

# Demystifying social cognition: a Hebbian perspective

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**For humans and monkeys, understanding the actions of others is central to survival. Here we review the physiological properties of three cortical areas involved in this capacity: the STS, PF and F5. Based on the anatomical connections of these areas, and the Hebbian learning rule, we propose a simple but powerful account of how the monkey brain can learn to understand the actions of others by associating them with self-produced actions, at the same time discriminating its own actions from those of others. As this system appears also to exist in man, this network model can provide a framework for understanding human social perception.**

Three primate cortical areas have been implicated in the capacity to understand the actions of others (Figure 1): the superior temporal sulcus (STS), area PF of the inferior parietal lobule and the premotor cortex (F5). Despite accumulating empirical evidence, little effort has been made to develop models of the interactions between these areas. Here we will review and compare the sensory and motor properties of all three areas. Based on the anatomical connections between them, and the Hebbian learning rule, we will propose a physiologically plausible model of how those three areas, working together, can learn to associate observed and heard actions with the monkey's own actions (i.e. mirror properties) and discriminate the monkey's own actions from those of others. Given that precise anatomical connections and single-cell properties are known only in the non-human primate, this review will focus on data from macaque monkeys.

## Review of the primate data

### Visual responses

**STS:** Bruce and colleagues [1] reported 15 neurons in the STS that responded best to the sight of walking. Perrett and coworkers later showed that this area contained cells responding selectively to a large variety of body movements including walking, articulation of the head, limbs and torso and goal-directed interactions with objects [2–5]. Different cell types were tuned to different hand actions (e.g. tearing, grasping, manipulating) [5]. Typically, such neurons have large receptive fields and respond independently of who performs the action. Figure 2a illustrates a neuron that responded vigorously

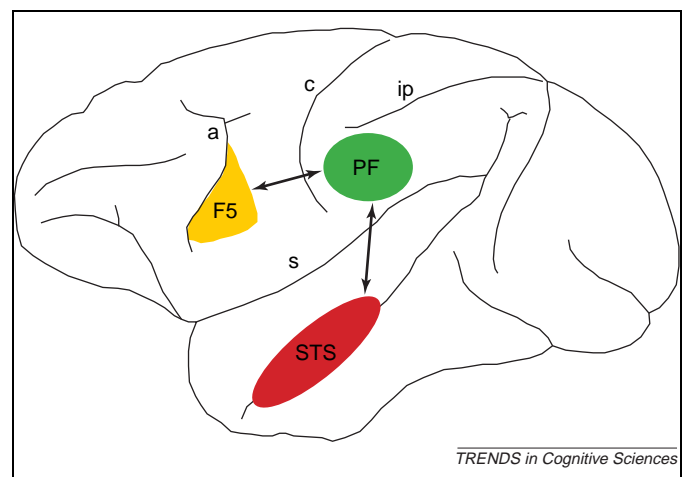
while observing a human releasing an object but not to the same movement without object or to the object movement alone. Changing the illumination, the distance to the experimenter or the speed of the movement often has little effect on such neurons. Although most neurons in the STS are sensitive to viewpoint, some respond similarly to many perspectives of an object or action, and are called 'object-centred' [3–8]. Such cells' firing appears to describe the stimulus at a high conceptual level corresponding to 'grasping' or 'dropping'.

**F5:** Responses to the sight of actions were also found in the premotor area F5. Different F5 neurons respond when the monkey sees another individual grasp, break or release an object [9–12]. Figure 2b shows an F5 neuron responding while the monkey sees a human grasp an object. The neurons' response is much less when a human mimes the same movement without an object (Figure 2b, bottom).

**PF:** Finally, in the inferior parietal cortex (area PF/PFG, termed PF hereafter), neurons also respond to the sight of grasping (Figure 2c) or other hand-object interactions [13].

STS, F5 and PF therefore all provide high-level visual descriptions of observed actions, being relatively invariant to changes in illumination, colour, distance and identity of the agent. There are, however, some differences between the areas.

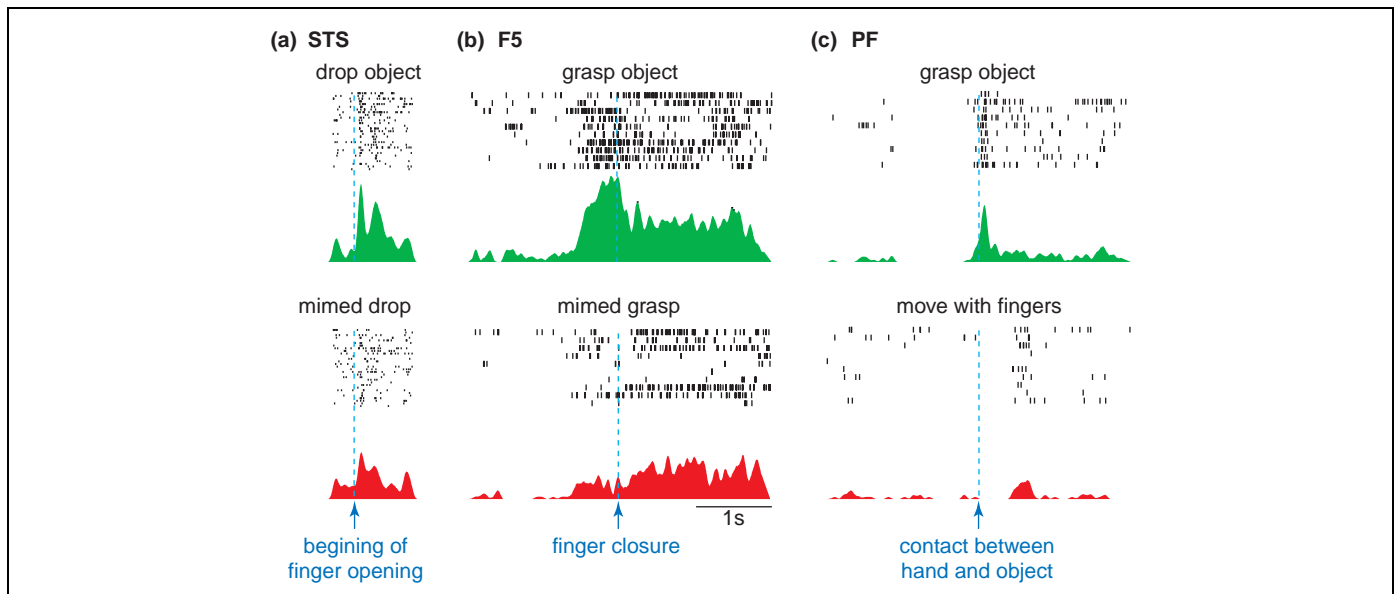
PF and STS cells often respond better to the sight of one hand performing the action than to the other, whereas in



**Figure 1.** Illustration of the location of premotor cortex (F5), area PF of the inferior parietal lobule (PF) and the superior temporal sulcus (STS) together with their anatomical connections (arrows) shown on a lateral view of the macaque brain (a, arcuate sulcus; c, central sulcus; ip, intraparietal sulcus; s, sylvian sulcus).

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**Figure 2.** (a) Response of an STS neuron while the monkey observed an experimenter open his hand to release an object (top). Watching the experimenter open an empty hand ('mimed drop') evoked a smaller response [18]. (b) Response of an F5 neuron while seeing the experimenter grasp an object (top) or perform the same movement in the absence of an object (bottom) [14]. (c) Example of a PF neuron that responded to the sight of grasping an object (top) but neither to the sight of the same fingers simply moving the object on a tray without grasping it, nor to a grasping movement performed without an object [13]. Both the STS and the F5 neuron are therefore critically tuned to hand-object interactions, but the PF neuron is less so.

F5, more than 60% of the cells respond equally well to the sight of either hand. Hand discrimination might depend on asymmetric receptive fields with better responses in the contra-lateral hemifield. Many STS neurons also respond well to movie or even point-light displays of actions [2] whereas F5 neurons respond poorly to videos of actions, even with stereoscopic presentation (L. Fogassi, pers. commun.).

Whereas the STS represents a wide variety of actions, including walking, face and hand actions, PF and F5 appear to be specialized for hand and mouth actions directed to objects. So far, there is no description of PF or F5 neurons responding more to the sight of whole body or facial movements not directed to objects, but other premotor or parietal structures might contain such neurons. Furthermore, in the STS >90% of the neurons are visual whereas in PF only ~60% [13] and in F5 <20% [10,11,14,15] show this property.

#### Non-visual sensory properties

PF is relatively less studied than the other two areas under discussion, but there are striking similarities between F5 and STS that merit some comment.

First, some STS neurons have been shown to respond strongly to the invisible presence of a human behind an occluding screen. These responses cannot be due to current visual input alone because the same human hiding in a different location often caused no response (Figure 3a; [16]). Instead, the response depends on what has been seen previously (a human walking towards one screen or the other), which is a property observed in other STS neuron types [17]. Similarly, some neurons in F5 respond to the sight of a human reaching behind an occluder, but only when the monkey previously saw an object being placed behind the occluder (Figure 3b; [14]), as if the monkey deduced that grasping occurs only if there

is an object. Both regions therefore supplement present visual input with deductions about what is not visible but can be inferred from cues.

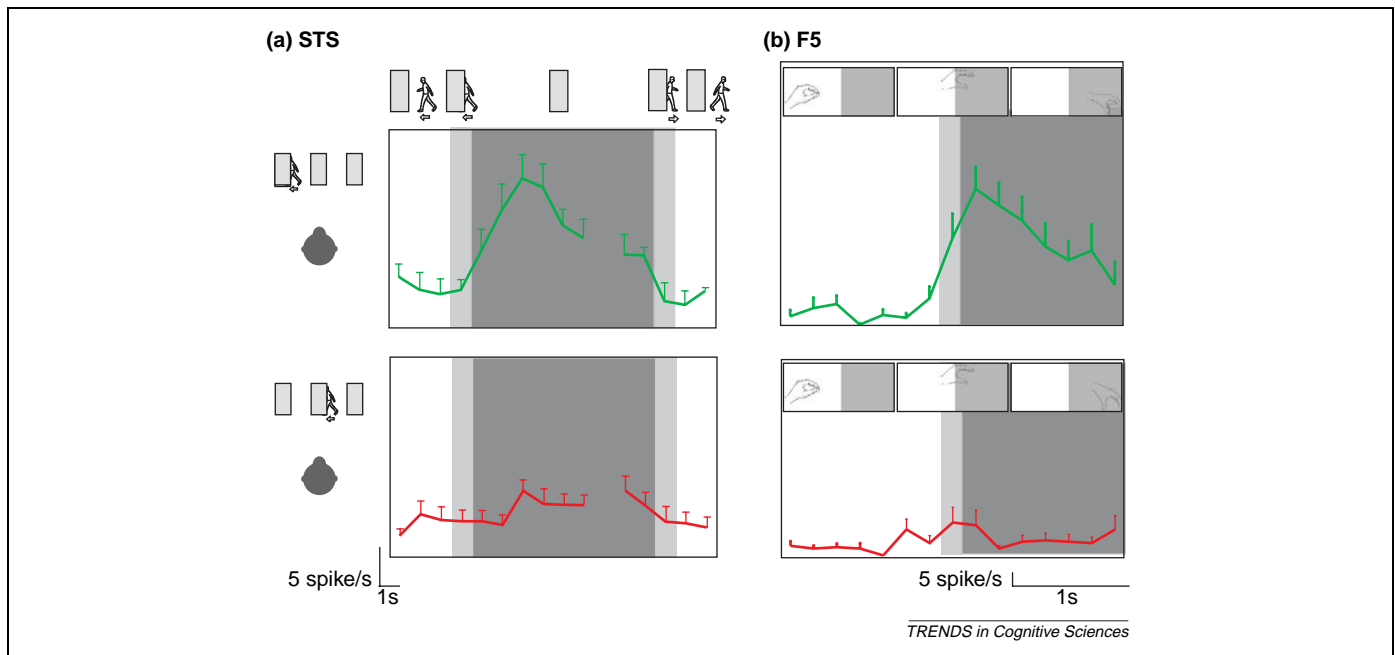
Second, both regions respond to actions that can only be heard (F5, [11,15]; STS, [18]). Some neurons respond to actions performed by other individuals both when they are seen and when they are only heard. Figure 4a illustrates an F5 cell that responds to its preferred action independently of whether it is seen or heard. Neurons with similar properties, but which respond to walking, have been found in the STS (Keyesers *et al.*, unpublished observations). Figure 4b shows an example of another type of STS neuron. It responded to the sight of hands tearing paper, but not to the sound of tearing alone. Combining both sound and vision produced the strongest response, demonstrating auditory input to that neuron [18]. Similar non-linear interactions are found in F5 [11].

In summary, areas F5, PF and STS all contain cells responding to the sight of a hand interacting with objects in particular ways. Both F5 and STS respond to the sound of actions, and to stimuli that are not fully visible.

#### Motor responses

A striking difference between STS, F5 and PF is the presence/absence of motor responses in these areas. Over 90% of F5 neurons responding to the sight of an action also respond when the monkey performs a similar action with eyes open or closed. In PF, the same is true for about two-thirds of the neurons. Although the STS has been explored less than the other areas, two years of searching has failed to reveal any reliable motor responses when the monkey cannot observe himself (Keyesers *et al.*, unpublished observations).

This difference in motor properties is corroborated by electro-stimulations: of the three areas, only in F5 does stimulation cause overt limb movements, including entire grasping sequences [19]. Similarly, reversible inactivation



**Figure 3.** (a) Response of an STS neuron while the monkey observed a human walk towards, hide behind and then reappear from an occluding screen. The top and bottom graphs illustrate the activity when observing the person hiding behind the left and centre occluder, respectively (see cartoon on the left). The different phases of the stimulus are illustrated above, and coded on the graph as a white background when the subject is fully visible, light gray when partially occluded and dark gray when fully occluded by the screen. The response is much stronger in the top case (green) than the bottom (red), even though in both occluded phases there were only three occluders to be seen without any visible individual [16]. (b) Response of an F5 neuron, while a human demonstrator reaches behind an occluding screen. In the top case, the monkey previously saw an object being placed on a tray before the occluder was placed in front of the tray. The discharge that begins as the hand starts to be occluded (light and dark gray background) is much stronger here than in the bottom case, although at that moment both visual stimuli (top and bottom) are equal [14]. Note that the scales are different in (a) and (b).

of premotor and inferior parietal cortex, but not STS, leads to deficits in grasping [20,21].

**F5 and PF:** In F5 and in PF, a neuron's visual and motor properties are usually congruent, which is why they are called 'mirror neurons' [10,13]. A mirror neuron responding when the monkey grasps a peanut also responds when someone else grasps a similar object. These visual responses are not the result of imitative behaviour [10]. The strictness of this congruence varies between neurons. Almost no F5 neurons and only a third of PF neurons respond to the observation of an action without demonstrating motor properties.

**STS:** In the STS, two types of cells have been described. In the lower bank, 'shape-selective' cells have been found to respond very selectively to hand-object interactions. These neurons respond similarly to the sight of the monkey's own movements and those of others [5,22]. Many cells in the upper bank are less selective for shape. These neurons respond similarly to any object, including hands, moving in particular directions. More than 80% of these fail to respond to the sight of the monkey's own movements [23]. Even the sight of a grating moved by the monkey is ineffective, whereas the same grating moved in similar ways by an experimenter evokes robust responses [24].

STS neurons have been tested while the monkeys moved their arms with their eyes closed (Keyser *et al.*, unpublished observations). There has been no consistent evidence in either the upper or the lower bank of the STS of neurons responding during the monkey's own limb movements in the absence of visual input. Taken together, current empirical evidence therefore suggests that kinaesthetic and/or motor information about the monkey's own limb movements have either no effect on shape-selective STS neurons, or an

inhibitory effect, counteracting the visual sensitivity to self-produced movements in the other neurons. For the latter, inhibition affects only the sight of the monkey's own movements: another simultaneous movement in the world can produce a full-blown visual response [23].

There is therefore a fundamental difference between F5 and PF neurons that respond during action execution even without visual input and shape-unselective STS neurons that fail to respond to the execution and sight of the monkey's own actions.

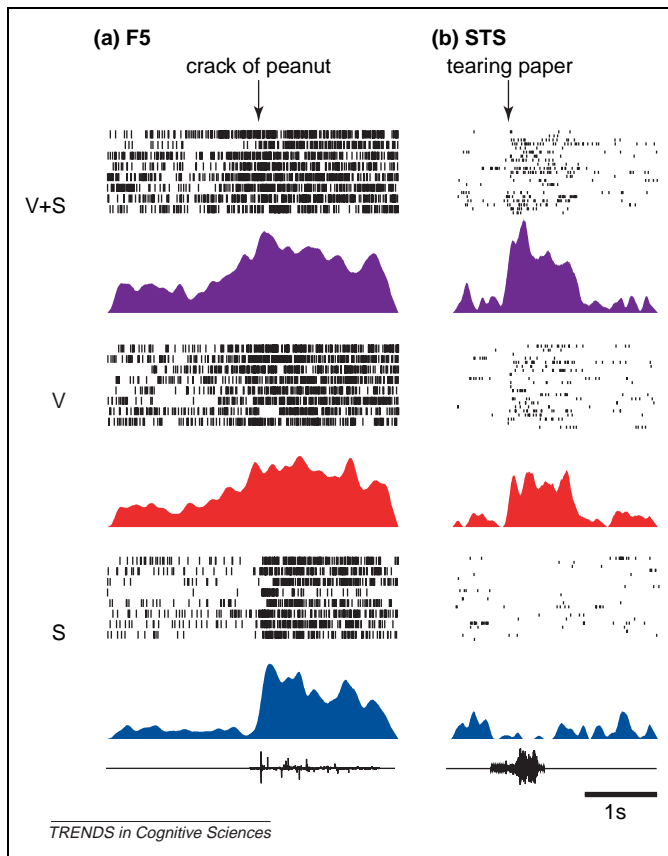
#### Anatomical connections

Anatomically, the three areas form a network of interconnected areas (Figure 1). The STS is reciprocally connected with the inferior parietal lobule (IPL) [25–29]. The IPL in turn is subdivided into multiple anatomical sectors, the most rostral of which is PF [30,31]. Whereas most of the IPL is connected with the STS, PF shows a pattern of patchy connections that overlaps particularly well with the locations in which neurons respond specifically to complex body movements [26]. PF also has strong reciprocal connections with the convexity of F5 where mirror neurons are found [31–34]. STS, PF and F5 should therefore be considered not individually but as a functional circuit, reciprocally connected, allowing information to be exchanged in both directions. How can this network perspective help us understand the functions of these areas?

#### The Hebbian model

##### *The emergence of mirror neurons for visible actions*

The existence of mirror neurons in the premotor cortex might be considered peculiar. How can cells respond both



**Figure 4.** Neural responses to the sight and the sound of actions. (a) Response of an F5 neuron to the sound alone (S) of cracking a peanut (bottom), to the vision of the action (V) and to the combined sound and vision of the action (V+S). The black plot at the bottom represents the sonograph of the action (data taken from [11]). (b) Same for an STS neuron. Here the effective action was tearing a sheet of paper. Note the lack of response to sound alone, but more response to V+S than V [18].

to the execution and the observation of an action? Several efforts have been made to describe the circuitry involved in action recognition [31,35,36] or to model the emergence of mirror neurons [37]. Unfortunately, the first set of studies [31,36,35] did not address the question of how the circuit they described could acquire mirror properties. The last study [37] elegantly showed how an *artificial* neural network can acquire mirror properties, but used a physiologically implausible learning rule. Here we provide a more physiological perspective by proposing that Hebbian learning (see **Box 1**) within the F5–PF–STS circuit can explain the existence of mirror neurons.

Both human and monkey infants observe their own actions carefully. During this process, their initially cumbersome movements occasionally lead them to grasp objects in particular ways. Action potentials in STS neurons responding to the sight of this type of grasping then overlap in time with activity in the PF and F5 neurons that cause the infant to grasp in that way, creating the prerequisites for Hebbian associations: neurons that fire together wire together. **Figure 5a** illustrates in more detail what happens in the brain. In our model, before learning, the STS→F5 connections are weak and unselective, that is, they reach both the precision grip (PG) and the whole hand prehension (WHP) neurons. Because the monkey is currently performing a precision grip, the synaptic signal from the STS finds only the PG neurons to be active in PF and F5. Hebbian learning

### Box 1. Hebbian learning

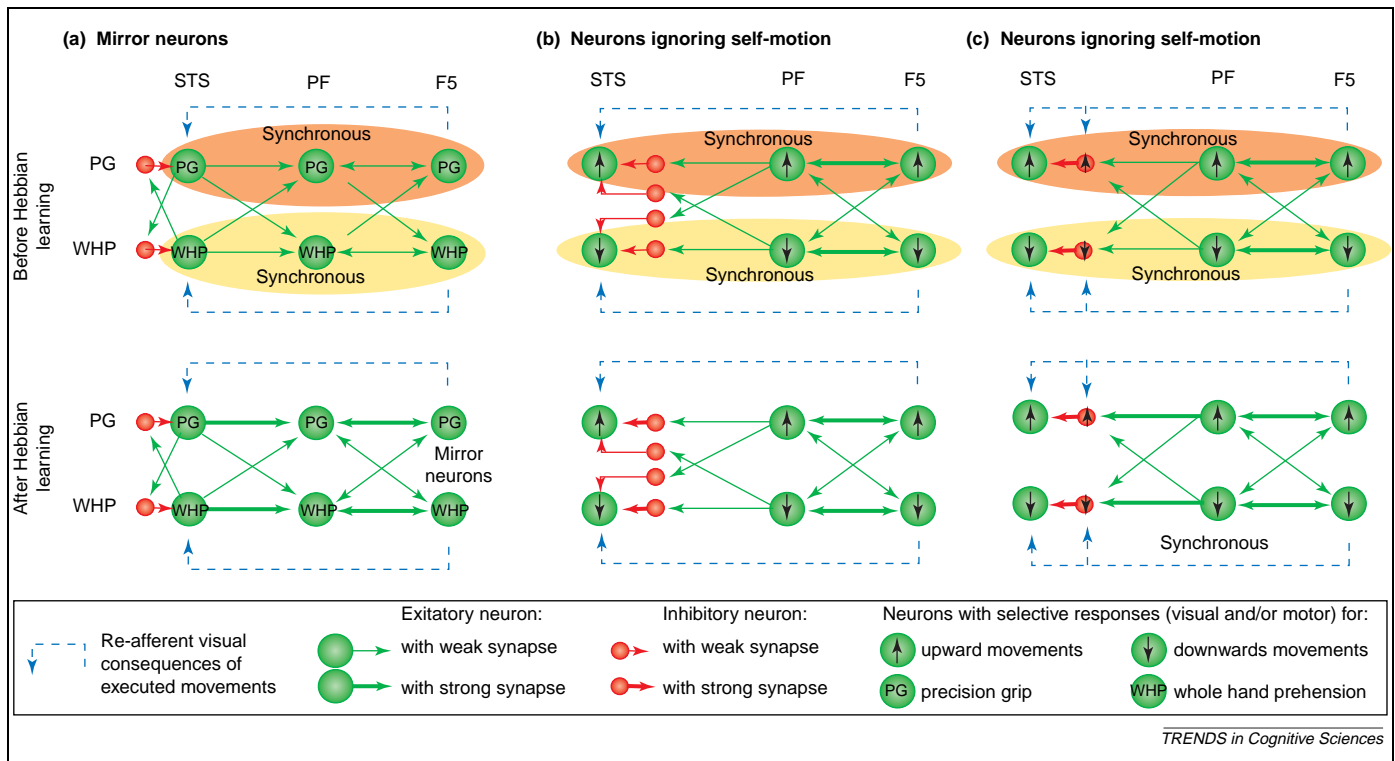
In his book *The Organization of Behaviour* [49], Hebb postulated: 'When an axon of cell A is near enough to excite cell B or repeatedly or consistently takes part in firing it, some growth or metabolic change takes place [...] such that A's efficiency, as one of the cells firing B, is increased'. Put in simpler words: 'neurons that fire together wire together'. Modern neuroscience now strongly supports his intuition [50]. Markram *et al.* [51] recorded from two connected cortical pyramidal neurons and noted that if the pre-synaptic action potential occurred 10 ms before, or during, the post-synaptic one, the efficacy of the synapse increased and that this was a lasting change. This form of synaptic plasticity has been termed 'Hebbian learning'. Importantly, Hebbian learning has also been observed in inhibitory GABAergic synapses [50].

will hence only reinforce the STS-PG to F5-PG connections. The same logic applies to WHP self-observation. Over time, neural associations will strengthen to the point where neurons in PF and F5 will respond to the visually- or auditorily-driven synaptic input from STS (**Figure 5a**, bottom). Many STS cells show some degree of viewpoint invariance (see above), and the same neurons therefore respond to the monkey's own actions and those of others [5]. After learning the association between F5 motor commands and auditory or visual STS descriptions of the monkey's own actions, the observation of someone else performing a similar action would then also activate the neurons in PF and F5, and mirror properties will have emerged.

According to our hypothesis, the emergence of mirror neurons in PF and F5 is a direct consequence of the anatomical connections between STS, PF and F5. All that it requires is Hebbian learning at interconnections. Similarly, events that systematically follow each other could be associated in Hebbian ways across modalities. For example, if the sight of reaching towards an object systematically precedes grasping, it could become associated with grasping execution, which could explain why the sight of reaching behind a screen can trigger responses in mirror neurons [14].

### Shared circuits for touch and emotions

We concentrate here on the STS–PF–F5 circuit responding to actions because enough is known about the anatomy and function of this system to develop a physiologically sound model. The main ideas, though, could apply to other cases where particular brain areas are involved both in observing and experiencing an event. First, seeing someone else being touched activates our secondary somatosensory cortex (i.e. the SII/PV complex) as if we had been touched ourselves [38]. When we are touched, the visual stimulus of the object touching our body overlaps in time with neural activation in the somatosensory cortices. Hebbian connections might therefore associate the sight of touch with the sensation of touch in SII/PV. These associations activate SII/PV even when we see someone else being touched. Second, observing someone else's disgust activates the insula of the observer as if he had been disgusted himself [39]. Hebbian enhancement of the connections between STS cells sensitive to (disgusted) facial expression [6,40] and insular cortex neurons responding to unpleasant odors [41] could account for this phenomenon; although we do not see our own facial



**Figure 5.** (a) Proposed model of the emergence of mirror properties. A chain of interconnected STS, PF and F5 neurons before (top) and after (bottom) Hebbian learning. The top row in each case represents neurons selective for precision grip (PG) be it seen (STS) or executed (F5), and the bottom row represents neurons selective for whole hand prehension (WHP). During self-observation of PG, F5 activity leads to motor output, and thereby to visual and auditory re-afferent activation of the STS-PG neurons (blue dotted arrow). The STS-PG neurons then send a signal to PF and F5. Inhibitory interneurons are shown in STS to account for competition [54] but are not necessary for the present model. Only STS→PF connections are shown, the reverse connections being considered in b. (b,c) Two alternative models accounting for the emergence of mirror neurons that ignore the monkey's own actions. Here upwards and downwards neurons are considered, and only the PF→STS axons that synapse on GABAergic interneurons are shown. During the execution of upwards movements, the visual consequences of the action activate upwards STS neurons. At the same time, a PF→STS corollary discharge conveys the motor and kinesthetic information regarding the action to the inhibitory interneurons controlling STS neurons sensitive to both upwards and downwards motion. Synchrony with the visually evoked activity occurs only in the upwards neurons, as the monkey is currently viewing his upward movement, resulting in Hebbian enhancement of only the matching synapses. The same logic applies to downwards movements. In (c) the inhibitory interneurons receive visual input, and Hebbian learning occurs between PF and STS in a way similar to (a) but with the opposite effect because of the inhibitory nature of the interneuron.

expressions, our mothers tend to mimic our facial expressions as babies. For disgust in particular, the sight of a baby vomiting causes a disgusted facial expression in most spectators. For the baby, his state of nausea is therefore correlated with the sight of disgusted facial expressions. This correlation is strengthened by the fact that our own disgust is often associated with other people's facial expressions of disgust because of common environmental causes of the emotion (e.g. a bad smell).

#### Mirror neurons for unseen actions

The intense facial imitation occurring between parent and child could also be essential for Hebbian training of mirror neurons responding to the sight of mouth movements. Despite the fact that we do not see our own mouth movements, the sight of the parent's mouth movements will become trained in a Hebbian way with the infant's matching motor program.

We both hear and see the actions of others, and the auditory and visual representations of these actions overlap in time in the temporal cortex, providing the basis for Hebbian association and audiovisual neurons in the STS [18]. The sound of our own actions resembles that of the actions of others. Listening to the sound of one's own actions hence triggers activity in audiovisual neurons in the STS that overlaps in time with motor activity in F5 and PF,

enabling the Hebbian emergence of audiovisual mirror neurons [11,15]. This scenario shows how the sight of others' actions can be matched to the execution of our own actions without ever seeing our own actions. It can therefore explain how mirror neurons can emerge for mouth movements (e.g. babbling) that we do not usually see, and has important implications for the acquisition of language [11,15].

Many forms of social learning could also be conceived as the result of such associations, including stimulus enhancement, response facilitation, contagion, emulation and imitation [42], whereby the sensory experience of others and their actions encourages the production of similar actions by the observer.

#### Cancellation of one's own actions in the STS

Hebbian learning also occurs at GABAergic synapses (see Box 1). Because GABA is inhibitory, the pre-synaptic input here 'learns' to inhibit post-synaptic activity. Figure 5b illustrates how such learned inhibition could account for the remarkable selectivity with which shape-unselective STS neurons ignore the sight of the monkey's own actions. Here 'upwards' and 'downwards' neurons are considered; that is, neurons that fire during the execution or observation of either upwards or downwards movements. The model predicts that, during an upward or downward movement, a PF→STS corollary signal to the inhibitory

interneurons results in Hebbian enhancement of only the matching synapses.

If the corollary signals from F5 and PF synapses project mainly onto inhibitory STS interneurons, Hebbian learning during self-observation would therefore result in the motor signal inhibiting the corresponding visual response. When the monkey observes the actions of someone else (or an unpredictable consequence of self-generated actions), the corollary motor signal is absent and the visual responses are not inhibited [23,24]. A similar inhibition of re-afferent sensory input was proposed in the classic accounts of the lack of movement perception during saccades [43,44]. By adding the Hebbian learning aspect to it, our model can account for the selectivity of the inhibition: only neurons with matching properties (i.e. selective for the same type of actions) will experience the coincident activity required for Hebbian learning. Our model thus predicts plastic and selective inhibition to develop even in the absence of selective pre-wiring (Figure 5).

Interestingly, both Figure 5b and 5c predict activity in the STS during the monkey's own movements in the inhibitory interneurons. Given that we focus on large spikes during extracellular recordings in our laboratories, the activity of the smaller inter-neurons are systematically ignored, which could account for why such activity was not observed during single-cell recordings. Functional MRI experiments, being sensitive to synaptic activity [45], indeed demonstrate STS activity during action execution [36] (see Box 2).

Shape-selective neurons in the STS are not shut down during self-observation [5], and therefore provide the required visual input to PF and F5 to train mirror neurons. Moreover, if a motor command has an unusual consequence (e.g. while wearing prism glasses), the corollary motor input will not inhibit the 'correct' re-afferent visual input [24] thus providing a salient error message. After repeated self-observation under the new conditions, the system will relearn to cancel the visual consequences of self-produced actions using the same Hebbian algorithm. This flexibility is an interesting property of our model.

#### *Origin and implications of the Hebbian system*

A similar system to the STS–PF–F5 circuit appears to exist in humans (Box 2). By responding both during the execution and the observation of actions, mirror neurons

#### **Box 2. Does a similar system exist in humans?**

Humans have a similar circuit to the STS–PF–F5 circuit in monkeys. F5 appears functionally similar to human BA44 and 6, PF/PFG to the human posterior parietal lobe (PPL, BA40 in particular), and STS to more mid and caudal sectors of the human STS [35,52,53]. In humans, all three areas are activated during the observation of the actions of others [35,36,47,48]. During the execution of actions, our model predicts increased excitatory activity in BA44/6 and PPL and increased inhibitory activity in the STS (see Figure 5 in main text). Given that fMRI reflects synaptic processing more than spike activity [45], and that inhibitory and excitatory synapses have similar metabolic costs, our model would predict increases in activity in all three areas, even if it is the result of inhibitory synaptic activity in the STS. This is exactly what has been observed [36].

#### **Box 3. Questions for future research**

- Are the anatomical connections from PF to the shape-unselective STS neurons inhibitory, as our model predicts (i.e. onto inhibitory interneurons)? Are those from STS onto PF and F5 excitatory?
- Can a similar model account for the emergence of mirror properties for touch and emotions?
- How does the brain use the mirror neurons that emerge from Hebbian learning for the purpose of social perception?
- Can we demonstrate Hebbian learning at synapses while learning new actions and observing ourselves?
- Can the tight correlations in activity between STS–PF–F5 that our model predicts be measured using multi-unit recordings in monkeys or, less directly, by dynamic causal modelling in neuroimaging? Does this correlation change as a new skill is acquired?
- Can an artificial neural network with Hebbian learning acquire mirror properties?

in F5 and PF can serve many purposes, including social understanding, language and imitation [11,15,46–48]. In addition, STS neurons remaining unresponsive to the observation of the agent's own movements, might be important for our capacity to distinguish ourselves from others. Both these properties emerge from the Hebbian STS–PF–F5 circuit, and the circuit might therefore underlie our remarkable capacity to relate intuitively to other people while at the same time not confusing ourselves with the people we empathise with: a combination of functions that none of the areas could fulfil alone.

Although this circuit might be central to these essential functions, it probably evolved for a different purpose. Together with Oztop and Arbib[37] we believe that information flow in the STS→PF→F5 direction probably arose initially to allow visual feedback to improve motor control. Information flow in the F5→PF→STS direction probably evolved to reduce the information processing load of the visual system by subtracting predictable and hence redundant information about the agents own movements from the visual scene. Once these circuits had evolved for these pragmatic purposes, they seem to have been used for the new social challenges of primate life.

To summarize, we have reviewed the available literature on the coding of actions in STS, PF and F5. We showed that neurons in all three areas respond to the sight and the sound of the actions of others, whereas only PF and F5 also respond to the monkey's own actions. Using a simple physiological learning rule – Hebbian learning – we showed how the mirror properties of F5 and PF and the cancellation of the agent's own movements in STS can be acquired by the STS–PF–F5 circuit by exploiting the correlations in time between the visual, auditory and motor representations of actions that occur during the subject's own actions and those of others. We hope that this simple, physiologically plausible model helps to demystify social cognition, by shedding new light onto its mechanisms and development (see also Box 3).

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