Dispatches

Social Neuroscience: Mirror Neurons Recorded in Humans

New single-cell recordings show that humans do have mirror neurons, and in more brain regions than previously suspected. Some action–execution neurons were seen to be inhibited during observation, possibly preventing imitation and helping self/other discrimination.

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Mirror neurons are defined by the property that they fire during both the execution and the observation of a specific action. Despite over ten years of intense research following their discovery in monkeys [1–3], until now there has been only indirect evidence for their presence in humans (see [4–8] for reviews). In this issue of *Current Biology*, Mukamel *et al.* [9] finally provide the critical *direct* electrophysiological evidence that humans have mirror neurons. This study additionally shows that the mirror neuron system in humans extends beyond the ventral premotor cortex and inferior parietal lobe traditionally associated with this system. Intriguingly, the study also reports evidence for the existence of 'anti-mirror' neurons, which might help us understand how our brain can perform motor simulations without moving our body, and how we might be able to discriminate our own actions from those we observe.

Humans Have Mirror Neurons

Itzhak Fried, a neurosurgeon at UCLA, helps patients with severe intractable epilepsy. Surgically removing the epileptogenic region that triggers the epilepsy can often cure the problem. To localize this region, he implants microwires in a number of likely foci (Figure 1). While waiting for spontaneous seizures to occur, many patients are eager to help research scientists by providing them with the unique opportunity to record from single neurons in their brain.

Mukamel and colleagues [9] presented 21 of these patients with movies of two types of facial expression (frowns and smiles) and two types of hand action (precision grips and whole hand prehensions). They also asked them to perform these four actions upon reading the written instructions 'Frown', 'Smile', 'Finger' or 'Hand' on a computer screen. The exciting finding of the team is that they recorded activity from 11 neurons that behaved exactly like broadly congruent mirror neurons in the monkey [1,9]: they discharged during both the observation and execution of one type of action (for example, whole hand prehension); and this activity exceeded that recorded during the observation and execution of at least one different type (for example, frowning and smiling). This combination of cross-modal activity and selectivity ensures that the firing of such a neuron can inform the brain, using motor simulation, that someone was performing one type of action rather than another [2].

Importantly, viewing the word describing the most effective action on a screen without performing the action did not produce a significant response in these neurons. Otherwise, rather than being mirror neurons, they could have been purely visual neurons that respond to the sight of an action and to the sight of the word describing that action.

Where Are the Mirror Neurons?

So far most researchers almost dogmatically associate mirror neurons with two brain regions: the ventral premotor (vPM) cortex and the inferior parietal lobule (IPL). The fact that mirror neurons were originally reported in these two regions in the monkey [1–3] somehow led to an irrational double standard. On the one hand, rather than critically examining whether visual activity in these regions truly overlapped with activity during motor execution of similar tasks [10], most enthusiastically attribute any activity in these regions to mirror neurons — even though, in the monkey, 90% of neurons in these regions are not mirror neurons [1,2]. On the other hand, glucose uptake [11], fMRI [12–14], transcranial magnetic stimulation [15] and magnetoencephalographic [16] experiments suggesting that the primary somatosensory cortex, the supplementary motor area (SMA) or the temporal lobe could also contain mirror neurons encounter skepticism and are ignored in most reviews on the mirror neuron system.

Mukamel *et al.* [9], however, could not choose where to look for mirror neurons. The position of their electrodes in humans was dictated by clinical considerations. Patients had electrodes in the medial wall (cingulate cortex, SMA and pre-SMA) and the medial temporal lobe (amygdala, hippocampus, parahippocampal gyrus and entorhinal cortex) — none of which is classically associated with mirror neurons. In accordance with what fMRI experiments suggested [6,12,13], mirror neurons were found in many of these areas: the SMA, the hippocampus and parahippocampal gyrus and the entorhinal cortex. These results suggest we should stop considering certain brain regions as intrinsically 'mirror neuron regions': instead, it would seem that mirror neurons are a minority of neurons, but exist in many brain regions.

Theories that propose that mirror neurons are the result of Hebbian learning [17,18] — 'what fires together wires together' — can explain this ubiquity: whenever we perform an action, all the neurons involved in executing this action will fire at

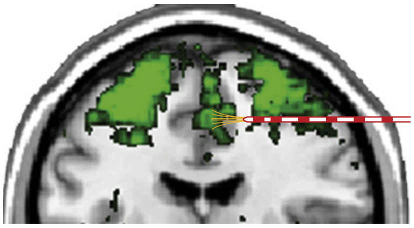

Figure 1. The experimental set-up used by Mukamel *et al.* [9].

The electrodes used to localize the origin of the epilepsy by Itzhac Fried (red) are sometimes placed in the SMA, where independent fMRI experiments happened to have measured 'mirror like' brain activity during action execution and observation (green), [12]. This has allowed Mukamel *et al.* [9] to record the first mirror neurons in humans.

approximately the same time as those involved in seeing, hearing and feeling ourselves perform the action. After repeatedly performing and perceiving ourselves perform the action, Hebbian learning would make many neurons, not only in the vPM and IPL, but also in the SMA and medial temporal lobe, have the property of being excitable both when we perform the action and when we see or hear someone else perform a similar action. The only prerequisite for such learning would be for a neuron to have connections with both sensory and motor systems—a frequent property in a brain that has evolved to connect perception and action.

To Do or Not To Do What I See: That Is the Question

The existence of mirror neurons always begged a question: if motor neurons are activated when we see the actions of others, why do we not always imitate what we see? Functional imaging studies showed that, unlike the premotor cortex, the primary motor cortex is sometimes deactivated when we see the actions of others [12]. It has been hypothesized that the SMA may be controlling this gate [12]. Mukamel *et al.* [9] confirm this idea: they found 11 'anti-mirror' neurons that increased their firing rate when the patient was executing a particular action, but *decreased* their firing rate below baseline when the patient observed someone else perform this action. Given the connections of the SMA, such neurons in this area would be ideally equipped to open the gate to M1 during action execution, and close it during action observation. Functional MRI is blind to the difference between mirror and anti-mirror neurons, because it simply measures increases in metabolism [19]: the synapses that inhibit anti-mirror neurons during observation would consume as much energy as those that excite mirror neurons in the same condition.

Another problem raised by mirror neurons is: if the brain represents the actions of others in its own motor system, how can it tell who is actually performing these actions? Anti-mirror neurons could disambiguate our own actions from those of others [9].

Conclusions and New Frontiers

Following a period in which it had become fashionable to claim that there is actually no evidence for mirror neurons in humans [7,20], the new work of Mukamel *et al.* [9] brings us two leaps further in our understanding of this system: we now know that humans have mirror neurons, and we know that mirror neurons are not restricted to the premotor and inferior parietal cortex. We also see that certain neurons seem to have 'anti-mirror' properties. In combination with mirror neurons, they could help the brain perform an inner simulation of other people's actions while at the same time selectively blocking overt motor output and disambiguate who performed the action.

What lies in front of us is a number of newer but equally challenging questions. What do mirror neurons do for us? How does the function of mirror neurons in various brain regions differ? How do mirror neurons in different brain regions interact with each other? How do we attribute actions to ourselves or to others, and what role do anti-mirror neurons play in this function?

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