, such that a movement can be induced by anticipating or perceiving sensory effects [7].

To date, researchers have specifically emphasized the potential social role of mirror mechanisms. Mirroring the actions of others might help to understand what another person is doing [2] or to predict what he/she is most probably going to do next (e.g. [8–12]). Finally, it might even underlie more sophisticated mental abilities, such as understanding the intentions of others (e.g. [13]). All these potential functions consider the possible role of mirror mechanisms from the perspective of the perceiver (c.f. Figure 1).

The functional analysis proceeds from (action) perception to action production (for an overview, see [10,14]) and can be subsumed under the notion of 'motor resonance'. Here, we suggest that this view is incomplete and perhaps even misleading. Social interactions involve at least two individuals who alternately take the role of perceiver and actor. To complete the picture, one also needs to consider the possible role of mirror mechanisms from the perspective of the actor. Given this view, the functional analysis must proceed from action production to action perception. We suggest that this perspective might reveal further important functions of mirror mechanisms, which we subsume under the term 'perceptual resonance'. Producing action will prime perception in a way that observers are selectively sensitive to action-related events in the environment and similar actions of conspecifics. The individual thus might be selectively sensitive to those actions that are related to and share features with his/her own actions. Perceptual resonance could therefore play a key role in grounding successful social interactions, as it provides a basis for sympathy, empathy and joint action.

The aim of this article is to draw attention to the effects of perceptual resonance to (others') action. These effects have so far largely been neglected in modern motor theories of social cognition. To this end, we will review recent empirical evidence showing when, how and why action modulates perception. Finally, we will also speculate that a mirror system might play an important role for constituting the mental self.

On-line effects of motor action on perception

A number of behavioural paradigms studied how the planning and execution of an action influence concurrent

Corresponding author: Schütz-Bosbach, S. (bosbach@cbs.mpg.de).
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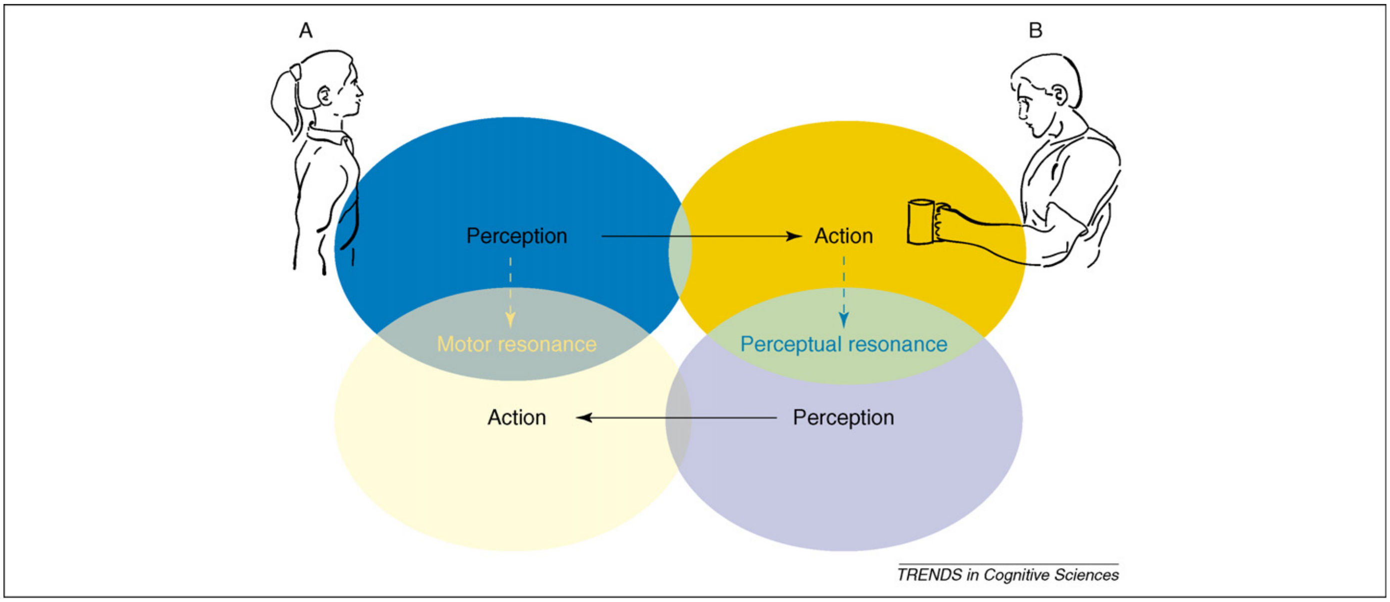

Figure 1. Motor and perceptual resonance. Modern theories of social cognition assume a direct relationship between action and perception, and argue that observed actions are mapped onto a motoric representation of the same action in the perceiver (individual A, who perceives actions of individual B). Perceiving action can thus induce motor resonance and a disposition to execute what one observes. A common representation of action and perception, however, also suggests that action production will prime action perception in the actor (individual B). Namely, it increases his perceptual sensitivity to those actions of other individuals that are similar to his own action (perceptual resonance).

perceptual encoding processes. The results suggest that action-induced modulation of perception can take the form of contrast or assimilation. Acting observers can be less sensitive (i.e. contrast effect) or more sensitive (i.e. assimilation effect) to visual stimuli that are similar to their action.

Contrast effects

One of the first examples is the effect of 'action-induced blindness' to response-compatible stimuli [15]. Researchers demonstrated that pressing or planning to press a left- or right-hand key impairs the identification of an arrow pointing in the congruent direction. That is, pressing a left-hand key impairs the identification of leftward-pointing arrows. In line with a common coding approach, it has been argued that, because of representing a certain direction (e.g. left) that specifies a current response, participants are temporally less sensitive to stimuli that share the directional feature of the response (e.g. left arrows) [7].

In a similar vein, Miall *et al*. [16] showed that producing hand movements facilitates the concurrent visual discrimination of deviant hand postures. These authors asked participants to detect an oddball hand image that diverged from other images presented in sequence. The oddball was detected faster when it appeared in a sequence of images that were congruent with the gestures that participants concurrently performed. This indicates that we are more sensitive to perceptual events that are deviant from the anticipated sensory effects produced by our own movements. This assumption has recently gained further support. Zwickel *et al*. [17] asked participants to move their hand along a predefined linear trajectory (c.f. Figure 2). At the same time, they watched an independent visual stimulus that moved on a screen. Critically, the visual stimulus motion deviated unpredictably in a corresponding or non-corresponding direction. Motion deviations of the visual stimuli were detected faster when they deviated in a direction that did not correspond to that of the produced hand movement.

A similar contrast effect has also been reported for complex body movements. Lifting or holding a box of varying weight can systematically affect perceptual judgments of the weight of a box lifted by another person [18]. Hamilton *et al.* asked participants to lift or hold a light or heavy box while simultaneously observing a movie of another person lifting an identical-looking box of varying weight. At the end of the movie, participants were required to estimate the weight of the box lifted by the actor in the movie. Interestingly, participants overestimated the weight of the box when they themselves had concurrently lifted or held a light weight, and they underestimated the weight when they lifted or held a heavy weight. Commensurate with this, other researchers reported an interference effect between observer movement and the visual analysis of a similar movement of another [19]. Stationary or walking observers were asked to judge the gait speed of another person who was presented as a point-light display in a movie. Walking observers showed significantly lower discrimination performance than stationary observers. However, walking in itself requires more attentional capacity than standing. Therefore, one cannot rule that the reduced perceptual sensitivity of walking observers simply reflects a capacity limitation due to the dual-task requirements (c.f. [20]). The empirical findings reviewed so far indicate that action can increase perceptual sensitivity to those events that do not share features with what a person is concurrently doing.

Assimilation effects

However, there is also evidence from several studies showing assimilative influences of action on concurrent perception. For instance, Wohlschläger [21] asked participants to turn a knob either from left-to-right or from

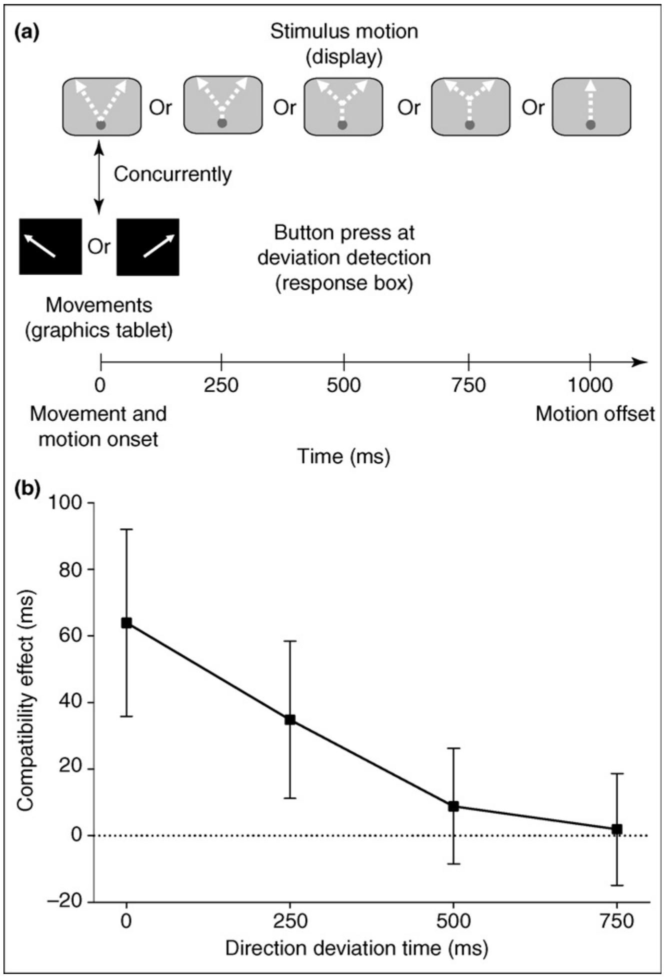

Figure 2. Experimental procedure and results described in [17]. **(a)** Participants were instructed to perform a diagonal hand movement to the left or right while they observed the motion of a single dot on-screen. Critically, the dot on the screen deviated to the left or right from its initial (vertical) direction at different time points, and this deviation either did or did not correspond to the ongoing movement that participants produced. Participants were required to press a button as soon as they detected a deviation in stimulus motion away from vertical. **(b)** Two major results were obtained. First, a reversed compatibility effect (i.e. compatible minus incompatible mean reaction times) was found, indicating that motion deviations were detected later (i.e. participants' reactions were slower) when the dot went in a direction that was compatible with that of the produced movements. Second, the results also showed that the size of the compatibility effect decreased with increasing onset time of the direction deviation of the visual stimulus. The later the deviation occurred, the smaller the compatibility effect, indicating that action-induced interference on perception is a function of the temporal overlap between movement production and motion perception (c.f. [16,23,24]). Reproduced with permission from [17].

right-to-left, while they observed a perceptually bistable apparent rotation of an object. The perceived motion direction turned out to be biased in the direction of the produced motion direction. A similar effect has also recently been demonstrated for the auditory domain [22]. Repp and Knoblich presented pairs of two tones that were related by a half-octave (tritone). Playing these tones in alternation normally produces in some listeners the illusion of a descending melody, but in others an ascending melody. Thus, the pairs of tones are perceptually ambiguous with respect to the direction of the pitch change between them. When skilled pianists produced a left-to-right key press sequence on a piano while listening to the bistable tone pairs, they significantly reported more often that the pitch between these tones went 'up'. Playing the piano from left-to-right always produces an ascending melody. Obviously, the auditory percept was directly influenced by the 'movement/pitch associations' of the pianists acquired through their own experience.

Taken together, these lines of research indicate that there are also situations in which action increases perceptual sensitivity to those events that share features with what a person is currently doing. This leaves us with the puzzling picture that current action production sometimes reduces and at other times increases our perceptual sensitivity to similar events in the environment. Indeed, this issue is so far poorly understood and needs to be investigated further. Some studies suggest that the time interval between action production and perceptual encoding is crucial to whether contrast or assimilation occurs. By increasing the interval, a previously observed contrast effect could be turned into an assimilation effect ([23,24]; c.f. also [16,17]). It has been argued that, because action and perception-related processes draw on identical cognitive codes (e.g. the feature RIGHT can specify an aspect of an action, but at the same time it can also refer to a feature of a visual object), those codes that are currently 'in use' for specifying a response are less available for perception. Increasing the time interval between action production and perceptual encoding might dissolve this competition of action and perception-related codes ([7]; c.f. also [8]). Thus, both phenomena seem to arise as a result of the tight linkage between action and perception, but the open question is which factors determine the occurrence of either contrast or assimilation (Box 1)?

Off-line effects of motor action on perception

Let us now consider studies that investigated off-line effects of motor action on perceptual judgments. The term 'off-line' refers to situations in which action-related processes are temporally separated from the relevant perceptual processing and contribute to it in a top-down fashion.

Influence of motor intention

Craighero *et al*. [25] aimed to investigate whether the preparation of hand actions can specifically affect responses to hand pictures. Participants were asked to grasp a bar in either a clockwise or counterclockwise orientation. Before the execution of this grasping movement, they were confronted with a picture of a hand, which served as a go signal for executing the preplanned action. Critically, the picture showed a grasp that either did or did not correspond to the grasp that participants had prepared to execute. Correspondence between the triggering hand stimulus and the

Box 1. Questions for future research

Why does action sometimes show a contrastive effect upon concurrent perception and at other times an assimilative effect?

What mechanisms enable us to distinguish our own actions from those of others?

What is the relation between action attribution and conscious self-experience or the self-concept in general?

Does impairment of the mirror system lead to deficits in the mental self concept?

Is the mirror neuron system sufficient for the emergence of the self?

required response indeed significantly reduced reaction times. Although the results can be interpreted in terms of motor-determined facilitation of visual processing, the study can unfortunately not entirely rule out the alternative possibility that the effect reflects a visual-determined facilitation of response initiation. That is, the occurrence of the response cue (i.e. picture of the hand), not the mentally prepared hand action, might have triggered the initiation of a congruent response.

More unambiguous support for motor/visual priming has recently been provided by Fagiolo *et al.* [26] (c.f. also [27]). Participants were asked to prepare to reach for or grasp an object placed in front of them. Before executing this particular action, they were required to look for a target that deviated with respect to size or location from other stimuli presented in a highly predictable sequence. Remarkably, location deviants were detected faster when participants prepared for a reaching (i.e. location-related) action and size deviants were detected faster when participants prepared for a grasping (i.e. shape-related) action. Together, these findings suggest that the preparation of a certain action can increase perceptual sensitivity to those events in the environment that are directly related to the motoric specification of this particular action.

Influence of motor learning

Also, non-visual motoric learning can directly and selectively influence the recognition performance of observed actions. For example, Casile and Giese ([28]; c.f. also [29]) trained participants to perform novel and unusual arm movements. In a subsequent visual task, they were asked to discriminate biological movement patterns presented as point-light displays. Remarkably, all participants showed improved visual discrimination of those displays that matched the previously learned motor movement. No improvement was found for displays that were unrelated to the learned motor pattern. Moreover, a significant positive correlation was obtained between how well a participant could perform the novel movement in the training phase and the magnitude of the visual discrimination advantage in the perceptual task (c.f. also [30]). This finding clearly suggests an intermodal mapping of proprioceptive representations of our own movements to observations of motor movements.

Influence of motor competencies

Visual encoding can also be influenced by knowledge of constraints that are characteristic of human movement. For instance, hand movements in a plane, such as drawing, can be described by the so-called two-thirds power law. This law specifies how movement velocity depends on the radius of curvature of the trajectory. Interestingly, this motor constraint is also effective in motion perception (see [31] for an overview): when observers are asked to judge when a dot traveling along an elliptical path appears to move at a uniform velocity, they select movements that follow the two-thirds power law [32]. In this case, the impression of a constant velocity was an illusion because the dot in fact accelerated and decelerated, depending on local curvature. Knowledge of the kinematic laws underlying human movement also seems to inform visual anticipation of the unfolding course of a moving object [33,34]. Estimations of the final position of a moving object are more accurate when the movement follows a biological rather than a non-biological velocity profile.

A similarly robust and well-studied phenomenon concerning the characteristics of human movement is Fitts' law, which refers to the relationship between speed and accuracy in produced movements. According to Fitts' law, the time needed to move as quickly as possible between two targets is a logarithmic function of the width of the targets and the distance between them. A recent study investigated whether Fitts' law also holds for action perception [35]. Researchers presented participants with apparent motion displays of a person moving his arm at different speeds between two targets of varying width and distance. The participants reported whether the observed person could move at the perceived speed without missing the targets. Remarkably, those trials were judged as being successful in which the movement speed was predicted by Fitts' law. Thus, it seems that participants somehow applied their knowledge of motor constraints to this perceptual task.

Another well-known demonstration of how knowledge of one's own motor capabilities influences perceptual judgments has been provided by Shiffrar and Freyd [36]. These authors showed that, depending on the time interval between two alternating static images of a human body, participants reported different impressions of physically impossible motion of human body parts (e.g. an arm passing through a leg). At short intervals, the physically impossible straight trajectory was perceived, but at longer time intervals the curved trajectory of a similar but plausible human movement was seen (e.g. the arm moved around the knee). This switch did not occur when objects instead of human bodies were shown. This perceptual difference was also accompanied by differences in brain activity [37]: increased activity was found in premotor and inferior parietal brain regions (i.e. areas that are normally involved in motor control and comprise the 'human mirror neuron system' [14]) when participants reported seeing biomechanically possible as opposed to impossible human motion (but see [38]).

A strong influence of motor knowledge on perception has also been demonstrated when participants watch recordings of their own movements. In this case, one can assume a closer or almost perfect match between the observed movements and stored motoric representations of the same movements. As a consequence, observers should show a greater perceptual sensitivity to and predictive accuracy of their own movements. This assumption has indeed gained empirical support.

For example, participants can recognize drawing movements as their own when these movements, produced without visual guidance shortly before the test phase, are presented as a single moving dot [39]. A similar recognition advantage for self-generated actions was found in a study in which participants threw darts at a target board [40]. In a test phase one week later, participants were confronted with videos showing their own or another person's throws. However, the video did not show the final landing position of the dart in a given trial. It was the participant's task to judge whether the dart would hit the board in the upper, middle or lower part. Prediction accuracy was highest when participants watched their own rather than another's dart throws.

Moreover, Loula *et al.* ([41]; c.f. also [42]) reported that participants are better at identifying themselves as point-light figures in a video display showing various actions such as dancing or jumping than they are at recognizing a friend or stranger. A purely visual explanation would actually have predicted recognition advantages for friends and strangers, as in our everyday life we see the movements of others more frequently than our own.

Finally, Grèzes *et al.* [43] reported earlier activation of premotor and inferior parietal areas in the brains of observers who watched videos of themselves lifting a box than when they saw somebody performing the same action. This finding suggests that the mapping of perceived motor patterns on stored motor representations is optimized when watching self-produced movements. Taken together, all these findings also suggest that the degree of correspondence between motor knowledge and perceptual input provides authorship cues (but see Box 2).

Box 2. Shared representations and the self/other distinction

The hypothesis of shared representations of others' and one's own actions (c.f. [55]) in a mirror neuron system [14] raises the problem of action attribution [56] — how do we know who has performed a certain action if we represent the actions of others in the same way as our own (c.f. [57])? Shared representations of actions should cause attribution errors. Indeed, Daprati *et al.* [58] found that participants frequently attributed another's hand to themselves when seeing video clips of either their own or another person's hand movements. Researchers have proposed a 'who' system, which should enable perceptual identification of self and other, perhaps on the basis of non-overlapping cortical activation simultaneous with activation of the mirror neuron system [56].

Consistent with the idea of a who system, a recent study has suggested social differentiation, not equivalence, within the motor system [59]. By using an established illusion to manipulate the sense of body ownership (the 'rubber hand illusion'; [60]) for a hand that in fact belonged to another person, it was found that the human motor system distinguishes the agent of an observed action. When participants clearly attributed an observed hand action to another person, a strong motor resonance effect was found (c.f. [61]), that is, motor-evoked potentials to single transcranial magnetic pulses recorded from participant's hand muscles showed a significant increase when participants passively watched another's hand making an action compared to when the hand was at rest. However, when they thought they were looking at their own hand (because the illusion was effective), an effect in the reverse direction emerged. Thus, activation of the motor system by observing actions critically depends on the attribution of the observed action. It remains to be investigated to what extent this sensorimotor-based social differentiation is involved in conscious distinctions between self and other.

Influence of motor expertise

Strong evidence for the claim that motor or action knowledge can govern action perception is provided by studies that investigated motor experts. Several studies have shown that motor experts indeed show a special perceptual sensitivity to actions and action effects that fall in their individual range of expertise. For instance, Drost *et al.* [44] asked pianists and guitarists to play a chord on their instrument in response to an imperative stimulus. Critically, the imperative stimulus was accompanied by a task-irrelevant piano or guitar chord that was either congruent or incongruent with the chord participants were required to play. Presenting an incompatible chord distractor led to significant slowing of the response. Interestingly, this effect only occurred when the chord distractor was produced by the participant's 'own' instrument. A similar result was obtained in a study that showed that just seeing letters can prime the execution of corresponding actions to produce these letters in typewriting experts [45]. Furthermore, Repp and Knoblich [46] showed that expert piano players are able to identify a recorded piece of music that they played earlier, even without auditory feedback, as their own. Remarkably, self-identification did not fail when participants listened to edited versions of the performances from which all information of expressive dynamics had been removed. Obviously, the pianists used the remaining motor-related information of expressive timing and articulation as cues for self-identification. Thus, they might have exploited the predictive capacity of their motor system when hearing the recordings.

Strong support for the hypothesis that the perceptual system is tuned to one's own motor capabilities also comes from the following study. Calvo-Merino *et al.* ([47]; c.f. also [30,48,49]) studied experts in classical ballet and experts in capoeira dancing. Greater activity in the premotor and parietal brain regions was found when dancers watched their own dance style (i.e. when ballet dancers watched ballet moves and capoeira artists observed capoeira moves). Thus, the motor system was more strongly engaged during action observation when participants already had a specific motor representation of the action they observed. In a further study, the researchers ruled out that this difference was purely due to visual familiarity [50]. Expert female and male ballet dancers were now investigated who watched videos of gender-specific ballet moves (c.f. Figure 3). The rationale behind this study was that male and female dancers should have the same amount of visual exposure to all moves, because they do their training together. Remarkably, greater activity in motor regions of the brain and also in the cerebellum was again observed when the dancers watched movies of their own gender-specific movement repertoire. Thus, participants clearly translated the observed body movements into their specific motor capabilities. As it is known that the cerebellum is involved in precise prediction, this finding furthermore can be interpreted as showing that dancers not only mentally simulated but also predicted the upcoming part of a move they observed on the basis of their own motor knowledge (c.f. [8]).

Finally, there are reasons to assume that impairment of the functional integrity of one's motor system can affect action perception. Bosbach *et al.* [51] studied two de-afferented individuals, GL and IW, who lost their senses of cutaneous touch and proprioception due to a rare viral infection. These individuals showed a selective deficit in interpreting the observed movement kinematics of another person as an indicator of whether or not this person had a

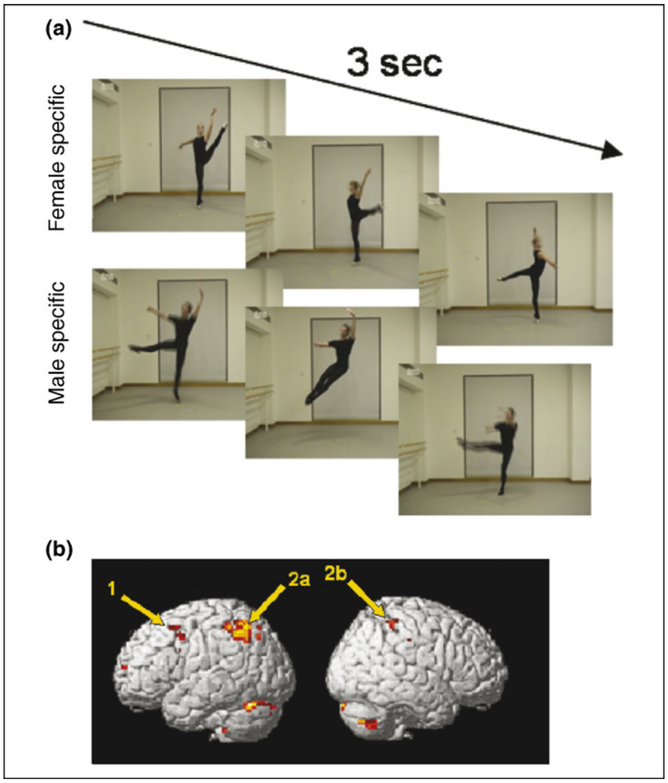

Figure 3. Effects of motor expertise on action perception. **(a)** Examples of video stimuli used in [50]. Female and male ballet dancers watched videos of standard classical female- and male-specific ballet moves. **(b)** Sagittal views of the regions in the left dorsal premotor cortex (1), the left intraparietal sulcus (2a) and the right intraparietal sulcus (2b) (the 'human mirror neuron system'; c.f. [14]) show higher activity when dancers watched movements from their own motor repertoire. Reproduced with permission from [50].

false expectation regarding the weight of a box he was required to lift. When IW was then asked to lift the previously observed object by himself, he was not able to attune his movements to his expectation of the object's weight. It is likely that this was the reason why he was also not able to deduce the expectations of others from their movements.

Impact of action on perception: why and what for?

A large body of evidence suggests that the processes of action and perception are intertwined and can influence each other by virtue of similarity: just perceiving an event in the outside world can automatically trigger the execution of a related action; conversely, the execution, intention or general knowledge of an action can constrain and even determine what is concurrently perceived. Here, we tried to draw attention to the so-far relatively neglected latter perspective and reviewed findings suggesting this conclusion. We speculate that perceptual resonance to action also fulfils an important, perhaps even the most important, social function: it might render an individual selectively susceptible to similar actions of conspecifics, perhaps even in the sense that we can only perceive and understand in others what we can do ourselves. Such a mechanism is decisive for grounding empathy and sympathy.

Moreover, we can also speculate on a further important function of a system that represents action and perception in a common medium, and thus provides a mirror-like representational device. Action mirroring not only might support the understanding of those actions (in the perceiver who does the mirroring), but also at the same time might help to build up and shape the notion of the mental self (in the actor who is being mirrored and thus perceives herself through the mirror of the other [52]). Of course, this requires that the two individuals engage in what one might call 'mirror games' — interactions in which they both mirror each other and perceive themselves being mirrored by the other. Such mirror games are well known in early infancy. For parents/guardians, the practice of reciprocating the baby's behaviour is common and widespread, perhaps even universal. For babies, these games seem to be of crucial importance for tuning in and becoming attached to others, as well as laying the foundations for perceiving and understanding themselves like others [53]. Such explicit mirroring can occasionally be observed in adults as well. For example, it is well known that people unconsciously tend to mimic the behavior of others (the 'chameleon effect'; [54]). This mirroring, however, often just reflects automatized behavior, which sometimes even needs to be suppressed, rather than controlled and cultivated practices. Nevertheless, this unconscious mirroring also enables people to perceive and receive their own behaviour through the mirror of somebody else (c.f. [52]).

In other words, mirror games provide self-related information through others. By engaging in mirror games, individuals are taking advantage of their capacity to understand intentional action in others for construing agency in themselves. These games thus exploit others for the constitution of the mental self (Box 1).

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