

Review

The role of motor contagion in the prediction of action

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Abstract

It has been proposed that actions are intrinsically linked to perception [James, W. (1890). *Principles of psychology*. New York, NY, USA: Holt; Jeannerod M. (1994). The representing brain – neural correlates of motor intention and imagery. *Behavioural Brain Sciences*, 17, 187–202; Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9, 129–154]. The idea behind these theories is that observing, imagining or in any way representing an action excites the motor programs used to execute that same action. There is neurophysiological evidence that neurons in premotor cortex of monkeys respond both during movement execution and during the observation of goal-directed action ('mirror neurons'). In humans, a proportion of the brain regions involved in executing actions are activated by the mere observation of action (the 'mirror system'). In this paper, we briefly review recent empirical studies of the mirror system, and discuss studies demonstrating interference effects between observed and executed movements. This interference, which might be a form of 'motor contagion', seems to arise specifically from the observation of biological movements, whether or not these movements are goal-directed. We suggest that this crude motor contagion is the first step in a more sophisticated predictive system that allows us to infer goals from the observation of actions.

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Keywords: Interference; Mirror neurons; STS; Observation of action; Goals; Intentions

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1. Overlapping neural networks associated with perception and action

The notion that actions are intrinsically linked to perception goes back to the 19th century when William James, in his ideomotor theory of action, claimed that “every mental representation of a movement awakens to some degree the actual movement which is its object” (James, 1890). The implication is that observing, imagining, preparing or in any way representing an action excites the motor programs used to execute that same action (Jeannerod, 1994; Prinz, 1997). Interest in this idea has grown in the last decade, at least in part due to the discovery of mirror neurons in the monkey ventral premotor cortex. These neurons discharge both when the monkey performs certain hand movements and when it observes another monkey or a human performing similar hand movements (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996; Rizzolatti, Fadiga, Fogassi, & Gallese, 1996a).

There are several notable properties of the mirror system. Firstly, mirror neurons respond to the sight of goal-directed actions only: they respond only when the monkey observes a hand grasping an object, and not to the sight of the hand or the object alone (Rizzolatti, Fogassi, & Gallese, 2001). Secondly, mirror neurons respond as long as a goal is achieved, even if the end of the action is out of the monkey’s sight (Umiltà et al., 2001). In this experiment, the monkey observed the experimenter reach for a peanut and in some trials the end portion of the action, in which the peanut was grasped, was occluded from the monkey’s vision. The neuron fired even if the actual grasp of the peanut could not be seen, as long as the peanut was present (the same neuron did not fire when the grasping action was ‘mimed’ in the absence of a graspable object). Thirdly, mirror neurons respond to the sound of an action, firing to the sound of a stick being dropped or paper being torn (Kohler et al., 2002). These observations suggest that mirror neurons represent general aspects of actions such as the overall goal, rather than some other more elementary property of movement such as specific motor commands, movement velocity, movement direction or muscle activity.

One condition necessary for mirror neurons to fire is that the observed goal-directed action is performed by an agent. Mirror neurons appear to distinguish between biological and non-biological motion, responding only to the observation of hand–object interactions and not to the same action performed by a mechanical tool, such as a pair of pliers (Rizzolatti et al., 2001). How do premotor neurons gain information about this aspect of an observed action? One possibility, proposed by Rizzolatti et al., is that the premotor cortex receives information about biological motion from the superior temporal sulcus (STS). Single cell studies in the macaque monkey have revealed that STSa cells selectively respond to depictions of the face and the body, either in action or represented by a static image (Oram & Perrett, 1994; Perrett et al., 1985a, 1985b; Perrett, Hietanen, Oram, & Benson, 1992). STSa neurons continue to respond to biological actions even when part of the action is occluded (Jellema

& Perrett, 2002). The response properties of neurons in STSa have been interpreted as demonstrating the contribution of the STS to the visual recognition of others’ actions (Emery & Perrett, 1994; Jellema, Baker, Wicker, & Perrett, 2000). This information would be useful for recognising the movements of other animate beings and categorising them as threatening or enticing, in order to predict their future actions and make an appropriate response.

The STS and the premotor cortex are connected via the parietal cortex (Rizzolatti et al., 2001). Recent results suggest that the parietal cortex might also contain neurons with mirror properties, responding to both movement execution and movement observation (Gallese, Fadiga, Fogassi, & Rizzolatti, 2002; Rizzolatti et al., 2001).

2. The human mirror system

There is a large body of evidence that, in humans, several brain regions are activated both during action generation and during the observation of others’ actions (Decety, Grèzes, Costes, Perani, & Jeannerod, 1997; Grafton, Arbib, Fadiga, & Rizzolatti, 1996; Hari et al., 1998; Rizzolatti et al., 1996b). Premotor and parietal cortices are activated both by the perception of action and by the execution of action. Furthermore, premotor and parietal cortices are activated to a greater extent when subjects observe movements with the intention to imitate them later compared with the intention simply to recognise them later (Grèzes, Costes, & Decety, 1999).

In some brain regions, the overlap between action observation and action execution is highly specific. Action observation activates premotor cortex in a somatotopic manner (Buccino et al., 2001). In this fMRI experiment, subjects observed actions performed by the mouth, hand and foot that were performed in isolation (mimicking chewing, grasping and kicking) or with an object (chewing food, grasping a cup and kicking a ball). The results demonstrated that watching mouth, hand, and foot movements alone (without objects) activates the same functionally specific regions of premotor cortex as making those respective movements. When actions involved objects the parietal cortex became activated. Again, different regions of the parietal cortex were activated according to the specific object-directed action being performed. Thus, it seems that the premotor activation is not dependent on the movement having a goal (an object), whereas the parietal cortex was activated only when the action was directed towards a goal.

Jeannerod (2001) has argued that the mirror system facilitates action understanding, suggesting that neural simulation allows us to plan our own actions and also to interpret the actions of others. Rizzolatti et al. (2001) have argued that imitating every observed action is unnecessary and that the purpose of the mirror system is not to reproduce observed actions. However, there is evidence that the motor system is geared up for making actions it observes (cf. Jeannerod,

1994). For example, people change their breathing when observing other people making effortful actions (Paccalin & Jeannerod, 2000) as if preparing to make such actions themselves.

Observing a movement has measurable consequences on the peripheral motor system (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). Fadiga et al. stimulated left primary motor cortex of human subjects using TMS while the subjects observed meaningless actions and grasping movements (and other visual control stimuli). Motor evoked potentials (MEPs) were recorded from subjects' hand muscles. It was found that during action observation – both goal-directed and meaningless actions – there was a decrease in the threshold needed to evoke MEPs in the hand muscles that would be used to make the observed movements. This was not the case for MEP thresholds from other muscles that would not be used to make the observed movement. Thus, the peripheral motor system seems to prepare to execute observed movements.

3. Interference between action observation and action execution

If the central and peripheral motor system becomes activated during the observation of action, what happens when we attempt to make an action while observing a qualitatively different action? Recently, several experiments have been

performed that provide evidence for an interference effect between observed and executed actions. In one study, subjects were instructed to perform a finger movement (tapping or lifting) in response to a visual Go signal. The Go signal was a photograph of a finger movement that was either the same (compatible) or the alternative (incompatible) finger movement to that being prepared by the subject. The results showed that the reaction time to initiate the prepared finger movement was significantly slowed down when the Go stimulus was a visual representation of a different finger movement (Brass, Bekkering, & Prinz, 2001). Note that the Go stimulus did not involve or imply a goal. The authors interpreted their findings as a facilitation effect in terms of the reaction time to carry out the action when there is high ideomotor compatibility between a prepared and an observed action. However, an equally plausible interpretation is that there is interference when the observed movement is incompatible with the movement being prepared.

In another psychophysical study, subjects prepared to grasp one of two bars that differed in orientation, being positioned on the diagonal, either clockwise or anticlockwise (Craighero, Bello, Fadiga, & Rizzolatti, 2002). The Go signal to grasp the bar was a photograph of the final hand posture necessary for the grasping action, which was either in the same orientation (congruent) or a different orientation (incongruent) from the prepared grasping response. In this experiment too, the Go signal had no discernable goal. Reaction

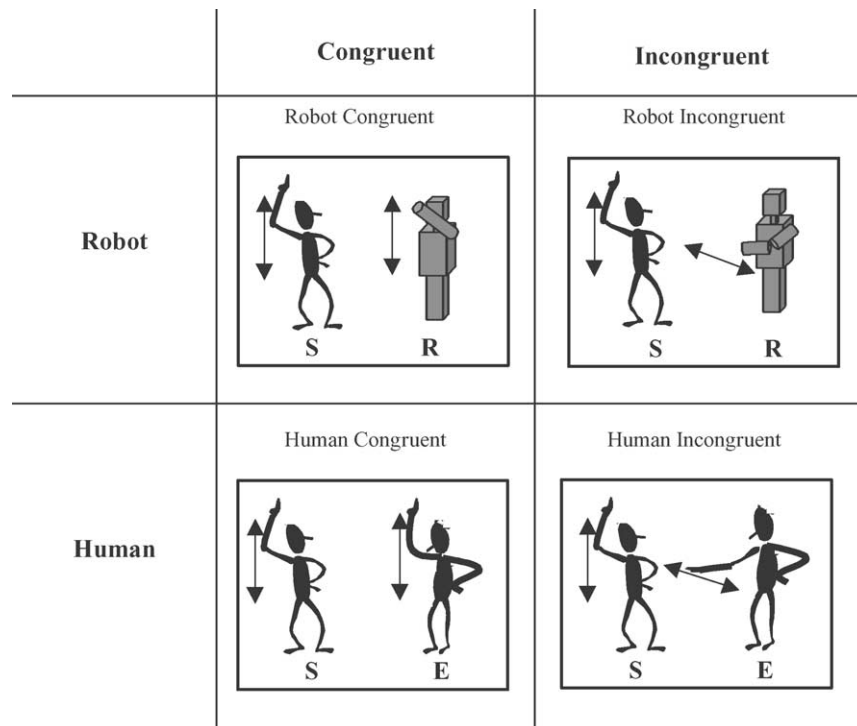


Fig. 1. Experimental design. Subjects made sinusoidal movements with their right arm at the same time as observing movements that were either congruent or incongruent with their own movements. In each condition, the subject (S) was instructed to make sinusoidal movements of their right arm from the shoulder, which were either vertical or horizontal at a rate of 0.5 Hz. While making these arm movements, the subject observed movements made by another effector situated facing the subject, either the right arm of the experimenter (E) or a robotic arm (R), that were either congruent or incongruent with the executed movements. In addition, there were two baseline conditions in which the subject moved their arm either horizontally or vertically without watching anything.

times to initiate the grasping action were measured and it was demonstrated that there was a facilitation when there was a similarity between the hand position in the Go stimulus and the grasping hand final position. This result was interpreted as demonstrating the close link between observed hand positions and specific motor actions. These results support the notion that, during observation of action, the specific neural networks subserving that particular movement are already tuned for action (Jeannerod, 1994).

If the motor system is geared up to execute observed movements, this should result in interference when the observed movement is qualitatively different from the *simultaneously* executed movement. To investigate this hypothesis, an experiment was performed in which subjects made sinusoidal movements with their right arm at the same time as observing arm movements that were either congruent or incongruent with their own movements (Kilner, Paulignan, & Blakemore, 2003). The subject made arm movements while observing arm movements made either by another *human* or by a *robot*, which were either in the same direction (*congruent*) or tangential (*incongruent*) to the subject's own arm movements (Fig. 1). In a baseline condition, the subject moved his arm without observing anything.

Arm movements were recorded using an Optotrak recording system and variance in the movement was used as a

measure of interference to the movement (Fig. 2). The results of this experiment revealed that there was a significant interaction effect between the observed effector (human or robot) and movement congruency (congruent or incongruent with executed movements) in terms of the variance of the subjects' arm movements. The significant interaction between observed effector and movement congruency was due to there being more interference in subjects' arm movements when subjects watched human arm movements that were incongruent with their own movements than in any other condition. The only condition that differed significantly from the baseline movement condition in terms of movement variance was the condition in which subjects watched the experimenter making incongruent arm movements.

These results demonstrate that observing non-goal-directed human arm movements significantly interferes with ongoing executed movements if the observed movements are qualitatively different from the movements being made. There was no significant interference to ongoing movements

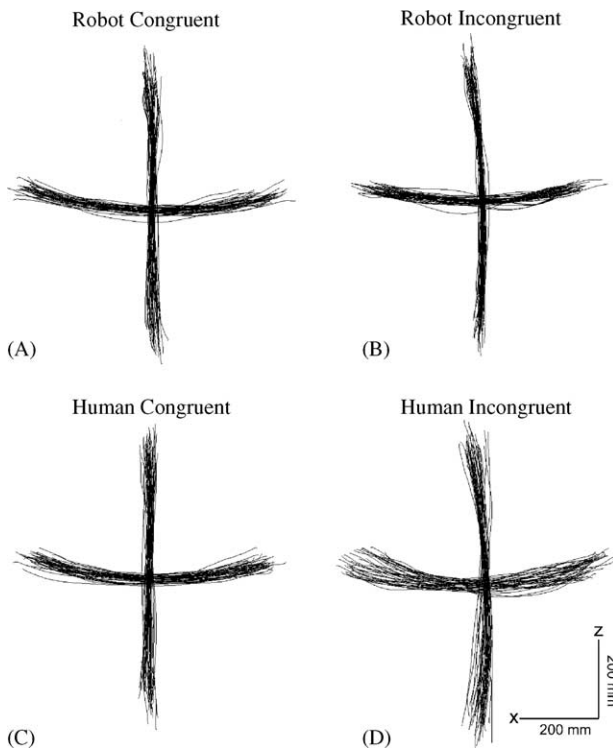


Fig. 2. Arm movement data from a single subject. (A–D) The individual movements in the XZ plane made by a single subject during four of the conditions. The plots show horizontal and vertical movements made by the subject while observing the robot making congruent movements (A), observing the robot making incongruent movements (B), observing the experimenter making congruent movements (C) and observing the experimenter making incongruent movements (D). The scale of all four plots is illustrated in (D).

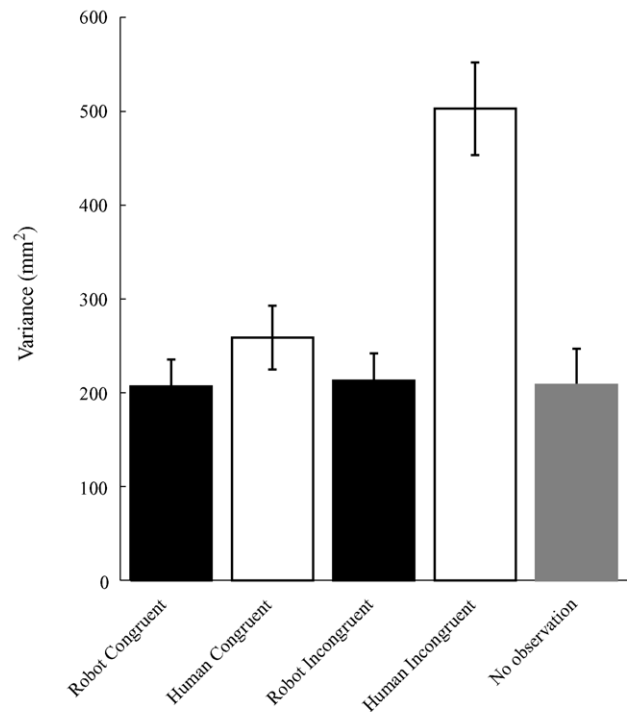


Fig. 3. Interference effect of observing biological movement on executed movements. For each segmented movement, the variance in the movement orthogonal to the dominant dimension of movement and in the dominant dimension of the incongruent movement was calculated. The mean of the movement variances was calculated across all trials for each condition. Mean variances (and standard error bars) are shown for five conditions: observing the robot making congruent movements (robot congruent); observing the experimenter making congruent movements (human congruent); observing the robot making incongruent movements (robot incongruent); observing the experimenter making incongruent movements (human incongruent); the baseline condition (no observation). The only condition that differed significantly from the baseline movement condition was the condition in which subjects watched the experimenter making incongruent arm movements ($P < 0.0005$). The other three comparisons were not significantly different ($P > 0.1$).

during the observation of incongruent movements made by a robot. Only the observation of another human making incongruent arm movements significantly interfered with the execution of arm movements (Fig. 3).

4. Interference effect is specific to observing biological motion

The finding that observing a robot making incongruent movements had no significant effect on executed movement demonstrates that the interference effect is not simply due to increased attentional demands, task complexity or any other confounding effect of observing an incongruent movement. Rather, it might be a consequence of the brain processing biological and non-biological movements differently.

There is a large body of evidence showing that distinct neural processing systems exist for these two types of movement, in particular in the STS. The ability to distinguish between biological and non-biological movement develops early: 3-month-old babies are able to discriminate between displays of moving dots that depict biological motion and displays in which the same dots move randomly (Bertenthal, 1993). This suggests that the detection of biological motion becomes hardwired in the human brain at an early age.

Several brain imaging studies have investigated the neural processing of the perception of biological motion in humans. One study used fMRI to compare brain regions activated by dot displays showing biological motion and regions activated by dot displays showing coherent motion in which all the dots moved at equal velocity in the same direction (Grossman et al., 2000). They found a specific area responsive to biological motion located within the ventral bank of the occipital extent of the STS. This activation was more pronounced in the right hemisphere than in the left hemisphere.

A second fMRI study compared dot displays showing biological motion and dot displays showing rigid object motion, in which an object appears to rotate (Grèzes et al., 2001). Activation specific to seeing biological motion was detected in the posterior portion of STS, more prominently in the right hemisphere, and in the left intraparietal cortex. A third fMRI study demonstrated that imagining biological motion activates the same region in the STS (Grossman & Blake, 2001). Other neuroimaging studies have detected activation in the right posterior STS in response to seeing hand, eye, and mouth movements (Puce, Allison, Bentin, Gore, & McCarthy, 1998; Rizzolatti et al., 1996b; Wicker, Michel, Henaff, & Decety, 1998). These data suggest that the human STS plays an important role in the perception of biological motion (Allison, Puce, & McCarthy, 2000; Frith & Frith, 1999).

The interference results described previously are in line with the proposal that observed movements are classified as biological (human) or non-biological (robot) and treated differently accordingly. Only the observation of biological movement interfered with executed movements. Observing a robot, whose movement was non-biological, making incon-

gruent movements had no significant interference effect on ongoing movements. The aspect of biological motion which is the trigger for interference, and which is absent in robotic movements, remains unknown. Whether the interference is caused by a characteristic component of biological motion (non-Newtonian motion, non-constant velocity, non-linear trajectory and acceleration, for example), or the presence of human features, such as limbs or eyes, or some other non-specific factor such as attention, needs exploring.

5. Does interference arise from mirror neurons?

The interference effect between observed hand postures and reaction times to move (Brass et al., 2001; Craighero et al., 2002) and between observed and executed arm movements (Kilner et al., 2003) may be due to interference within a common neural network that encodes both observed and executed movements. This network includes the premotor cortex and the parietal cortex. Furthermore, there is evidence that mirror neurons in the premotor cortex distinguish between biological and non-biological actions, responding only to a hand movement and not to the same movement performed using a pair of pliers (Rizzolatti et al., 2001). This distinction between the observation of biological and mechanical movement in terms of the mirror responses in premotor cortex might explain the finding that interference effects seem to be specific to the observation of incongruent human movements, and do not occur when observing non-biological incongruent movements.

There is, however, another important distinction that needs to be considered, that is between movements and goal-directed actions. The mirror neurons in monkey premotor cortex make this distinction (Rizzolatti et al., 2001) since they respond only to actions (a hand grasping an object) and not to movements (the hand moves in the absence of an object to grasp). In contrast, thresholds are reduced in motor cortex during observation of meaningless movements as well as goal-directed actions (Fadiga et al., 1995). Like wise in the various demonstrations of interference between observation and action that we have already discussed, the subjects were observing pictures of hands or movements with no obvious goal (Brass et al., 2001; Craighero et al., 2002; Kilner et al., 2003). Thus, it appears that simply observing movements causes a form of ‘motor contagion’ that interferes with the execution of movements if these are different from those being observed. This system is distinct from the mirror neurons described in monkey premotor cortex since the interference arises from any kind of movement and is not restricted to goal-directed actions.

The distinction between movements and actions is seen most clearly in studies of imitation (e.g. Wohlschläger, Gattis, & Bekkering, 2003). If a child sits opposite an adult and is asked to imitate her, then, when the adult moves her right hand, the child imitates mirror-wise, i.e. she moves her left hand. Does this mirroring also occur at the physiologi-

cal level? When there is an obvious goal to the action then the distinction between movement and action becomes even clearer. If the adult picks up an object on a table, the child perceives the action to be imitated as picking up the object and will use the most efficient movement to achieve this goal. If the adult picks up an object on his left by moving his right hand across the mid-line then the child will pick up the object (on her right) with her right hand thus avoiding moving across the mid-line. If no object is present then the child will imitate the adult's movement by moving her left hand across the mid-line.

At the physiological level these observations could be seen as the end result of the combination of two processes. There is contagion by which the motor system of the observer is primed to produce the movement observed and there is affordance by which the motor system of the observer is primed to interact efficiently with the object.

This analysis suggests that mirror neurons are part of a much wider 'mirror' system, which has at least three levels. At the lowest level there is automatic contagion from movements as long as these are made by biological entities. At a higher level there is mirroring of specific goal-directed actions (with an involvement of mirror neurons). There is likely to be an even higher level at which intentions are mirrored. But in order to mirror intentions, at some level we have to know what these intentions are.

6. The role of motor contagion in reading the goals of others' actions

It has been proposed that the mirror system might facilitate communication, empathy and the understanding of other people's minds (Gallese & Goldman, 1998; Jeannerod, 2001). The internal imitation of other people's actions would trigger an action representation from which the underlying goals and intentions could be inferred on the basis of what our own goals and intentions would be for the same action (Goldman, 1992). The mirror system would allow the observer to "get into the mental shoes of the target" (Gallese & Goldman, 1998). However, such a system has costs. First, as discussed above, automatic simulation of observed actions can interfere with the observer's current behaviour. Second, representing actions of the self and others in common could lead to confusion as to who is performing the action (see, for example, Georgieff & Jeannerod, 1998).

Another way of using the system that controls our own actions to read the goals and intentions of others is based on the idea of the MOSAIC model (Wolpert, Doya, & Kawato, 2003). This approach depends upon predicting what is going to happen next on the basis of our prior knowledge. In this way, we learn about the world we are interacting with on the basis of differences between our predictions and what actually happens. Our knowledge of the world is continually updated and improved. In this approach, we start with some idea of the goal of the person we are observing and use our

motor system to predict what he will do to achieve this goal. If he does something different we have to update our representation of his goal. For this approach to work there has to be a starting point (initial value or seed) for the estimated goal of the person we are observing. We suggest that the contagious processes we have discussed above could provide one such seed. Contagion would bring the observer one step closer to the actor so that the observer would be in a better starting point from which to predict the actor's next action. An example of how contagion might be useful in this way is given by the effect of social stereotypes on behaviour. Bargh, Chen, and Burrows (1996) exposed their subjects to words relating to stereotypes about old people (lonely, grey, Florida, etc.). When the subjects left the lab after this exposure they walked more slowly than before. This effect would automatically enable them to simulate the movements of elderly people more accurately.

7. Conclusions

We suggest that there are many levels at which observed actions cause contagion. Consider the simple situation in which the possible goals are different objects for which the person (the actor) may reach (see Castiello, 2003 for a related account). At least three contagious processes might operate in an observer (but only when the actor being observed moves in a 'biological' manner). First, the observer will automatically look in the same direction as the actor (Farroni, Csibra, Simion, & Johnson, 2002). Second, if the observer attends to an object as a result of the gaze shift, then the sight of that object will automatically activate representations of the movements appropriate for reaching that object (Kritikos, Bennett, Dunai, & Castiello, 2000). Note, however, that the appropriate movements for the observer to reach the object are not usually the same as the appropriate movements for the actor since actor and observer are in different positions relative to the object. Third, the arm movements made by the actor will automatically activate representations of the same movements in the observer (Kilner et al., 2003). All these effects are combined to suggest that the actor is making a goal-directed movement towards one particular object. On this basis, predictions are made about the precise form his movements should subsequently take.

This outline of a mechanism for the first step in automatically inferring a goal-directed action provokes many questions. With regard to the contagious effects of action observation we need to identify the crucial features of the observed movement that causes interference. We need to identify what is special about biological movements. Of particular interest is the process by which the representation of an observed movement (in egocentric coordinates) gets converted into the representation of a goal-directed action (in object centred coordinates). Twenty years after the publication of the classic review on the visual control of reaching movements

(Jeannerod & Prablanc, 1983) there is still much to be learned from the observation of action.

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