Beyond simulation? Neural mechanisms for predicting the actions of others

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Our ability to attribute mental states such as beliefs and desires to other people has been proposed to involve simulating their mental processes in our own brains. A new imaging study shows that predicting the actions of others does involve areas in the human action control system, but not the same areas that are activated when we plan to perform the same actions ourselves.

How can we read the intentions of other people and thereby predict their future actions? The cognitive basis of this ability, known as 'having a theory of mind' (ToM), is currently the subject of vigorous debate. Do we attribute mental states to others by simulating their cognitive processes or do we use inferential and deductive processes that do not require simulation[1]? In this issue, Ramnani and Miall[2] make a significant contribution to the debate between 'simulation theorists' and 'theory theorists' by investigating the neural processes involved in the prediction of a very simple action made by another person.

Their results show that areas within the human action control system are indeed activated when predicting another's actions. However, they are not the areas activated when we prepare to make the same action ourselves. Furthermore, predicting another's action also leads to activation in brain areas that are typically engaged in tasks that involve complex mental state attributions[3]. These findings are interesting for two reasons. First, they suggest that a simple form of simulation cannot be the only mechanism involved in predicting actions and understanding intentions of others. Second, they provide evidence that even representing the action that someone else performs in a simple task elicits processes involved in ToM .

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When we watch a traffic light change from red to green, we can predict the behavior of a driver waiting in his car in front of it. Does this prediction involve a simulation of the driver's cognitive processes used to plan accelerating? Or does one use inferential and deductive processes that do not involve simulation to come to the conclusion that he will accelerate? To find out whether the neural processes involved in preparing our own actions are also used to predict the future actions of others, Ramnani and Miall developed a clever associative visuomotor task, in which subjects learned to associate arbitrary visual instruction cues with finger movements (**Fig. 1**). During the actual experiment, they were led to believe that another participant who had undergone training together with them was performing the task in another room. The color of the instruction cue specified who should perform the action: the participant being scanned (first person), the training partner in the other room (third person) or a computer (non-biological agent). On some trials, the shape of the instruction cue specified the finger movement that was to be performed, so that a subsequent trigger cue only indicated when the action should be initiated (specific instruction). In this case, the action could be planned in advance. On other trials, the shape of the instruction cue did not indicate the finger movement, which was specified only by the trigger cue (unspecific instruction). In this case, the action could not be planned in advance.

The comparison between specific versus non-specific instruction cues

for the first-person condition showed differential activity in dorsal premotor cortex (PMd). This finding is in line with previous studies showing that PMd is activated when subjects plan to perform arbitrary stimulus-response associations[4]. The comparison between third person and computer across the two instruction types reveals the main effect of intentional stance—anticipating the action of a human actor versus a non-biological agent[5]. As expected from prior results, this

Figure 1 Training phase of the associative visuomotor task. Participants learned to anticipate the actions of their training partner to prepare them for the subsequent fMRI experiment.

comparison showed differential activity in paracingulate cortex and superior temporal sulcus (STS), areas typically involved in mental state attribution[3,6,7]. The crucial question, then, was whether PMd, the area involved in one's own action preparation following specific instructions, would also be active following specific third-person instruction cues. Such a result would be strong evidence for 'simulation theory'. In contrast, mental state attribution through a mechanism like 'theory theory' should lead to activation in areas outside the motor system. Ramnani and Miall did not observe activity in PMd when subjects

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anticipated the action of their partner. Instead, this comparison activated two other neural systems: areas associated with ToM tasks, including paracingulate cortex and posterior superior temporal sulcus, and motor areas, including ventral premotor cortex (PMv).

This new study[2] extends our present knowledge of action understanding in two ways. First, by using a task that requires dorsal premotor cortex rather than ventral premotor cortex, Ramnani and Miall were able to show that the area in PMv usually associated with action understanding and imitation (BA 44/45), is involved in action prediction, even when it is not part of the subsystem used for action planning. Previous studies of action understanding have used standard visuomotor stimulus-response tasks, which involve PMv. Thus, in these studies, PMv was activated during action execution and action observation.

Accordingly, the results from these studies suggested that a common neural mechanism may underlie the planning of actions and the observation or anticipation of these actions, supporting simulation theory[8]. Ramnani and Miall's results show that PMv is activated when observing someone else making an action, even though execution of that same action activates PMd.

Ramnani and Miall suggest two possible interpretations of the co-activation of STS and PMv. On the one hand, it could be that one predicts the other's action by first simulating the execution of the action oneself. On the other hand, forming a mental image of the other's action could also account for the activation in these areas. We consider the first possibility unlikely. If simulating an action is equivalent to preparing to perform it oneself, then in this task we should see activation of PMd. This was not the case. The idea that we predict an action by imagining the other person performing it seems more plausible. It is believed that PMv has a specific role in action when a visual stimulus directly indicates the form of the action required[9]. This is the case when reaching for an object where the shape of the object indicates the form and orientation of the hand needed for grasping, but not when the visual stimulus is an arbitrary sign as in the Ramnani and Miall experiment. However, the sight of another person performing an action also directly indicates the action required to imitate the response. Indeed there are 'mirror neurons' in PMv that respond during the observation of specific actions[10]. In the Ramnani and Miall experiment, no action could be observed, but the subjects had previously observed their partners responding to the cues seen during scanning. The activity in PMv might therefore be associated with imagining the partner performing the action.

The second way in which the new study[2] extends our knowledge concerns the way the other person's task is represented. The activation in areas typically engaged in mental state attribution suggests that an explicit representation of the other person as an intentional agent was formed. It is generally believed that the

mirror system does not provide an explicit representation of other agents or tasks[11]. Therefore, an additional mechanism must be assumed, linking particular stimuli to particular actions. Such a link could be achieved by forming a representation of an intentional relation[1]. Barresi and Moore[12] define intentional relations as relations that involve an agent (in this case, the other participant), an object (a particular stimulus) and the activity connecting agent to object (pressing a specific response button upon seeing the stimulus). Thus, a specific stimulus is associated with the other's intention to act. It seems possible that forming and holding such an intentional relation in mind relies on areas also involved in more complex ToM tasks[3]. In the Ramnani and Miall study, participants were encouraged to pay attention to the other's actions through a monitoring task. Evidence from studies on task representation when two people act at the same time suggests that an intentional relation may be formed even when there is no need to take the other agent into account[13]. It would be interesting to find out whether similar results can be obtained in the absence of a monitoring task that encourages mentalizing about the other person. Finally, investigating individuals with autism in the task developed by Ramnani and Miall seems like a promising way to address the question of whether the ToM deficits in individuals with autism are restricted to the attribution of complex mental states to others or also affect the representation of intentional relations[14].

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