

When mirroring is not enough: that is, when only a complementary action will do (the trick)

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It is well known that perceiving another person's body movements activates corresponding motor representations in an observer's brain, a process which appears to be imitative in nature. However, it is also true that simply imitating another person's action/s in many situations is not an effective or appropriate response, as successful interaction often requires complementary rather than emulative behavior. This manuscript presents a review of the recent efforts to identify the mechanisms responsible – once observed actions have been mapped onto an observer's motor system – for the switch from the tendency to imitate actions to the inclination to carry out a nonidentical context-appropriate response. The putative human mirror neuron system seems to play a particularly important role in this process because of its prominent function in action observation and execution. Recent

findings indicate, however, that acting in a complementary fashion might entail the recruitment of neural systems outside of the human mirror neuron system. *NeuroReport* 24:601–604 © 2013 Wolters Kluwer Health | Lippincott Williams & Wilkins.

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Introduction

Findings supporting the concept that there is a basic neurophysiological system underlying the ability in an onlooker's brain to match another person's body movements with motor representations have been drawn from different methodological approaches. First and foremost, single-cell recordings demonstrated the existence of 'mirror' neurons (MNs), discharging not only when a macaque monkey grasped three-dimensional objects but also when the primate observed a similar action being performed by the experimenter [1]. Functional MRI, magnetoencephalography, and transcranial magnetic stimulation (TMS) studies have provided indirect evidence that similar neural mechanisms exist in the human brain (for recent reviews, see Hickok and colleagues [2–4]). Findings from these studies indicate that activated motor representations appear to be imitative in nature, reflecting an automatic resonance mechanism of motor structures paralleling observed movements.

However, we are tempted to ask: what happens when the automatic tendency to 'mirror' is inappropriate, out of order, or even dangerous, and a complementary action rather than an imitative one would be expected, required, or appropriate? If, for example, someone holding a mug by its handle hands it to us, instead of imitating that individual's action we simply and automatically select the right grip to take it. In this case, the two grips adopted by the two individuals are complementary (mismatched). Mirroring an observed action, we would all agree, often proves detrimental for successful interaction with others. So how does the brain resolve the possible conflict

between the automatic tendency to 'mirror' and that to perform context-related complementary actions? This manuscript reviews recent studies focusing on action observation calling for complementary rather than emulative movements. Although some evidence suggests that the mirror neuron system (MNS) is involved to some degree in the process of preparing for a complementary response, it also seems to be implicated in recruiting a more integrated neural network specifically tailored to support joint/collaborative actions.

Imaging evidence of 'complementary' neural activity

The role of the human mirror neuron system (hMNS) in coding complementary actions was investigated during experiments in which participants were instructed to execute imitative or complementary actions [5] after they observed an actor grasping a manipulandum using either a precision or a power grip (these grips are defined by the position of the thumb and the fingers. In the former, the intermediate and distal phalanges and the thumb press against one another, and in the latter the fingers clamp down on an object with the thumb generating counter pressure). In the imitative context, the participants were instructed to perform the same action (imitative) that they had observed [e.g. using a precision grip (PG)]; in the complementary context, they were expected to execute a complementary type of grasp [using a power, whole-hand grip (WHG)]. The results indicated that the hMNS can link observed actions with nonidentical responses as long as they serve a common goal. Key areas of the MNS seemed to be activated to a

stronger degree when corresponding actions were complementary rather than imitative. The BOLD signal in the right inferior frontal gyrus and in the bilateral inferior parietal lobes was, in fact, stronger when complementary rather than imitative actions were being prepared, suggesting that hMNS is involved, in a context-dependent manner, in dynamic coupling action observation and execution. These findings make sense if there are two kinds of MNS: strictly congruent ones, which are activated when the action observed and the one that is executed are identical, and broadly congruent ones, which are activated when the action observed calls for a nonidentical, complementary one. Different sets of MNS might, according to this hypothesis, serve to integrate observed actions and appropriate responses during social interaction [5].

Another hypothesis postulates that the putative MNS is only partially involved in integrating complementary actions [6] because F5 neurons, which respond during action observation, show a fixed reaction in the face of both observed and executed actions [1]. In the same way, broadly congruent visuomotor neurons, which can include complementary types of responses (e.g. execution of grasping and observation of placement), always showed fixed reactions in all trials. The MNS might then be able to promote complementary actions by constantly linking action observation to the motor programs needed to perform incongruent actions, but it might not have the flexibility needed for the rapid task-dependent reorganization implied in carrying out these actions. In other words, shifting from 'doing the same thing' to 'doing something different' in situations in which a complementary action is called for seems to go beyond the known properties of the MNS. It is possible that collaborative actions indirectly recruit the hMNS, which translates observed and executed actions into a common code and then transmits this information to an integration network specifically tailored to support complementary actions [6–8].

Findings confirming this hypothesis emerged from a functional MRI study during experiments in which participants were at times required to carry out similar actions and at other times complementary ones in cooperation with a partner [6]. This experiment showed such coordinated efforts recruit two separate sets of areas: one that translates motor and visual codes and another that integrates the information to achieve common goals. The former includes regions of the hMNS, including the premotor and parietal areas. The latter includes regions of the prefrontal, posterior parietal, and temporal lobe adjacent to the hMNS. These findings showed that although the hMNS may play a critical role in joint, coordinated two-party efforts by translating all actions concerned into a common code, the flexible remapping of all these actions seems to be performed somewhere else. Joint actions could, therefore, be characterized by a dual process during which one set of areas (including the hMNS) transforms observed actions into corresponding

representations through a combination of inverse and forward models [6] and another set utilizes the common code to flexibly integrate the actions observed with those needing to be carried out to achieve joint goals.

Corticospinal excitability reveals reciprocity

TMS studies indicate that an observer's motor system is facilitated by merely observing someone carrying out motor actions [9–12]. In a pioneering study carried out by Fadiga *et al.* [9], single-pulse TMS was applied over the motor cortex of participants observing a model reaching for and grasping three-dimensional objects. Those investigators demonstrated that observing a grasping action induces an enhancement of the motor-evoked potentials (MEPs) recorded from the participants' hand muscles corresponding to those involved in the action being observed. Our motor system simulates, underthreshold, observed actions in a strictly congruent, temporally matched manner – the muscles involved are the same as those being used by the person carrying out the observed action [13].

The existence of an MNS in humans was corroborated by recent studies focusing on the link between corticospinal facilitation effects that are contingent upon action observation and the frontoparietal regions of the putative hMNS [14,15]. MNS involvement in congruent activity during action observation and execution has also been confirmed in the primary motor cortex of macaque monkeys [16].

Motor facilitation effects have recently been analyzed in an attempt to uncover whether corticospinal excitability is related solely to an observed action or whether it can be dissociated from it in the event the action to be executed is not identical to the one observed [14]. During the first part of a study using TMS to induce MEPs in hand abductor muscles, individuals were instructed to watch a video showing a subject moving the fingers of his hand. As was to be expected, MEPs were found to be greater in the participants' index finger when the video showed an index finger abduction and in their little finger when the video showed a little finger abduction. This is, of course, the classic 'mirror' MEP effect. The investigators then trained the participants to move their fingers in a way that was incongruent with respect to the hand in the video. They were instructed to move their little finger when the video showed an index finger movement and to move their index finger when the video showed a little finger movement. After training, MEPs were found to be greater in the participant's little finger when an index finger movement was observed, and vice versa. 'Mirror' effects can then be trained by sensory–motor association. The important implication of these findings is that the human 'mirror system' can be dissociated from motor actions that are being observed.

Subsequent studies specifically focused on the 'complementary' nature of observed actions [17–19]. MEPs from

right hand muscles were recorded at two time points while participants observed action sequences which, at times, elicited a complementary response. During a video, a model was seen grasping a coffee-filled thermos using a WHG and pouring coffee into three espresso coffee cups placed near her on the table. Thereafter, the model moved her arm/hand as if she intended to pour coffee into the fourth cup, which was placed farther away with respect to the other three and was located on the other side of the table in the video foreground, seemingly closer to the participant watching the video. (Anyone on that side of the table wanting to pick up that cup would need to use a PG.) The MEPs recorded at the time the participant initially observed the model grasping the thermos elicited both ADM and FDI muscle facilitation, and, in effect, both are usually recruited for a WHG. In contrast, when the model moved as if she intended to pour coffee into the fourth cup located farther away, only FDI muscle activation was observed (needed to carry out a PG). These results confirm that action observation does not inevitably lead to an imitative kind of motor facilitation but differs depending on the action context – when the context calls for a complementary action, the excitability pattern reflects an underthreshold activation of muscles that would be involved in a complementary action. In contrast, when the context calls for an imitative action, the observer's corticospinal activity reflects symmetrical motor resonance.

Some researchers hypothesized that the potential conflict emerging between observed actions and non-identical complementary responses can be resolved flexibly in a double-step manner by the system itself. During the first step, the observed action gives clues on what will take place, and in what way the observer may be involved. During the second step, associations are made between the action that is observed and nonidentical movements to prepare, if necessary, for a complementary action.

Although findings from the studies described above indicate that there is a shift from simulation to reciprocity, it was unclear as to when exactly that switchover takes place. A study was thus specifically designed to verify at what point the automatic reaction of mirroring another person's actions becomes the inclination to carry out an appropriate complementary action. The paradigm used was similar to the one described above, except for the fact that TMS was delivered at five different time points during action observation [18]. The results demonstrated that the transition from simulation to reciprocity was acknowledged very early by the corticospinal system, even before the prospect of a complementary action became explicit. Observers seem to be attuned to advanced movement information and are able to use it to anticipate a future course of action and to prepare for appropriate complementary actions.

The mirror system and complementary actions: a working memory hypothesis

The results outlined here seem to suggest that a dual process lies behind joint actions – a low-level mirror one, which stores and analyzes information on observed actions (allowing the onlooker to experience what is being observed) and a high-level more abstract one, which flexibly integrates the individual's actions with those of others and selects the most adequate course to achieve joint goals [20]. It is possible, we hypothesize, that the mirror system function is similar to that of the working memory but is specifically tailored for action. According to this hypothesis, the mirror system's primary role is, as demonstrated by studies outlining its multisensory nature, to keep on hold the neuronal activation linked to the visual, auditory, or imaging aspects of motor actions [21]. As in the case of working memory, distinct elements are kept on-line while a larger structure is being processed [22]. Complementary actions might be the ideal way to test this hypothesis. During complex social interaction, an individual needs to keep both simulative and complementary tendencies simultaneously active in an attempt to process both an observed action and its relative response. The working memory permits an individual to manipulate distinct components of a scene to extract meaning from it in view of achieving a final goal. Similarly, during social interactions, the mirror system might be involved in keeping action-related information on hold to enable other brain areas to extract the meaning of the observed action so as to achieve the joint goal.

Conclusion

The world would be a strange place if all observed actions led to imitative behavior by people who are observing them. Most sports would be impossible to play, as observing an object-directed action (e.g. throwing a ball) would activate the same action in an observer when a very different action (e.g. catching or blocking) would be called for. Absurdity would reign in the ballpark and wherever two or more people are doing just about anything.

The results outlined here suggest that, when an observed action calls for a nonidentical complementary one, there is an interplay between the automatic tendency to resonate with what is being observed and the inclination to implicitly prepare for a complementary action. Observed actions in which an implicit complementary request is embedded seem, then, to have the ability to prompt nonidentical responses.

These findings also provide evidence of flexible stimulus–response adjustments that are necessary whenever individuals interact and cooperate with one another. Neuroimaging and TMS studies confirm that action observation mechanisms tend to simulate what was observed; however, they also seem to be involved in a

more flexible context-dependent action observation process. An interplay seems to exist, then, between an initial simulation process, which allows the observer to experience what is being observed, and a subsequent one, which elaborates the consequences of the initially observed actions in relation to their context and intentions. Understanding the process of how humans coordinate actions in social situations in which the task at hand does not call for imitation [23–25] is yet another step forward in the attempt to comprehend the workings of the neural networks. Further studies are of course warranted in view of the potential application of action observation in the clinical setting.

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Conflicts of interest

There are no conflicts of interest.

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