The mirror mechanism: recent findings and perspectives

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Content

• basic properties of mirror neurons

• new findings on visual properties of mirror neurons

• the role of the mirror mechanism in planning actions and in understanding the intention underlying the others’ motor acts
Background

- Mirror neurons first described
  - monkey ventral premotor area F5
  - monkey inferior parietal area PFG

*Figure 1.* Lateral view of the monkey brain showing the subdivisions of the agranular frontal and posterior parietal cortices. The intraparietal and arcuate sulci have been opened to show the areas buried inside them. Agranular frontal areas have been labelled according to Matelli et al. [22,23]. Note that area F5 is formed by three further subdivisions: F5c, F5p and F5a [24]. Posterior parietal areas are defined according to Pandya and Seltzer and Gregoriou et al. [25,26]. The areas buried inside the intraparietal sulcus are defined according to functional criteria (for references, see [27]). AI, inferior arcuate sulcus; AIP, anterior intraparietal area; AS, superior arcuate sulcus; C, central sulcus; DLPF, dorsolateral prefrontal cortex; FEF, frontal eye field; IO, inferior occipital sulcus; L, lateral fissure; LIP, lateral intraparietal area; Lu, lunate sulcus; MIP, medial intraparietal area; P, principal sulcus; ST, superior temporal sulcus; VIP, ventral intraparietal area; VLPF, ventrolateral prefrontal cortex.
Basic properties of monkey mirror neurons

• In area F5
  - purely motor neurons
  - visuomotor neurons
    ‘canonical neurons’ - responsive to the presentation of three-dimensional objects
    ‘mirror neurons’ - responsive to the observation of motor acts performed by others
Basic properties of monkey mirror neurons

• main properties of F5 motor neurons
code the goal of the motor acts
evidence supporting this point is provided by neurons that discharge when the monkey grasps an object (e.g. food) with its right hand, left hand and the mouth

• visual properties of mirror neurons (premotor and parietal cortices)
congruence between the executed and the observed motor act
  - a strict correspondence between the effective observed and executed motor act
  - a correspondence in the goal of the observed and executed motor act, but not in the precise movements necessary to achieve the goal
Basic properties of monkey mirror neurons

The mirror neuron circuit

Figure 2. (a) Overview of MR brain activations (recorded with 3T fMRI) during the observation of grasping acts. Leftmost image: lateral view of reconstructed left hemisphere indicating the six different antero-posterior levels at which coronal slices shown on the right have been taken. Right: statistical parametric maps activation for the contrast: hand action versus static control. The data are from a single monkey, overlaid onto its coronal anatomical sections. Numbers on each slice indicate y-coordinate (antero-posterior from interaural plane). as, arcuate sulcus; ips, intraparietal sulcus; sts, superior temporal sulcus.
Basic properties of monkey mirror neurons
The mirror neuron circuit

**Figure 2.** (c) Temporo-parieto-premotor grasping observation pathways in the monkey brain. Flattened representation of STS, IPS/IPL and IAS with ROIs indicated. Arrows and areas coloured in red and blue indicate, respectively, the STPm–PFG–F5c pathway and the LB2–AIP–F5a/p pathway.

AIP, anterior intraparietal area; FEF, frontal eye fields; F5c, F5 convexity; F5p, F5 (bank) posterior; F5a, F5 (bank) anterior; FST, fundus of the STS; **IAS, inferior arcuate sulcus;** LIPa, anterior part of the lateral intraparietal area; MT/V5, middle temporal area; MSTd, middle superior temporal area, dorsal part; MSTv, middle superior temporal area, ventral part; **STS, superior temporal sulcus;** IPS, intraparietal sulcus.
New visual properties of mirror neurons

• Space-sensitive mirror neurons
  • possible influence on mirror neuron discharge of the spatial location of the observed actions

• View-dependent mirror neurons

• Mirror neurons sensitive to the value of an observed action
New visual properties of mirror neurons
Space-sensitive mirror neurons

**Figure 3.** (a) Schematic view of the visual conditions of the experimental paradigm: the monkey observes an experimenter executing a grasping act in the peripersonal (left) and extrapersonal (right) space of the monkey.  
(b) Examples of the responses of three mirror neurons during observation of grasping acts executed in the monkey's peri- and extrapersonal space and during monkey execution.
New visual properties of mirror neurons
Space-sensitive mirror neurons

**Figure 3.** (c) Operational encoding of the monkey peri- and extrapersonal space. The top part shows the experimental conditions: the experimenter grasps an object in the extrapersonal (left) or in the peripersonal space without (centre) or with (right) a frontal panel impairing the monkey's reach into its peripersonal space. Note that in this latter condition, the object (and the act performed by the experimenter) is metrically in the monkey's peripersonal space, but operationally outside it. The lower panels show the visual responses of a mirror neuron in the three conditions. The vertical lines mark the time of contact between the experimenter's hand and the object.
Responses of mirror neurons to grasping observed from three visual perspectives.

(a) Experimental conditions (subjective view: 0°; side view: 90°; frontal view: 180°). (b) Examples of the responses of four mirror neurons during observation of grasping from the three perspectives. Rasters and histograms are temporally aligned (vertical grey line) with the moment at which the observed hand touches the object. Neuron 1 is selective for the subjective view, neuron 2 for the frontal view, neuron 3 for the side view. The activity of neuron 4 discharged equally well for all points of view.
Figure 5. (a) Motor task. The monkey, starting with its hand from a fixed position (left), reaches and grasps a piece of food (or an object), then it brings the food to the mouth and eats it (grasp-to-eat condition I) or places it (or the object) into a container (grasp-to-place condition) located near the mouth (II) or near the target (III). Visual task. The experimenter, starting with his hand from a fixed position (left), reaches and grasps a piece of food or an object (right), then he brings the food to the mouth and eats it (grasp-to-eat condition I) or places it (or the object) into a container located near the target (grasp-to-place condition II).
Motor intention and mirror neurons
Coding of motor sequences in the parietal and premotor cortex

Figure 5. (b) Examples of the discharge of three IPL neurons during the motor task. Neuron 67 is selective for grasping to eat, neuron 161 shows the opposite behaviour, while the response of neuron 158 is not affected by the action goal. (c) Examples of the discharge of three IPL neurons during the visual task. Neuron 87 discharges stronger during observation of grasping to eat, neuron 39, on the contrary, during observation of grasping to place, while neuron 80 discharges equally well in both conditions. In both (b) and (c), rasters and histograms are aligned (vertical bar) with the moment when the monkey or the experimenter, respectively, touched the food/object.
Motor intention and mirror neurons
Coding of motor sequences in the parietal and premotor cortex

Figure 5. (d) Congruence between the visual and the motor response of mirror neurons encoding action goal in area PFG. (i) Example of a neuron discharging stronger during grasping for eating than during grasping for placing, both when the action is executed and when it is observed. Conventions as in (b) and (c). (ii) Population-averaged responses, showing the same pattern of differential activity between the preferred (white bar) and not preferred (black bar) action during motor and visual tasks. Depending on the neuron, the preferred action could be grasp-to-eat or grasp-to-place.
Coding motor intentions in humans

- Enourmous amount of studies devoted to action observation in humans
- Only a limited number of studies devoted to the issue of understanding motor intention in humans
Coding motor intentions in humans

• fMRI study
• 3 experimental conditions
  • “context“ (a scene composed of objects either for the beginning of breakfast or the end of it)
  • “action“ (empty background, grasping a mug)
  • “intention“ (grasping a mug within the context)

• Areas belonging to cortical mirror system were activated both in the “action“ and “intention“ conditions
• The contrast between the “intention“ and “action“ conditions showed activation in the right caudal inferior frontal gyrus

Conclusion

• The mirror mechanism allows one to unify action production and action observation. This motor-based action and intention understanding appears to represent the primary way for interindividual interactions.

• the link between the mirror mechanism and mentalizing will be achieved only if it becomes possible to record single neurons from awake human beings during such processes