



**Mirror Neurons Differentially Encode the
Peripersonal and Extrapersonal Space of Monkeys**
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impact mediated much of this effect further supports this notion.

Finally, students' psychological state sheds light on how affirmation processes interact with the recursive cycle. African Americans, a stereotyped group, displayed greater psychological vulnerability to early failure. For them, early failure may have confirmed that the stereotype was in play as a stable global indicator of their ability to thrive in school. By shoring up self-integrity at this time, the affirmation helped maintain their sense of adequacy and interrupted the cycle in which early poor performance influenced later performance and psychological state. Students' performance and psychological trajectory can be strongly influenced by timely actions, even when apparently small, that alter or reset the trajectory's starting point.

Other factors, such as teachers' expectancies of their students, could contribute to the longevity of the treatment's effect (21). For instance, that fewer affirmed children were assigned to remediation suggests that the intervention's effects were not only noted by the academic system, but acted upon by it.

The findings demonstrate how initial psychological processes, triggered by an apparently subtle intervention, can have psychological and pragmatic effects that perpetuate themselves over extended time spans, in the present case 2 years (6, 13). They demonstrate the role of such processes in long-term intellectual achievement and also sug-

gest a practical strategy for addressing the achievement gap. Effective psychological interventions depend on the presence of positive and sufficient structural, material, and human resources. Together with such resources and other educational programs, psychological interventions can help individuals perform to their potential and produce lasting positive changes in equity and opportunity.

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18. For the adequacy outcome, the racial group \times condition \times prior performance interaction was significant [$B = -0.31$, $t(328) = -2.54$, $P = 0.011$], indicating that while there was no condition \times prior performance interaction among European Americans [$B = 0.11$, $|t| < 1.1$], there was such an interaction among African Americans [$B = -0.20$, $t(155) = -2.75$, $P = 0.007$].
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Mirror Neurons Differentially Encode the Peripersonal and Extrapersonal Space of Monkeys

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Actions performed by others may have different relevance for the observer, and thus lead to different behavioral responses, depending on the regions of space in which they are executed. We found that in rhesus monkeys, the premotor cortex neurons activated by both the execution and the observation of motor acts (mirror neurons) are differentially modulated by the location in space of the observed motor acts relative to the monkey, with about half of them preferring either the monkey's peripersonal or extrapersonal space. A portion of these spatially selective mirror neurons encode space according to a metric representation, whereas other neurons encode space in operational terms, changing their properties according to the possibility that the monkey will interact with the object. These results suggest that a set of mirror neurons encodes the observed motor acts not only for action understanding, but also to analyze such acts in terms of features that are relevant to generating appropriate behaviors.

Mirror neurons are a set of neurons, first described in the monkey premotor area F5, that respond both when the monkey performs an active goal-directed motor act and when he observes the same motor act performed by others (1, 2). The most accepted interpretation of the function of mirror neurons is that they are involved in action understanding. Here, we investigated whether mirror neurons, besides playing a role in this function, also encode aspects of the observed actions that are relevant to subse-

quent interacting behaviors. A way to test this hypothesis is to examine the effect of relative distance between observer and actor on mirror neuron responses. Although completely irrelevant for "understanding" what the actor is doing, a precise knowledge of the distance at which the observed action is performed is crucial for selecting the most appropriate behavioral reaction.

To investigate quantitatively the possible degree of spatial modulation of the visual responses of mirror neurons, we first isolated hand

movement-related neurons in area F5 of two rhesus monkeys by measuring the neurons' discharge while each monkey was executing hand goal-directed motor acts. The visual properties of these neurons were then assessed by having the experimenter perform the same motor acts in the monkey's peripersonal and extrapersonal (3–7) space, respectively (Fig. 1, A and B). The position of the experimenter's body was the same in all conditions, and actions were performed in the middle sagittal plane of the monkey's body. The selectivity for one of the two regions of space was then assessed by means of quantitative statistical analysis of the response patterns of 105 mirror neurons recorded from two monkeys (8).

Figure 2A shows the visual responses of three mirror neurons to motor acts executed in the peri- or extrapersonal space of the monkey. All three neurons responded during active movements of the monkey. However, their visual responses exhibited different types of tuning depending on whether the observed actions were executed in the monkey's peri- or extrapersonal space. Of all F5 mirror neurons tested, 26% ($n = 27$) exhibited a

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selective visual response when the motor acts were performed in the monkey's extrapersonal space and 27% ($n = 28$) showed instead a selectivity for the monkey's peripersonal space. The remaining 47% ($n = 50$) responded to the visual presentation of actions independent of the spatial location at which they were performed (Fig. 2, B and C, and fig. S1). These results indicate that in monkey area F5, the visual responses of mirror neurons were modulated by the location in space at which observed actions were performed. In particular, a subgroup of these neurons exhibited significantly different responses during observation of actions performed in the monkey's peri- and extrapersonal space, respectively.

We performed an additional experiment in which motor acts were executed at five different distances, with the middle one marking the border between the peri- and extrapersonal regions of the monkey (Fig. 3A). Figure 3B shows the average responses of 27 space-selective mirror neurons as a function of distance. In this figure, distances shorter than 37 cm (corresponding to the length of the monkey's extended arm) lie inside the monkey's peripersonal space, and distances longer than 37 cm are in the monkey's extrapersonal space. As the curves show, the population activity varied in a quasi-monotonic manner with the distance from the monkey's body. That is, it decreased with the distance from the monkey's body for mirror neurons exhibiting selectivity for the peripersonal space and conversely increased for mirror neurons exhibiting selectivity for the extrapersonal space.

We next investigated whether space-selective neurons encode the peri- and extrapersonal regions in a metric format (i.e., the boundary between the

two regions is fixed and only depends on the distance from the monkey's body) or in an operational format [i.e., the boundary between the two regions is dynamic and depends on the workspace of the monkey (3, 9–11)]. In this experiment, visual responses of mirror neurons to motor acts performed in the peripersonal space were measured, in one monkey, under one additional condition in which the frontal panel of the primate chair was closed, thus preventing the monkey from reaching for objects close to his body. Nine (43%) of the 21 tested space-selective mirror neurons changed their tuning as a result of this experimental manipulation. More specifically, after closure of the frontal panel, neurons selective for the extrapersonal space started to respond also in the peripersonal space (similarly to neuron 1 in Fig. 4), while neurons selective for the peripersonal space ceased to respond (similarly to neuron 2 in Fig. 4). This experiment suggests that mirror neurons sensitive to a specific part of space fall into two categories: One encodes peri- and extrapersonal space in a purely metric format; the other parcellates space in an operational manner and changes its properties according to the possibility that the monkey will act.

Taken together, our results seem to suggest that mirror neurons, in addition to their basic properties of encoding observed motor acts, also encode the distance at which they are performed with respect to the observer. However, there is a possible caveat to this conclusion, namely the possibility that the responses of those neurons that we interpret as responding only to actions in peripersonal space might actually reflect the mere presence of an object close to the monkey's body. Such responses are present in adjacent area F4

(3–5). However, this interpretation can be rejected for two reasons. First, neurons in the ventral premotor cortex visually responding to objects close to the monkey's body also exhibit somatosensory responses. In our experiments, when tested for somatosensory responses, none of the mirror neurons responding to motor acts performed in the monkey's peripersonal space discharged during tactile stimulation of body parts. Second, no discharge was observed when three-dimensional objects were presented in isolation in the monkey's peripersonal space.

Another possible interpretation of the selective neuronal responses to the observation of motor acts performed in the monkey's peripersonal space is that the presence of an object close to the monkey's body induced a motor preparation to grasp the object. This interpretation can also be refuted for two reasons. First, as the monkeys received no reward, the number of attempts to grasp the object quickly decayed to virtually zero. Second, as mentioned earlier, the mere presentation of an object elicited no neuronal response. Such responses also during object presentation—and not only during action observation—would have been expected if they were related solely to motor preparation. Finally, we can also exclude the possibility that differential responses in the monkey's peri- or extrapersonal space are due to differences in the amount of attention allocated during these two experimental conditions, as only those trials in which the monkey was fixating the observed action were considered for further analysis. Furthermore, off-line analysis of eye position records revealed no significant difference in the duration of fixations in the two experimental conditions (8).

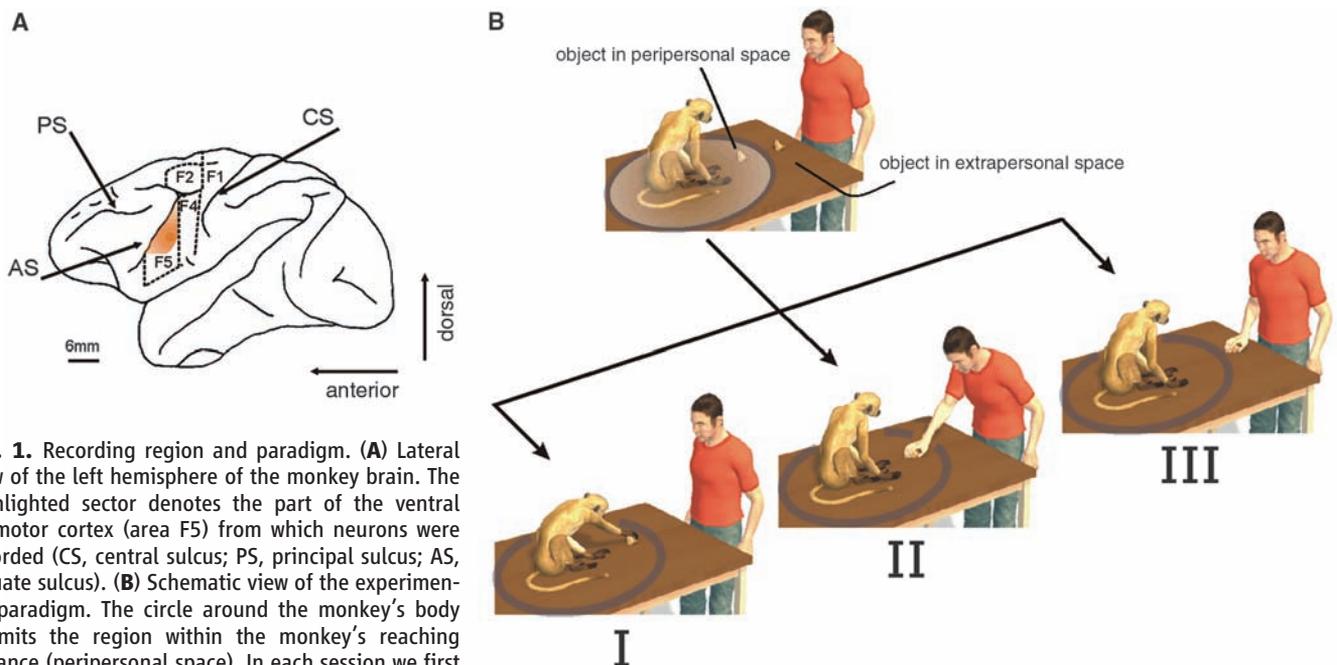


Fig. 1. Recording region and paradigm. **(A)** Lateral view of the left hemisphere of the monkey brain. The highlighted sector denotes the part of the ventral premotor cortex (area F5) from which neurons were recorded (CS, central sulcus; PS, principal sulcus; AS, arcuate sulcus). **(B)** Schematic view of the experimental paradigm. The circle around the monkey's body delimits the region within the monkey's reaching distance (peripersonal space). In each session we first tested the motor responses of neurons during active movements of the monkey (I). The visual responses of these neurons were further tested with the experimenter executing goal-directed motor acts in the peripersonal (II) and extrapersonal (III) space of the monkey. The order of conditions II and III was counterbalanced across sessions.

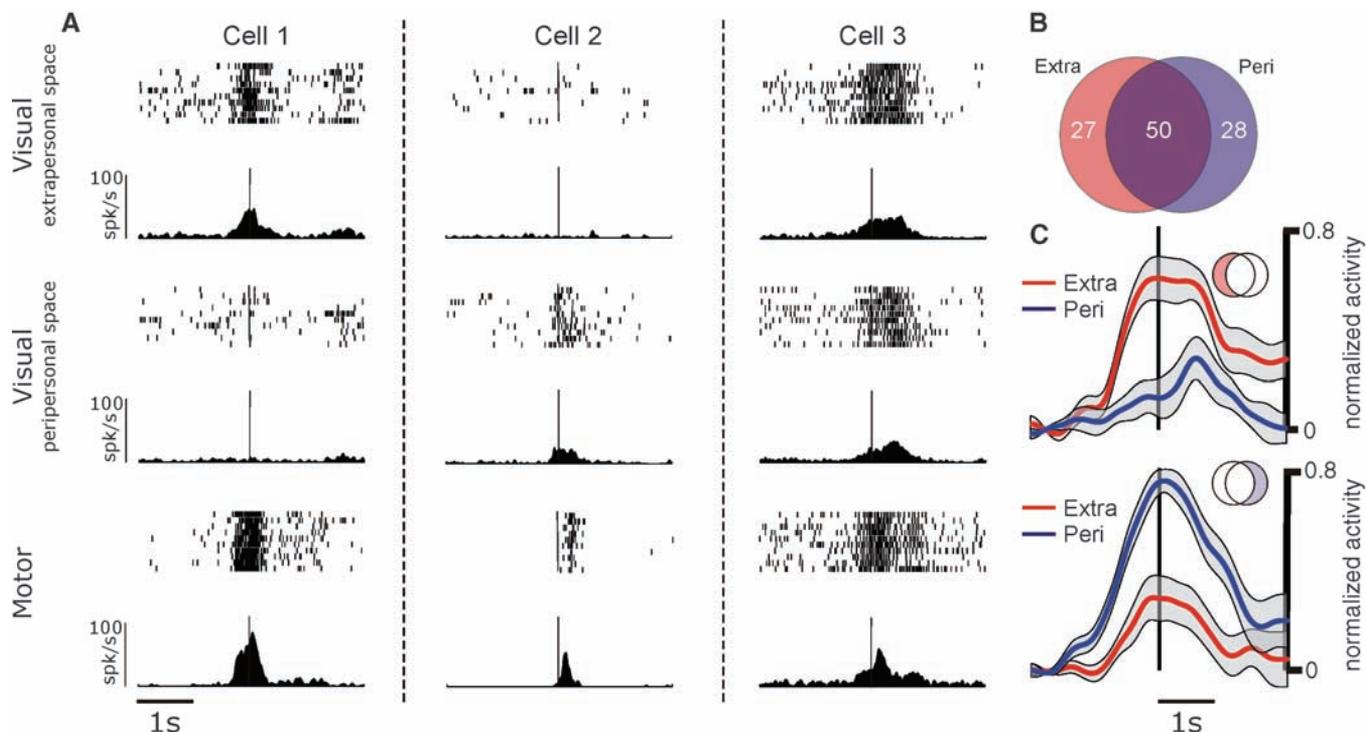


Fig. 2. Single-unit responses and population activity of mirror neurons during observation of actions executed in the monkey's peri- and extrapersonal space. **(A)** Responses of three mirror neurons during observation of motor acts performed in the monkey's extrapersonal (top row) and peripersonal (middle row) space, respectively, and during execution of motor acts (bottom row). Each panel shows a raster plot (top) and a peristimulus spike density function (bottom) of the cells' responses. Raster plots and spike density functions are aligned with the time of contact of the experimenter's or monkey's hand with the object. Cells 1 and 2 exhibited a visual preference for motor acts performed in the monkey's extrapersonal and peripersonal regions, respectively. Cell 3 instead responded to the visual presentation of motor acts independent of the spatial region in which they were performed. **(B)** Venn diagram illustrating the number of mirror neurons

showing a preference for the monkey's peri- or extrapersonal space. The intersection of the two circles represents neurons whose discharges exhibited no statistically significant difference in the two experimental conditions. Neurons not contained in the intersection responded with a significantly stronger discharge during one of the two experimental conditions. **(C)** Population responses to the preferred and nonpreferred conditions of mirror neurons exhibiting a spatial selectivity. The upper and lower panels show the average visual response of mirror neurons selectively discharging during observation of motor acts performed in the monkey's extrapersonal and peripersonal space, respectively. The shaded regions around each curve represent standard error. Vertical lines represent the time of contact between the experimenter's hand and the object. See fig. S1 for an analysis of visual selectivity for specific motor acts.

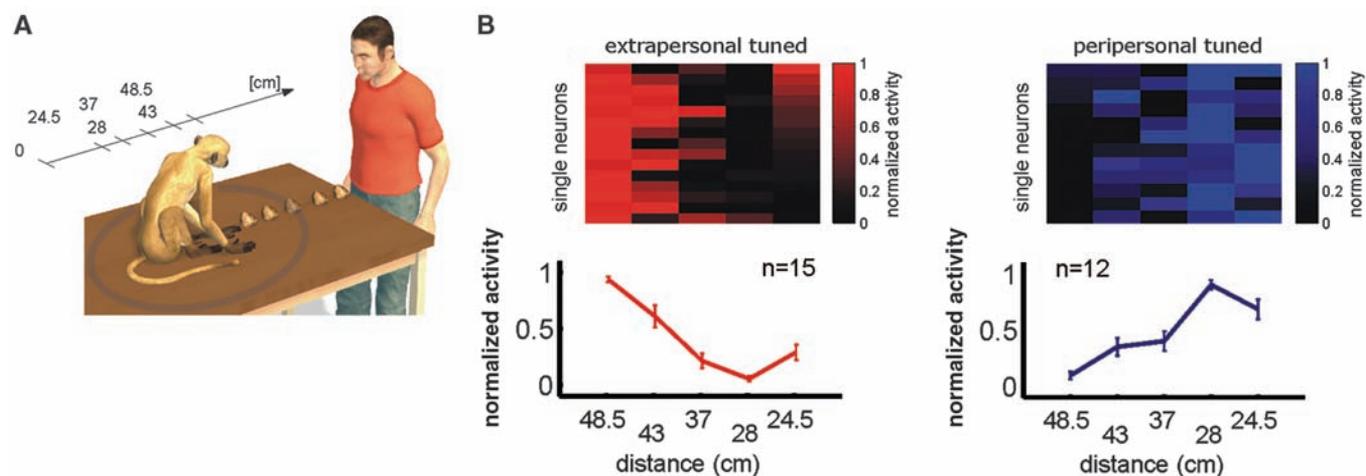


Fig. 3. Experiment in which actions were executed at five different distances, thus more finely sampling the monkey's peri- and extrapersonal space. **(A)** Schematic view of the experimental setup. **(B)** Population responses of mirror neurons as a function of the distance between the monkey and the observed action. The curves represent the normalized population activity of mirror neurons selectively responding to motor acts performed in the monkey's extrapersonal (left panel, $n = 15$ units) or

peripersonal (right panel, $n = 12$ units) space, respectively, tested in this experiment. The horizontal axis signifies the distance between the object and the monkey's body. A distance of 37 cm represents the maximum extension of the monkey's arm and thus marks the border between the monkey's peri- and extrapersonal regions. Vertical lines represent standard errors. The panels above each curve show the normalized activities of the single neurons.

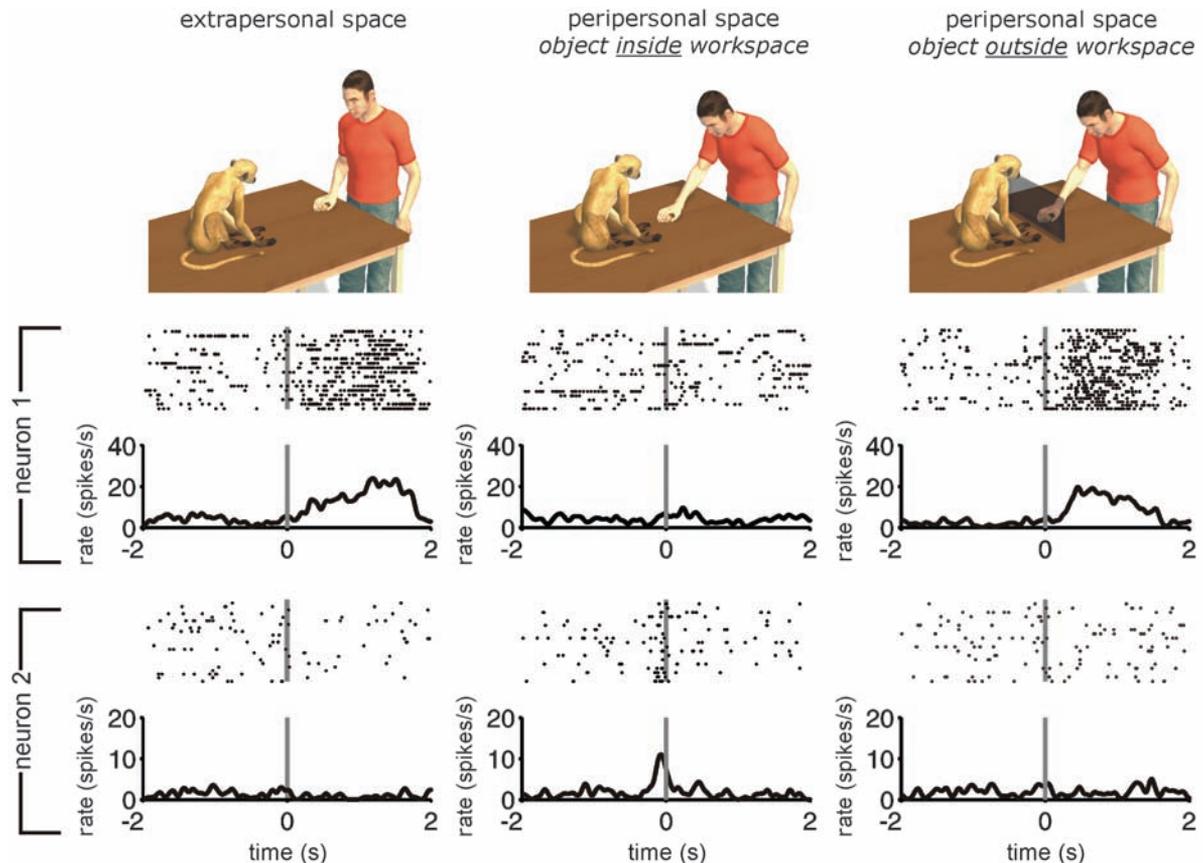


Fig. 4. Dynamical encoding of the monkey's peri- and extrapersonal space. The three columns show the responses of two mirror neurons (neuron 1 and neuron 2) to actions performed in the extrapersonal space (left column) and in the peripersonal space under two different experimental conditions: (i) The monkey is free to perform actions close to his body (central column), and (ii) the frontal panel of the primate chair is closed, thus preventing the monkey from reaching toward objects close to his body (right column). The vertical lines mark the time of contact of the experimenter's hand with the object. The two mirror neurons in the figure encoded space in an operational manner and showed complementary responses. Before closure of the frontal panel (left,

neuron 1 exhibited visual responses only during observation of motor acts executed in the monkey's extrapersonal space; it did not respond when motor acts were executed close to the monkey's body (center). However, after closure of the frontal panel of the primate chair, this neuron discharged also during observation of motor acts performed close to the monkey's body for which it was previously unresponsive (right panel). Neuron 2, before closure of the frontal panel, exhibited visual responses only for motor acts executed in the monkey's peripersonal space (left and center). After closure of the frontal panel, this neuron no longer visually responded to motor acts performed close to the monkey's body (right). See also fig. S3.

These considerations suggest that we are indeed dealing with mirror neurons differentially responding to motor acts performed in different regions of space. What is the possible functional meaning of the different types of mirror neurons described in this study?

The distance between observer and actor is a feature that plays virtually no role in "understanding" the meaning of an observed motor act; nonetheless it is important for evaluating adequate subsequent interacting behaviors. Although an observer can immediately interact with an individual acting in the observer's peripersonal space, interactions in the observer's extrapersonal space are possible only through intermediate steps (e.g., approaching the observed agent or removing an obstacle). The fact that the responses of a subpopulation of mirror neurons exhibit spatial selectivity suggests that these neurons might encode observed actions for subsequent different types of behavioral responses—for example, an approaching behavior in the case of motor acts performed in the extrapersonal space, or a competitive be-

havior in the case of motor acts performed in the peripersonal space. The presence of mirror neurons that encode space not in metric but in operational terms, and that modify their properties according to behavioral contingencies (such as the possibility or impossibility of reaching the observed agent), further supports this interpretation.

Our results suggest a cognitive role for mirror neurons as a system that not only encodes the meaning of observed actions but also contributes to choosing appropriate behavioral responses to those actions. In particular, a stimulating (although admittedly speculative) interpretation of our results is that mirror neurons not only may represent a neuronal substrate for understanding "what others are doing," but also may contribute toward selecting "how I might interact with them."

References and Notes

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References

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