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Neural mechanisms of imitation

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Recent advances in our knowledge of the neural mechanisms of imitation suggest that there is a core circuitry of imitation comprising the superior temporal sulcus and the 'mirror neuron system', which consists of the posterior inferior frontal gyrus and adjacent ventral premotor cortex, as well as the rostral inferior parietal lobule. This core circuitry communicates with other neural systems according to the type of imitation performed. Imitative learning is supported by interaction of the core circuitry of imitation with the dorsolateral prefrontal cortex and perhaps motor preparation areas — namely, the mesial frontal, dorsal premotor and superior parietal areas. By contrast, imitation as a form of social mirroring is supported by interaction of the core circuitry of imitation with the limbic system.

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Introduction

Over time, the scientific community has markedly changed its view of imitation. Until few decades ago, imitation was definitely not considered to be associated with high forms of intelligence; however, first, the advent of the 'cognitive revolution' and, later, the emergence of the 'embodied cognition' approach have changed this perception so much that a recent interdisciplinary collection on imitation describes it as, "a rare ability that is fundamentally linked to characteristically human forms of intelligence, in particular to language, culture, and the ability to understand other minds" [1].

With the exception of a very special form of imitation (birdsong learning, the neural correlates of which have been studied extensively over the years [2]), detailed studies of the neural correlates of imitation have emerged only in the past few years. This surge of interest in the neural correlates of imitation has been probably inspired — at least in part — by the discovery of 'mirror neurons' in macaques. These neurons are active when the monkey performs a goal-directed action and when the monkey observes somebody else performing the same action [3–5]. Mirror neurons have been found in the ventral premotor cortex (area F5 [3,5,6]) and in the rostral sector of the inferior parietal lobule (area PF [7••]). F5 and PF are anatomically interconnected [8]; in addition, PF connects with the superior temporal sulcus (STS) [9]. In the STS, there are higher-order visual neurons that respond to seeing the actions of others [10]. Thus, in the macaque, there seems to be a circuitry composed of the STS, PF and F5 that codes the actions of others and seems to be able to map these actions onto the motor repertoire of the observer.

These neurophysiological properties seem optimal as precursors of neural mechanisms of imitation in humans. Indeed, functional imaging studies in humans adopting imitative tasks have identified a similar circuitry in the human brain [11–14]. This circuitry comprises the human STS and the human mirror neuron system — namely, the inferior frontal cortex [11], which seems particularly important for coding the goal of the imitated action [13], and the rostral part of the inferior parietal lobule [15,16].

Two main questions emerged from the initial work on the neural mechanisms of imitation in humans. First, given the overlap between the areas activated by imitation tasks and classical areas of language (an overlap that supports the hypothesis that mirror neurons might be important neural elements in the evolution of language [17]), is the activation of classical language areas during imitation essential to imitative behavior or is it simply an epiphenomenon due to internal verbalization [18,19]? Second, given that monkeys have mirror neurons but do not seem to be skilled imitators, what is the role of mirror neurons in monkeys and how do mirror neuron areas in the human brain support imitation? In this review, I will discuss recent studies that have addressed these questions.

Virtual lesion approach to studies of imitation

The advent of functional neuroimaging has made it possible to study in detail the neural correlates of all sorts of human behavior; however, functional neuroimaging cannot provide information on how essential a brain area is to the behavior under investigation. With transcranial magnetic stimulation (TMS), by contrast, it is possible to induce a 'transient lesion' in the stimulated area and to measure the behavioral effects of such a lesion [20,21]. If the area stimulated is essential to the task, then a behavioral effect will be observed. To rule out nonspecific effects, it is important to have a control task and a control stimulation area. With this design, if a behavioral effect is observed only in the experimental task, and then only in the investigated area and not in the control area, it can be reasonably argued that the area under investigation is essential to the task. This approach is even more powerful when TMS is 'image-guided', that is, when it is possible to use structural or functional neuroimaging data to guide the brain stimulation [22].

Image-guided TMS has been used in a recent study on the links between pars opercularis of the inferior frontal gyrus (a classical language area) and imitation. Subjects were stimulated while they imitated finger movements directed at various keys on a keypad and while they performed a control visuomotor task in which the motor output was identical to the imitation task but the visual input was simply due to a red dot jumping over the keys of the keypad. The data demonstrated that TMS reduced performance during imitation, but not during the control visuomotor task, when applied to pars opercularis of the inferior frontal gyrus. By contrast, no effect was observed for either imitation or the control visuomotor task when TMS was applied to the control stimulation site in the occipital lobe [23]. These data show that pars opercularis of the inferior frontal gyrus is essential to imitation, and they support the hypothesis that this brain area contains the human homolog of area F5 of the macaque [17]. Notably, TMS disrupted only some aspects of the imitation process — namely, the goal of the imitated action. This observation is in line with previous imaging findings showing that pars opercularis of the inferior frontal gyrus is particularly active when imitating actions with visible goals [13].

Mirror neurons and imitation

Mirror neurons fire during both the execution of one's own actions and the observation of the actions of others — properties that seem relevant to imitation. Moreover, functional neuroimaging studies in humans have shown that areas of the human brain that are relevant to imitation seem to be the homolog of the mirror neuron areas in macaques. Taken together, these observations suggest that mirror neurons are important cells in imitation. However, the degree of imitative ability in monkeys is subject to debate [24,25], although there is a general consensus that monkeys do not imitate well or often and do not learn quickly by imitation. What is the role, then, of mirror neurons in monkeys? Furthermore, what is the relationship between mirror neurons and imitative learning?

To address the first question, it is useful to consider a recent behavioral study in macaques. In this study, two experimenters performed actions simultaneously with the macaques. One experimenter copied the actions of the monkey precisely, while the other experimenter performed other types of action that were in the monkey's motor repertoire but were not being performed by the monkey at that time. Under these conditions, macaques preferred to look at the human that was imitating them, showing that they recognized being imitated [26]. Macaques might have used their mirror neurons to perform this recognition. More generally, mirror neurons in macaques might provide the ability to recognize the actions of others and the intentions associated with them. In fact, two recent studies in macaques [7••] and humans [27•] have demonstrated that mirror neurons can code the likely future actions of others so that observers are able to anticipate the intentions of others.

These functional properties could be the basis for those forms of imitation that are important for social interactions, mutual identification and empathy (see later); however, the ability to recognize and even to imitate actions that are already in the motor repertoire of the observer is not helpful in learning new actions. Imitative learning is highly appealing because it provides a form of learning that avoids time-consuming trial-and-error learning. Are mirror neurons sufficient to support imitative learning?

Recent single-cell studies suggests that mirror neurons might have the ability to change their responses to the visual input received and that this could represent an initial step toward imitative learning. Classical early studies of mirror neurons showed that these cells fire at the sight of a grasping action but do not fire when the object is grasped with a tool rather than directly with the hand [3,17]. Because macaques do not use tools, it made sense to propose that their mirror neurons would not fire at the sight of an action that did not belong to their motor repertoire. Recently, however, a contingent of mirror neurons with neural responses that are stronger to the sight of actions using tools than to the sight of grasping actions has been observed [28•]. The most likely interpretation of these findings is that these neural responses were induced by the repeated exposure of the monkeys to the sight of tool-use actions performed by the experimenters. Whether these experience-dependent neural responses are relevant to the ability to learn new actions remains to be tested.

Neural correlates of human imitative learning

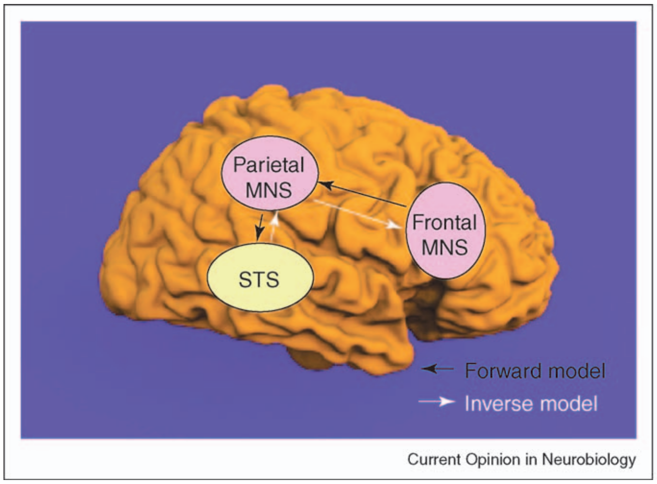
Recent attempts have been made to clarify the role of the mirror neuron system in imitative learning. These attempts can be categorized into two domains: theoretical and empirical. Initial imaging work suggested that there is a flow of information processing across the three principal cortical areas for human imitation — namely, the human STS and the two frontoparietal mirror neuron areas. First, the STS provides a higher-order visual description of the observed action. Second, this description is fed into the frontoparietal mirror neuron system, where the goal of the action and the motor specification on how to achieve it is coded. Last, efference copies of the motor imitative plan are sent from the frontoparietal mirror neuron system to the STS, where there is a matching between the predicted sensory consequences of the planned imitative action and the visual description of the observed action [29].

This information flow has been recently mapped onto a theoretical framework of paired forward and inverse internal models called MOSAIC, which was developed in the motor learning field [30,31]. According to MOSAIC, internal models are input–output functions that mimic experience-dependent sensory-motor states. The inverse model is a controller that retrieves the motor plan necessary to achieve a desired sensory state (or goal), whereas the forward model is a predictor of the sensory consequences of a motor plan. Thus, the inverse model is updated on the basis of the forward model. In neural terms, the input of the inverse model would be the STS output that is sent to the frontoparietal mirror neuron system, and the output of the inverse model would be the output of the frontoparietal mirror neuron system downstream to motor areas. Efference copies of motor commands originating from the frontoparietal mirror neuron system would provide the input of the forward model, whereas its output would be the matching process occurring in the STS [32,33] (Figure 1).

A recent study suggests that the origin of the efference copy of imitated actions that is sent to the STS is located in the ventral sector of pars opercularis of the inferior frontal gyrus [34••]. In that study, the data from seven functional magnetic resonance imaging (fMRI) experiments on hand action imitation and observation were pooled together and re-analyzed, and the results were plotted onto probabilistic cytoarchitectonic maps of the human brain [35,36]. Two peaks of activity emerged in probabilistic Brodmann area 44 (BA44), which corresponds to pars opercularis of the inferior frontal gyrus. A dorsal peak was active during both the imitation and observation of action, corresponding to the pattern of a classical mirror neuron. A ventral peak was active during action imitation, but not action observation. Surprisingly, this peak was not even active during a control motor task in which the performed action was identical to the action performed during imitation. Thus, the activity in the ventral sector of pars opercularis is specific to imitation and might represent the origin of the efference copy. In fact, imitation requires a precise matching of the performed action onto the observed one; thus, a predictor is useful during imitation. The control motor task, by contrast, could be performed by simply selecting the appropriate action and thus does not require a predictor. It should be noted, however, that this recent study pooled together imaging studies of relatively simple, overlearned actions. The real question for imitative learning is what is happening during the imitation of novel actions that do not belong to the motor repertoire of the observer?

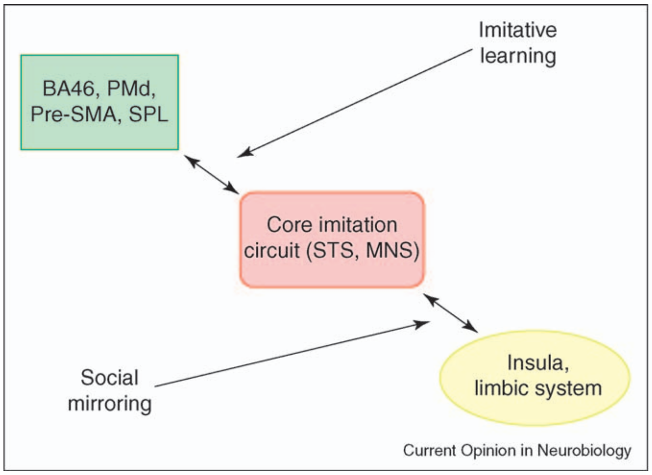
A recent fMRI study has addressed this question. Musically naive subjects were studied while they observed and subsequently executed guitar chords. As expected, the frontoparietal mirror neuron system was active during both the observation and the execution of the guitar chords. The imitation of novel actions, however, yielded additional activation of the dorsolateral prefrontal cortex (BA46) and of cortical areas relevant to motor preparation — namely, dorsal premotor cortex, mesial frontal cortex and superior parietal lobule [37••]. The activity in BA46

Figure 1



Neural mechanisms of imitation. Shown is a representation of the core circuitry for imitation on the lateral wall of the right cerebral hemisphere, together with the internal models the circuitry implements during imitation. Abbreviations: MNS, mirror neuron system; STS, superior temporal sulcus.

Figure 2



Neural mechanisms of imitative learning and social mirroring. In this model, imitative learning is implemented by interactions among the core imitation circuit, the dorsolateral prefrontal cortex (BA46) and a set of areas relevant to motor preparation (PMd, pre-SMA, SPL), whereas social mirroring is implemented by the interactions among the core imitation circuit, the insula and the limbic system. Abbreviations: BA46, Brodmann area 46; MNS, mirror neuron system; PMd, dorsal premotor cortex; pre-SMA, pre-supplementary motor area; SPL, superior parietal lobule STS, superior temporal sulcus.

seems to reflect the selection of motor acts that are appropriate for the task [38], a role that would not be specific to imitation but would also be crucial to other forms of sensory-motor behavior [39]. Thus, imitative learning seems to be supported by a core circuit for imitation composed of inferior frontal, inferior parietal and superior temporal areas and an additional circuit comprising motor preparation areas and BA46 (Figure 2).

Imitation as a form of social interaction

Imitation also seems to be a pervasive form of social communication and identification [40]. People tend to imitate each other during social interactions [41]. The more that people tend to imitate others, the more that they tend to be empathic and concerned with the emotional states of others [41]. This suggests that the core circuitry for imitation might interact with the limbic system (the neural system concerned with emotions) during social mirroring [42]. A recent fMRI study of the observation and imitation of facial emotional expressions has revealed a large-scale neural network that comprises the core circuitry for imitation (the mirror neuron system and the STS), the insula and the limbic system [43]. Subsequent studies of the imitation or observation of emotions have supported the idea that empathy has a sensory-motor, mirroring basis [44–46].

It is conceivable that disorders of social behavior might be due to dysfunction in this circuit. In particular, whether one of the core deficits in autism is a dysfunction in the mirror neuron system has been actively investigated [47,48•,49•]. A recent magnetoencephalography-based study has indeed shown that during the imitation of lip movements adults with Asperger's syndrome activate the same areas as control subjects, but these activations tend to lag behind the temporal progression observed in the control group [50•]. Moreover, recent fMRI data show that during the observation and imitation of facial emotional expressions, children with autistic spectrum disorder have reduced activity in both mirror neuron areas and the limbic system as compared with typically developing children [51••], thereby providing the first developmental evidence of a dysfunction in this circuit in autistic children during a task involving social mirroring.

Conclusion

Recent advances in our understanding of the neural mechanisms of imitation suggest that imitative learning and social mirroring are both associated with activity in a core 'imitation' circuit comprising the frontoparietal mirror neuron system and the STS. However, during imitative learning the core circuitry for imitation interacts with dorsolateral prefrontal cortex (BA46) and motor preparation areas, whereas during social mirroring it interacts with the insula and the limbic system. Future studies in this field should encompass the typical development of these large-scale networks and their dysfunctions.

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