OPINION

Neurophysiological mechanisms underlying the understanding and imitation of action

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What are the neural bases of action understanding? Although this capacity could merely involve visual analysis of the action, it has been argued that we actually map this visual information onto its motor representation in our nervous system. Here we discuss evidence for the existence of a system, the 'mirror system', that seems to serve this mapping function in primates and humans, and explore its implications for the understanding and imitation of action.

We live in a world full of objects, sounds and movements. Among all of these stimuli, the movements of other living creatures — especially of our conspecifics — are particularly important for us. How do we understand the actions of other subjects? What are the neurophysiological bases of this ability? Unlike other cognitive capacities, such as object recognition or space perception, action understanding has never been a main focus of research in neuroscience, despite its crucial role in social behaviour. Action is a rather generic term that describes several different types of phenomenon, ranging from a movement directed to attain a specific goal, to behaviours in which means and ends are temporally far apart. In this article, we will use the term action in two ways: as a generic term that indicates any type of intentional motor behaviour, and as a specific term referring to goal-directed behaviours that produce a reward for the acting individual. This distinction will become relevant later in the article, when we discuss imitation and understanding of meaning.

What are the neural mechanisms that underlie action understanding? By action understanding, we mean the capacity to achieve the internal description of an action and to use it to organize appropriate future behaviour. Broadly speaking, there are two hypotheses that might explain how action understanding occurs. The first one, which we will refer to as the 'visual hypothesis', states that action understanding is based on a visual analysis of the different elements that form an action, and that no motor involvement is required. For example, when we observe a hand grasping an apple, the analysed elements would be the hand, the apple and the movement of the hand towards the apple. The association of these elements, and inferences about their interaction, would be sufficient to allow the observer to understand the witnessed action. If this view were correct, action understanding would essentially be mediated by the activity of the extrastriate visual areas, the inferotemporal lobe and the superior temporal sulcus (STS). In both monkeys and humans, these areas respond selectively to objects, body parts, biological motion and, in the case of some neurons of the STS, interactions between hands and objects[1–7].

An alternative hypothesis, which we will refer to as the 'direct-matching hypothesis', holds that we understand actions when we map the visual representation of the observed action onto our motor representation of the same action. According to this view, an action is understood when its observation causes the motor system of the observer to 'resonate'. So, when we observe a hand grasping an apple, the same population of neurons that control the execution of grasping movements becomes active in the observer's motor areas. By this approach, the 'motor knowledge' of the observer is used to understand the observed action. In other words, we understand an action because the motor representation of that action is activated in our brain. This view, although defended by some theoreticians, was never particularly popular in neuroscience. However, the idea that we understand others through an 'internal act' that recaptures the sense of their acting was defended by several philosophers, especially by PHENOMENOLOGISTS (for example, REF. 8; see REF. 9 for a detailed account). Of course, the hypothesis that action understanding is based on a direct-matching mechanism does not exclude the possibility that other, more cognitive processes based on object and movement descriptions could also participate in this function. It stresses, however, the primacy of a direct matching between the observation and execution of action.

Here we will review evidence that an action observation/execution matching system does exist in monkeys and humans, and will discuss its implications for the understanding and imitation of action.

Mirror system in monkeys

Mirror neurons are a particular class of visuomotor neurons, originally discovered in a sector of the ventral premotor cortex of monkeys, called area F5 (REFS 10,11). Area F5 is characterized by the presence of neurons that code goal-related motor acts such as hand and mouth grasping[12–14]. Some of these cells are motor neurons, others also respond to visual stimuli. Some of them are activated by the presentation of three-dimensional objects, whereas others — mirror neurons — require action observation for their activation. The main functional characteristic of mirror neurons is that they

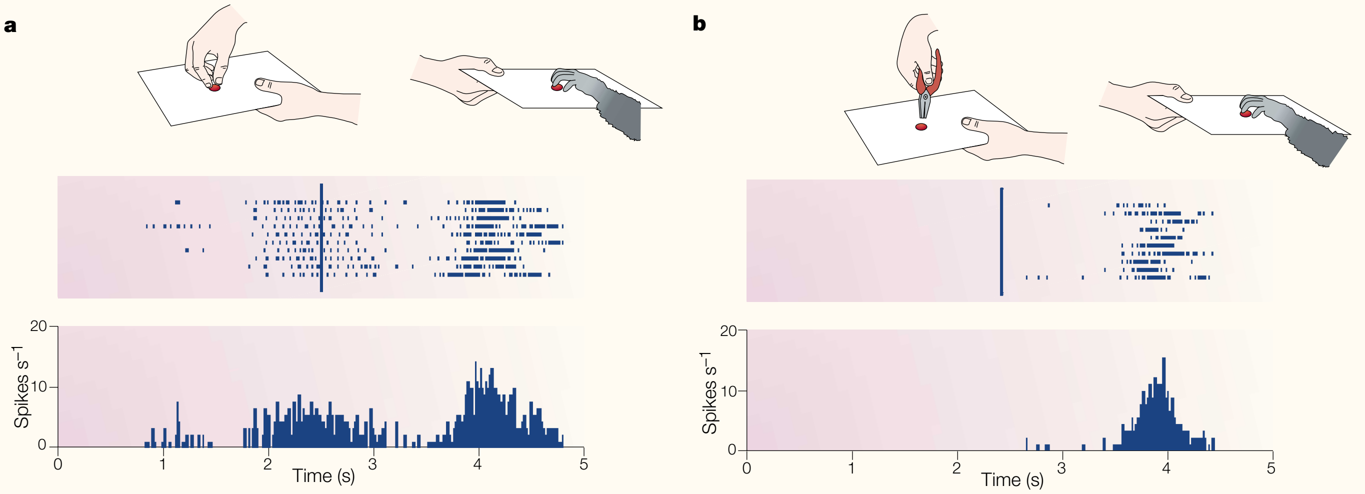

Figure 1 | **Visual and motor responses of a mirror neuron in area F5. a** | A piece of food is placed on a tray and presented to the monkey. The experimenter grasps the food, then moves the tray with the food towards the monkey. Strong activation is present in F5 during observation of the experimenter's grasping movements, and while the same action is performed by the monkey. Note that the neural discharge (lower panel) is absent when the food is presented and moved towards the monkey. **b** | A similar experimental condition, except that the experimenter grasps the food with pliers. Note the absence of a neural response when the observed action is performed with a tool. Rasters and histograms show activity before and after the point at which the experimenter touched the food (vertical bar). Adapted with permission from REF. 11 © 1996 Elsevier Science.

become active both when the monkey makes a particular action (for example, when grasping an object or holding it), and when it observes another individual (monkey or human) making a similar action (FIG. 1). Typically, mirror neurons do not respond to the sight of a hand mimicking an action in the absence of the target. Similarly, they do not respond to the observation of an object alone, even when it is of interest to the monkey[10,11].

Most mirror neurons in F5 show a marked similarity in their responses to the observation and execution of effective actions. This congruence is sometimes extremely strict. In such cases, the effective motor action and the effective observed action coincide both in terms of goal (for example, grasping) and in terms of how the goal is achieved (for example, precision grip). However, for most neurons, the congruence is broader and is confined to the goal of the action. These broadly congruent neurons are of particular interest, because they seem to generalize the goal of the observed action across many instances of it.

The novelty of these findings is the fact that, for the first time, a neural mechanism that allows a direct matching between the visual description of an action and its execution has been identified. Such a matching system constitutes a parsimonious solution to the problem of translating the results of the visual analysis of an observed action — devoid, according to the 'direct-matching hypothesis' of meaning (see also below) — into an account that the individual is able to understand.

Before addressing the issue of what the functional roles of the mirror system might be, it is important to discuss how and from where such a system originates. More than 10 years ago, Perrett and his coworkers found that the STS harbours a rostrally located region — the STSa — where neurons discharge when the monkey observes biological actions[4,15–17]. Some of the movements effective in eliciting responses were walking, turning the head, bending the torso and moving the arms. A small set of neurons discharged during the observation of goal-directed hand movements, such as grasping objects[16] — actions that were similar to those coded by F5. It is important to note that, although this issue was not systematically addressed, STSa neurons do not seem to discharge during active movements, or if they do express motor-related activity, it is not as prominent as in F5.

So, both STSa and F5 contain neurons that are responsive to the observation of biological actions. The two areas are not directly connected; however, both of them are linked to the inferior parietal lobule, namely to area PF (Brodmann area (BA) 7b)[18–22]. The properties of area PF have recently been re-investigated with the specific purpose of finding out whether this area contains neurons that respond to biological motion[23,24]. The results showed that more than half of the PF neurons that were recorded responded to visual stimuli. Among them, neurons that respond selectively to the observation of actions are particularly interesting. These neurons represent about 40% of the visually responsive neurons. Actions that are effective in activating them include grasping, bimanual interaction, holding, placing and reaching. About half of the action-observation neurons responds to one action only, whereas the other half responds to two actions (for example, grasping and releasing, see FIG. 2). But the most important finding was that most neurons that were responsive to action observation also discharged during action execution. They were therefore defined as PF mirror neurons[23,24]. As in the case of F5, there was a clear relationship in most PF mirror neurons between the observed action they responded to and the executed action that triggered their discharge.

It therefore seems that there are three interconnected areas in the monkey brain that contain neurons that are responsive to biological movements. These areas differ in their motor properties. In F5, almost all of these neurons discharge during action execution. In area PF, about two-thirds of them have this characteristic. In the STSa, neurons with motor properties do not seem to be common, although, as mentioned above, no systematic investigation of motor properties in STSa has been carried out so far.

However, it is important to stress that these findings do not exclude the possibility that other areas are involved in the description of biological movements and the understanding of action. As a matter of fact, in addition to its connection to area PF, STSa is also part of a circuit that includes the amygdala and the orbitofrontal cortex[25]. Such a circuit is probably involved in the elaboration of the affective aspects of social behaviour[6,26,27].

Brothers and colleagues[28,29] described neurons in the monkey amygdala that were responsive to the observation of complex social stimuli, such as monkeys displaying threatening facial expressions. A possible role of the amygdala in processing social stimuli is consistent with several brain-imaging studies in humans. Using POINT-LIGHT STIMULI, Bonda *et al.*[30] measured cerebral metabolic activity by positron emission tomography (PET) during the observation of biological motion. They found activation of the amygdala and the rostrocaudal part of the right superior temporal sulcus and adjacent temporal cortex during the observation of signs conveyed by expressive body movements. However, it must be clarified that these data do not detract from the direct-matching hypothesis. Indeed, there is preliminary evidence that the amygdala becomes active during the expression of facial emotions, especially when imitation is involved (REF. 31, and M. Iacoboni, unpublished observations). It is important to add that patients with MOEBIUS SYNDROME, who are congenitally incapable of moving their facial muscles, seem to have difficulties in appreciating emotions conveyed by the faces of others[32,33]. This finding strongly supports the possible existence of a matching system, not only for stimuli devoid of emotional content, as in the case of the F5 mirror system, but also for emotionally charged stimuli[34].

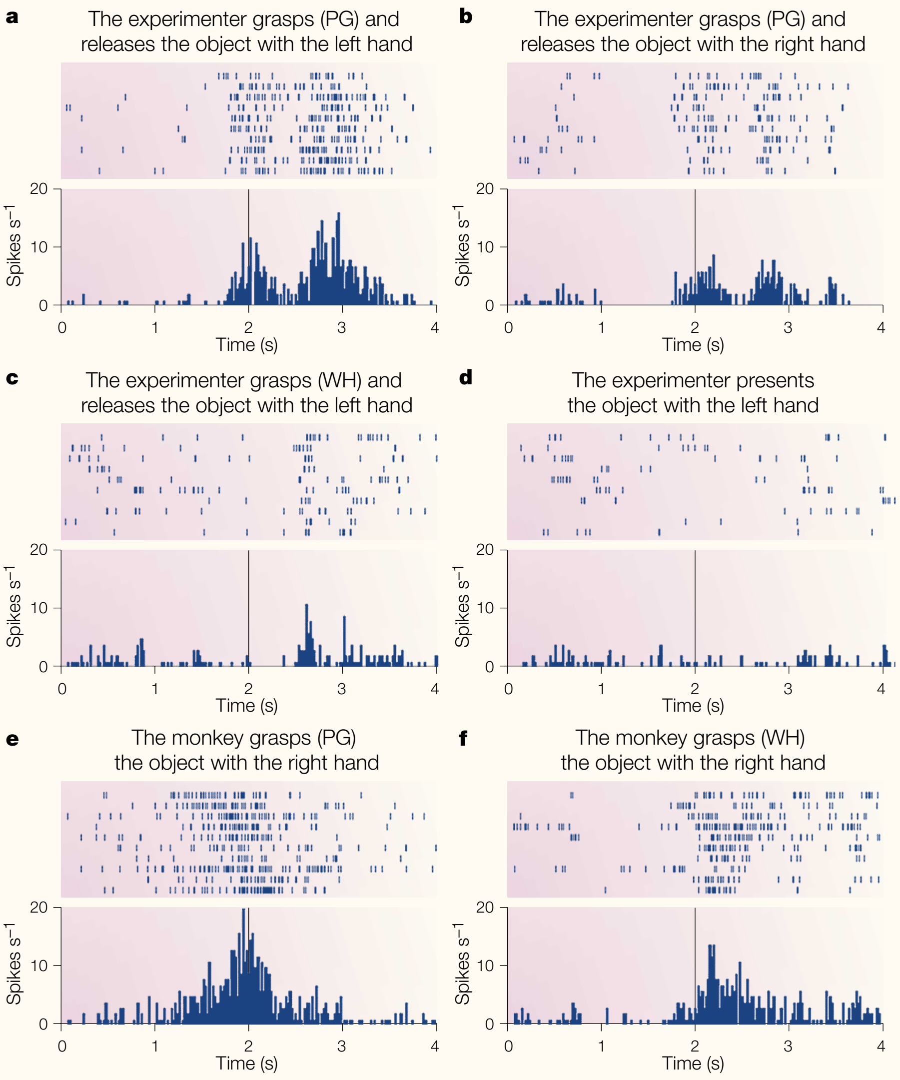

Figure 2 | **Visual and motor responses of a mirror neuron in area PF.** Rasters and histograms showing the response to a series of actions of a neuron in area PF of the right hemisphere. **a** | A piece of food was placed on a tray and presented to the monkey. The experimenter grasped the food with the left hand by means of a precision grip (PG), and subsequently released it, moving the hand away from the food. Note the strong response during the observation of both the grasping and releasing actions. The neuron did not respond during presentation of the food on the tray. **b** | A similar experimental condition executed with the right hand. Note that the magnitude of the neural response was much smaller in this condition. **c** | The experimenter grasped a large piece of food, apprehending it with the whole left hand (WH), and subsequently released it, moving the hand away from the food. **d** | The experimenter presented a piece of food to the monkey with the left hand. Note the absence of neuronal responses in **c** and **d**. **e** | The monkey grasped a small piece of food with its right hand by means of a PG in the dark. **f** | The monkey grasped a large piece of food, apprehending it with its right hand in the dark. The point at which the monkey (**e**,**f**) or the experimenter (**a**–**c**) touched the food, or the experimenter's hand started moving to present the food to the monkey (**d**), is marked with a vertical line. Adapted with permission from REF. 24 © 2001 Oxford University Press.

Mirror system in humans

Electrophysiological evidence. Probably the first evidence, albeit indirect, in support of a mirror system in humans came from studies carried out by Gastaut and Bert[35], and by Cohen-Seat *et al.*[36], on the reactivity of cerebral rhythms during movement observation. Traditionally, electroencephalography (EEG) studies have distinguished between two rhythms at rest, both of which occur in the alpha frequency range (8–13 Hz): a posterior alpha rhythm and a central mu rhythm. In addition to their differing topography, these two rhythms differ in their functional significance. The posterior alpha rhythm is present when the sensory systems, particularly the visual system, are not activated, and disappears on the presentation of sensory stimuli. The mu rhythm is present during motor rest, and disappears during active movements and somatosensory stimulation[37]. Gastaut and Bert[35], and Cohen-Seat *et al.*[36], showed that observing the actions of another human blocks the mu rhythm of the observer. This finding was recently confirmed by Cochin *et al.*[38,39], and by Ramachandran and colleagues[40,41].

Evidence for a matching between action observation and execution also comes from magnetoencephalography (MEG) studies. Among the various rhythms recorded from the central region, rhythmic oscillations around 20 Hz originate in the precentral cortex inside the central sulcus[42,43], and the level of 20-Hz activity is enhanced bilaterally less than 500 ms after median nerve stimulation[42,44]. This post-stimulus rebound is a highly repeatable and robust phenomenon that can be used as an indicator of the state of the precentral motor cortex. Interestingly, it is abolished when the subject manipulates an object after median nerve stimulation[44]. This post-stimulus-rebound method was used to test whether action observation affects the 20-Hz rhythms[45]. Participants were tested in three conditions: at rest, while they were manipulating a small object, and while they were observing another subject performing the same task. As expected from previous findings, the post-stimulus rebound was strongly suppressed during object manipulation. But interestingly, it was also significantly reduced during action observation. Because the recorded 15–25-Hz activity is known to originate mainly in the precentral motor cortex, these data indicate that human motor cortex is activated both during the execution of a motor task and during action observation. This finding strongly supports the existence of an action observation/execution matching system in humans.

Another body of evidence in support of the existence of a mirror system in humans comes from TRANSCRANIAL MAGNETIC STIMULATION (TMS) studies. Fadiga *et al.*[46] stimulated the left motor cortex of normal subjects using TMS, while these subjects observed meaningless, INTRANSITIVE MOVEMENTS of the arm, as well as hand-grasping movements performed by an experimenter. Motor-evoked potentials (MEPs) were recorded from various arm and hand muscles. As a control, motor cortex was stimulated during the presentation of three-dimensional objects and during a dimming-detection task that is highly demanding on the subject's attention. The results showed a selective increase in MEPs in the regions that the subjects normally use for producing the observed movements. This increase was found during the observation of goal-directed movements and of intransitive, meaningless arm movements.

Strafella and Paus[47] recently extended these observations. By using the DOUBLE-PULSE TMS technique, the authors showed that the duration of intracortical recurrent inhibition that occurs during action observation is similar to that seen during action execution. This finding strongly supports the idea that there is analogy at the cortical level between the mechanisms that mediate action observation and those involved in action execution.

By using the H-REFLEX technique, Baldissera *et al.*[48] studied the excitability of the spinal cord during action observation. They found that the H reflex recorded from flexors rapidly increased in size during the observation of finger extension (hand opening), and was depressed during the observation of finger flexion (hand closing). The converse behaviour was found in extensors. So, whereas modulation of cortical excitability varies in accordance with the observed movements, excitability of the spinal cord changes in the opposite direction. The absence of an overt repetition of the observed movement, despite cortical motor activation, might therefore depend, at least in part, on this inhibitory spinal mechanism.

In conclusion, neurophysiological experiments clearly show that action observation is related to activation of cortical areas that are involved in motor control in humans. In addition, they indicate that the observation of intransitive actions might produce an activation of the motor cortex. This finding differs from those made in monkeys, at least in area F5, where only transitive actions are effective in activating motor areas.

> "… the 'direct-matching hypothesis' … holds that we understand actions when we map the visual representation of the observed action onto our motor representation of the same action."

Evidence from brain imaging. The neurophysiological experiments described above, although fundamental in showing that action observation elicits a specific, coherent activation of the motor system, do not allow the localization of the areas involved in the phenomenon. Data on the localization of the human mirror system have been obtained using brain-imaging techniques.

Experiments carried out by various groups showed that ventral premotor/inferior frontal cortical areas become active when subjects merely observe arm or hand actions[49–52]. Broca's area — a region traditionally considered to be exclusively devoted to speech production — is one of the motor areas that was activated in these experiments. These results indicate that Broca's area also contains a representation of the hand (see also below), similar to its monkey homologue — area F5. These data can also be taken as evidence of an interesting evolutionary scenario, linking the origin of language with the comprehension of hand actions (see REF. 53).

The STS and the inferior parietal lobule are other areas that become engaged during the observation of hand actions. The activation is clearer when action observation is contrasted with object observation rather than with observation of a static hand (for example, see REF. 50). The activation of the STS is consistent with data in monkeys showing activation of the STSa (see above), and with numerous reports that this region becomes active during the observation of different types of biological movement (see REF. 6 for review). Similarly, the activation of the posterior parietal lobe is consistent with data in monkeys obtained by Fogassi *et al.*[23] and Gallese *et al.*[24].

In the experiments reviewed so far, subjects were tested while observing actions. The conclusion that human premotor areas have mirror properties was only indirect, based on the fact that the activated areas belong to the motor system (see below) and, in the case of Broca's area, by its homology with area F5 in monkeys[54,55]. The last inference has been strongly corroborated by the finding that Broca's area is actived during hand movements[56–58]. Direct evidence for an observation/execution system in humans was recently provided by experiments using functional magnetic resonance imaging (fMRI)[59] and event-related MEG[60].

Iacoboni *et al.*[59] tested normal human volunteers in two basic conditions: 'observation only' and 'observation/execution'. In the observation-only tasks, subjects were simply instructed to pay attention to the stimuli — a moving finger, a cross that appeared on a stationary finger, or a cross on an empty square. In the observation/execution tasks, the subjects were told to lift a finger in response to the movement of the observed finger (imitation) or in response to the appearance of the cross. The results showed that activation in three cortical areas — the left inferior frontal cortex (Broca's area, BA 44), right anterior parietal region and right parietal operculum — was significantly stronger during imitation than during other observation/execution tasks. The left inferior frontal cortex and the right anterior parietal region were also active during observation-without-execution tasks, whereas the parietal operculum became active only during observation/execution conditions.

Nishitani and Hari[60] addressed the same issue using MEG. In their experiments, subjects were requested to grasp a manipulandum (execution), to observe the same movement performed by an experimenter (observation), and to observe and simultaneously replicate the observed action (imitation). The results showed that during execution there was an early activation in the left inferior frontal cortex (BA 44), with a response peak appearing about 250 ms before touching the target. This activation was followed in 100–200 ms by activation of the left precentral motor area, and 150–250 ms later by activation of the right precentral motor area. During observation and during imitation, the pattern and sequence of frontal activations were similar to those found during execution, but they were preceded by occipital activation due to visual stimulation.

Activation of Broca's area during the observation of hand actions could be interpreted as reflecting verbal mediation. Although it is improbable that every time a subject observes an action he describes it to himself verbally, this possibility cannot be discounted *a priori*. If the interpretation based on verbal mediation is correct, Broca's area should be active regardless of the type of action that is observed and the effector used. But if activation of Broca's area reflects a specific anatomical and functional localization for hand actions, the activation should be absent while observing actions of other effectors, such as the foot. Furthermore, if activation of Broca's area were due to verbal mediation, no premotor activation during the observation of motor actions should be expected.

This point was recently tested in an fMRI experiment[61], in which participants were instructed to observe actions made by mouth, hand and foot. The observed actions were biting an apple, reaching and grasping a ball or a small cup, and kicking a ball or pushing a brake. But in addition to actions directed towards an object, the participants were also shown actions that did not involve one: chewing, mimicking a reaching movement, and pretending to kick a ball or push a brake. The observation of both object- and non-object-related actions of different parts of the body was contrasted with the observation of a static face, a static hand and a static foot. The results showed that observing both object- and non-object-related actions led to the somatotopic activation of the premotor cortex. The activation pattern was similar to that of the classical motor cortex homunculus, with the mouth represented laterally and the foot medially (FIG. 3). During the observation of object-related action, a roughly somatotopic activation was found in the posterior parietal lobe.

In conclusion, these data tell us three things. First, they show that the activation of Broca's area during observation of hand actions reflects a genuine mirror phenomenon. Second, they indicate that the mirror system is not limited to hand movements. Third, in agreement with previous data by Grafton *et al.*[50], Grèzes *et al.*[52] and Iacoboni *et al.*[59], they show that the parietal lobe is part of the human mirror system and, most importantly, that it is strongly involved when a subject observes object-directed actions.

Action understanding

As mentioned in the introduction, there are two main hypotheses that might explain how the brain implements action understanding — the visual hypothesis and the direct-matching hypothesis. The visual hypothesis states that action understanding is based on a visual analysis of the different elements that form an action, with no motor involvement. The direct-matching hypothesis, on the other hand, holds that we understand actions when we map the visual representation of the observed action onto our motor representation of the same action.

The central point of the visual hypothesis is that a description of motor events in visual terms is sufficient for action understanding. According to this hypothesis, the brain builds progressively more complex descriptions of biological motion that culminate in the description of goal-directed actions. This description allows the viewer to understand the behaviour of others and facilitates social interactions[17]. The visual properties of some STSa neurons recently described by Perrett and coworkers[62] seem to support the visual hypothesis. Of particular relevance in this respect are neurons that combine information about the direction of gaze of an agent with the action performed by that agent. These neurons become active when the monkey sees the reaching action, but only if the action is performed with the agent's gaze directed to the intended target of reaching. So, if the agent performs an identical reaching action while looking away from the position to which the reach is directed, the neurons do not respond[62]. It therefore seems that these higher-order visual neurons combine the output of neurons that are specifically responsive to the observation of arm reaching with the output of neurons that are specifically responsive to the direction of attention, as conveyed by the direction of gaze. Also, the behaviour of other STSa neurons, such as those that respond to goal-directed hand actions[16], can be taken as evidence in support of the visual hypothesis.

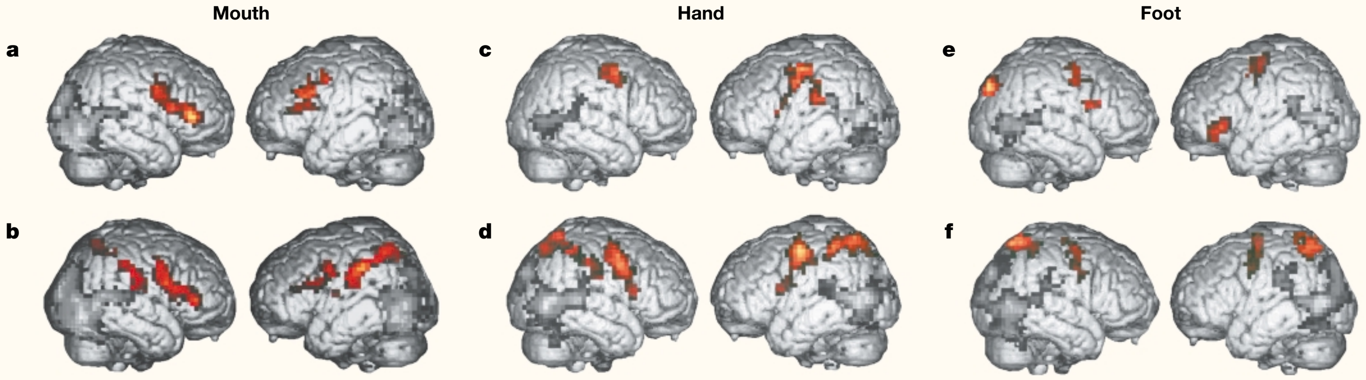

Figure 3 | **Brain activation in frontal and parietal areas during the observation of mouth, hand and foot actions. a**,**b** | Activation foci during the observation of non-object-related (chewing; **a**) and object-related (biting an apple; **b**) mouth actions. In both cases, activations were present in Brodmann areas (BA) 6 and 44 in both hemispheres, and in BA 45 in the right hemisphere. During the observation of object-related mouth action, two additional activation foci were found in the parietal lobe: rostrally in area PF and caudally in area PG (REF. 104). **c**,**d** | Activation foci during the observation of hand actions that were non-object related (mimicking grasping an object; **c**) and object related (actually grasping an object; **d**). During the observation of mimicked hand actions, BA 6 was activated bilaterally. This activation was dorsal to that found during the observation of mouth actions. Observing object-related hand actions also led to bilateral activation of premotor cortex and BA 44. Two additional activation foci were present in the parietal lobe: the rostral activation was located inside the intraparietal sulcus, caudal and dorsal to that found during the observation of mouth actions; the caudal activation was in area PG. **e**,**f** | Activation foci during the observation of foot actions that were non-object related (mimicking kicking an object; **e**) and object related (actually kicking an object; **f**). In both cases, the dorsal sector of BA 6 was activated. During the observation of object-related actions, there was an additional activation of the posterior parietal lobe (including area PE) that partially overlapped with activations seen during the observation of mouth and hand actions. Frontal and parietal activation foci are presented in colour. Other activations (mostly occipital) are shown in grey. Adapted with permission from REF. 61 © 2001 Federation of European Neuroscience Societies.

The properties of these neurons show that the visual analysis of action reaches a surprising level of complexity in the STSa. But the existence of these neurons and, more generally, of neurons that bind different types of visual features of an observed action, is not a sufficient condition for action understanding *per se*. The main weakness of the visual hypothesis is that it does not indicate how the 'validation' of the meaning of the observed action is achieved, and it is by no means obvious how the complex properties of STSa neurons could have emerged.

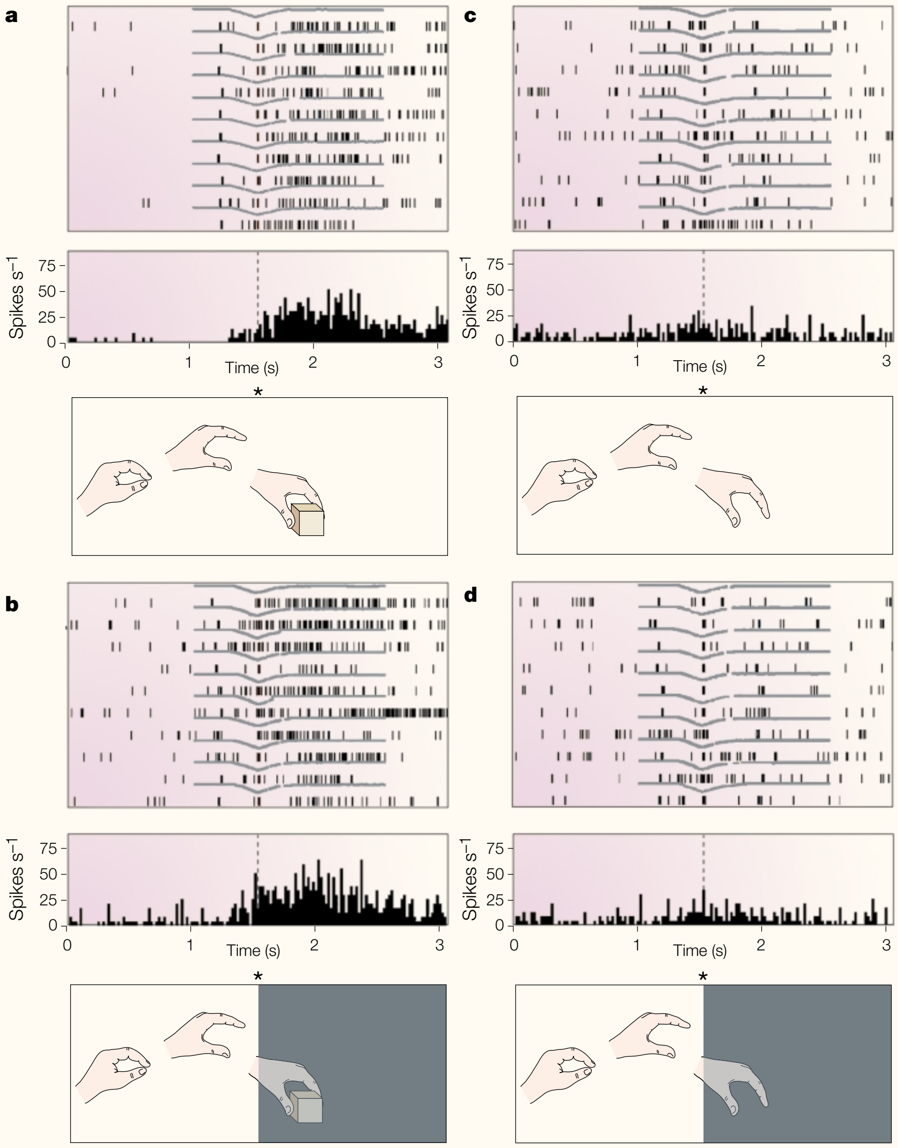

Figure 4 | **Activity of a mirror neuron in F5 in response to action observation in full vision and in hidden conditions.** The lower part of each panel illustrates the experimenter's action as observed from the monkey's vantage point: the experimenter's hand moving towards an object and grasping it (panels **a** and **b**) or mimicking grasping (panels **c** and **d**). The behavioural paradigm consisted of two basic conditions: full vision (**a**) and the hidden condition (**b**). Two control conditions were also performed: mimicking in full vision (**c**) and mimicking in the hidden condition (**d**). So, in panels **b** and **d**, the grey square represents an opaque sliding screen that prevented the monkey from seeing the experimenter's action performed behind it. In rasters and histograms, the vertical line shows the point at which the experimenter's hand was closest to a fixed marker that, in the hidden condition, indicated the point at which the experimenter's hand began to disappear from the monkey's vision. The upper part of each panel shows rasters and histograms of 10 consecutive trials recorded during the corresponding experimenter's hand movement. Kinematic recordings (gray traces) of the experimenter's hand are shown above each raster. The illustrated neuron responded to the observation of grasping and holding in full vision (**a**) and in the hidden condition (**b**), in which the interaction between the experimenter's hand and the object occurred behind the opaque screen. The neuronal response was virtually absent in the two conditions in which the observed action was mimicked (**c** and **d**). Adapted with permission from REF. 63 © 2001 Elsevier Science.

The situation becomes less obscure in considering the motor aspects of gaze/reach coordination. From a motor point of view, the gaze/reach association does not develop by chance, as should be assumed when considering it from a purely visual perspective. Instead, this association is learned in early life, as infants discover that they have a better chance of reaching objects if they look at them. As this behaviour is rewarded by its consequences, it becomes part of the normal adult behavioural repertoire. So adults know that gaze direction indicates action direction in most circumstances. When the motor system resonates because a similar action is made by another individual, the attentional aspect of the observed reaching action is recognized. By contrast, when there is a discrepancy between gaze and reaching direction, the action remains ambiguous to the observer.

We argue that the sensory binding of different actions found in the STSa is derived from the development of motor synergistic actions. Efferent copies of these actions activate specific sensory targets for a better control of action. Subsequently, this association is used in understanding the actions of others. However, the question of how motor actions could bind sensory information is outside the scope of this review, and we will not discuss it here.

Some recent findings on the properties of F5 mirror neurons argue against the need for a visual description of action for action understanding, and therefore oppose the visual hypothesis. As described above, mirror neurons typically discharge when there is an interaction between a biological effector (for example, a hand) and an object. Is this interaction absolutely necessary? Recently, Umiltà *et al.*[63] addressed the question of whether viewing the hand/object interaction was indeed necessary to evoke a response of mirror neurons. The alternative hypothesis was that mirror neurons would fire, even in the absence of a visual description of the action, if the monkey had sufficient cues to work out what the experimenter was doing.

Umiltà *et al.*[63] studied the responses of F5 mirror neurons in two conditions (FIG. 4). In the first one, the monkey could see the whole action made by the experimenter (full-vision condition). In the second, the monkey could see only the beginning of the same action; the crucial part — the hand/object interaction — was hidden from view (hidden condition). In the hidden condition, the monkey was shown that an object or some food had previously been located behind the screen. So, the

Glossary

DOUBLE-PULSE TMS
A variant of the transcranial magnetic stimulation technique, in which two coils are used to generate magnetic fields in quick succession over the same cortical region or in different regions at the same time.

H REFLEX
Also known as the Hoffmann reflex, the H reflex results from the stimulation of sensory fibres, which causes an excitatory potential in the motor neuron pool after a synaptic delay. Exceeding the potential threshold for a given motor neuron generates an action potential. The resulting discharge will cause the muscle fibres innervated by that neurone to be activated.

INTRANSITIVE MOVEMENT
A movement not directed towards an object.

MOEBIUS SYNDROME
A disorder characterized by facial paralysis, attributed to defects in the development of the sixth (abducens) and seventh (facial) cranial nerves.

PHENOMENOLOGY
A philosophical movement founded by the German Edward Husserl, dedicated to describing the structures of experience as they present themselves to consciousness, without recourse to theory, deduction or assumptions from other disciplines, such as the natural sciences.

POINT-LIGHT STIMULI
Stimuli devised by the Swedish psychologist Johannson to study biological motion without interference from shape. Light sources are attached to the joints of people and their movements are recorded in a dark environment.

TRANSCRANIAL MAGNETIC STIMULATION
A technique used to stimulate relatively restricted areas of the human cerebral cortex. It is based on the generation of a strong magnetic field near the area of interest which, if changed rapidly enough, will induce an electric field sufficient to stimulate neurons.

meaning of the experimenter's action could be inferred from the monkey's knowledge of the situation and the view of the hand disappearing behind the screen. The results showed that more than half of the recorded mirror neurons also discharged in the hidden condition. This indicates that, despite the fact that the monkey did not see the action, it knew its meaning; its neurons signalled 'the experimenter is grasping' or 'the experimenter is holding' (FIG. 4).

These data are consistent with the idea that monkeys, like humans, can infer the goal of an action, even when the visual information about it is incomplete[64,65]. Importantly, they show that this inference might be mediated by mirror neurons in the absence of visual information. It is important to stress that we are not claiming that, in the experiment of Umiltà *et al.*[63], the monkeys understood the intention of the agent of the action (that is, why the observed action was performed), but only that they understood the action meaning (that is, what the agent did).

A theoretical objection to the direct-matching hypothesis is that activation of the motor system during action observation might be related not to action understanding, but to motor preparation. In the case of mirror neurons, the specificity of the neuronal response rules out a generic motor preparation — the mere readiness to move. Yet, even in the case of mirror neurons, it is possible to argue that motor activation is present because the observer tends to copy the observed action. However, this interpretation seems unlikely. In conditions in which mirror neurons become active, hardly any imitation would be useful. When the monkey observes another monkey grasping a piece of food, the obvious action to take would be, for example, to approach the other monkey, but certainly not to repeat the observed action. Furthermore, ethologists maintain that monkeys do not imitate hand or arm actions[66,67]. It is therefore clear that, as the monkey is not going to perform the observed action and never actually repeats it, the activation of mirror neurons during action observation does not serve a motor function. Of course, the fact that monkeys do not imitate hand action does not exclude the possibility that monkeys might express some imitative behaviour — as has been found in other species, such as birds — and that this behaviour might be mediated by a mechanism similar to that of the mirror system. This point will be discussed below.

Another piece of evidence that oppose the idea that the primary function of the mirror system is to provide a motor copy of the observed action comes from brain-imaging experiments. In a PET study, Grèzes *et al.*[52] asked humans to observe meaningful arm actions, either to understand their purpose or to imitate them. They found significantly stronger activation of premotor areas when the subjects had to understand the motor actions than when they had to imitate them. If the main purpose of premotor activation during action observation is to have a motor copy of the observed action for imitating it, stronger activation of premotor areas would be expected when the subjects were instructed to imitate, and not the opposite, as was found.

> " … there is analogy at the cortical level between the mechanisms that mediate action observation and those involved in action execution."

As we discuss in the following sections, the mirror mechanism serves several functions that depend on the part of the motor system that resonates. If the task requires action understanding, then the motor sectors that code actions (PF and premotor areas) become active. If the stimuli have emotional content, it is possible that subcortical structures such as the amygdala become active[31]. When the task does not require action understanding, other regions are activated[34,68]. Finally, when the task requires action understanding and imitation, the activity is shared between the motor regions on which understanding depends and other circuits that store sensory copies of the action.

Imitation

In addition to action understanding, imitation is another function which involves the mirror system. The verb 'to imitate' has various meanings. In everyday life, it simply means 'to do after the manner of' or 'to copy'. It is obvious that this broad definition includes a large variety of phenomena. In some cases, imitative behaviour is a consequence of attending to certain parts of the environment, allowing the observer to express, nonspecifically, responses that are appropriate to it (stimulus enhancement)[69,70]. But apart from this kind of behaviour, imitation concerns motor behaviours that are determined by the observation of similar motor behaviours made by a conspecific. Imitation can be accompanied by an understanding of the action meaning, it might be an approximate or a precise replica of the observed action, and it might concern a series of motor acts never before performed by the observer. According to most ethologists, true imitation concerns only this type of behaviour (for a discussion of imitation from an ethological point of view, see REFS 66,67,71–74).

In our view, a fundamental phenomenon that forms the basis of imitation is that which has been referred to as 'response facilitation' — the automatic tendency to reproduce an observed movement[74]. Response facilitation can occur with or without an understanding of the meaning of what has been observed.

Response facilitation without understanding of meaning. This type of response facilitation seems to be an ancient function that is present in many species. The best-studied example is arguably the behaviour of shore birds when a dangerous stimulus appears. As soon as the stimulus is detected, one or a few birds start flapping their wings, others start repeating the behaviour and, eventually, the whole flock flies to flee[70,75]. This behaviour does not necessarily require an understanding of the action. What is important here is that the action emitted by the first bird could act as a 'release' signal for the behaviour of all the other birds, coordinating their behaviour[75].

Response facilitation without an understanding of the meaning of an action is also seen in humans. A famous example, first described by Meltzoff and Moore[76], is the capacity of newborn infants to imitate buccal and manual gestures. Although the response is certainly important for the infant, because it creates a link between the observing infant and the performing adult[77], there is not much to understand in the observed buccal or hand action.

Examples of response facilitation are also present in adult humans. For example, in *The Expression of the Emotions in Man and Animals*, Darwin[78] mentions the case of sports fans who, while observing an athlete performing an exercise, tend to 'help' him by imitating his movements. Other examples include laughing, yawning, crying and, as shown recently by Dimberg *et al.*[79], involuntarily mimicking facial expressions. It is probable that the purpose of these behaviours is to create an interpersonal link between subjects.

Response facilitation with understanding of meaning. Adult human observers typically imitate movements made by other people, having an understanding of what the other person is doing. There is an important theoretical distinction that we want to make here. Apart from symbolic or 'quasi-symbolic' gestures, such as arm movements to invite another individual to approach or to go away, there are two different types of goal-related behaviour: motor acts and 'motor actions'. By motor act[12], we simply mean a movement directed towards an object (or the body), which eventually allows an effective interaction between the used effector and the target of the movement. Examples of motor acts are grasping an object, holding it, or bringing it to the mouth. By 'motor action', as briefly mentioned in the introduction, we do not refer to any type of intentional motor behaviour. Instead, we will use the term 'motor action' in referring to a sequence of motor acts that, at its end, produces a reward for the acting individual. For example, a 'motor action' might be composed of a sequence of motor acts that allow feeding (reaching for a piece of food, grasping it, holding it and bringing it to the mouth).

The distinction between motor acts and 'motor actions' is not only logically motivated, but also corresponds to the way in which the motor system is organized. There is evidence from monkey studies that motor acts are coded at the single-neuron level. For example, there are neurons in area F5 that code specifically for grasping, holding, tearing and so on[12,13,80,81]. Similarly there are neurons in the ventrorostral part of F2 and in F4 that code proximal arm movements such as arm reaching[12,82,83]. Of course, we cannot exclude the possibility that 'motor action', as defined above, is also represented at the individual-neuron level. However, convincing evidence for this is lacking at present.

> "… the mirror system could underlie other fundamental cognitive functions, such as language understanding and mind reading."

Mirror neurons are elements that, on the one hand, code motor acts and, on the other, allow imitation to take place. If we accept this hypothesis, then the mechanism of imitation can be divided into three submechanisms: retrieval of a motor act, construction of a sequence of motor acts, and refinement of the motor act or of the motor sequence. All of these stages require the mirror system.

The mere observation of a motor act typically determines the activation of its motor representation. The difference between imitation and understanding is that, in the case of imitation, the observed act is not only internally represented, but must also be externally manifested. The overt repetition of the observed motor act is of little use in most circumstances and, in some cases, even dangerous for the observing individual. Therefore, in normal conditions, imitation occurs for social reasons or as a learning mechanism.

The mechanism that underlies the capacity to imitate a 'motor action' (as defined above) is much more complex. An interesting hypothesis to explain how this can occur was recently advanced by Byrne in his discussion of what he refers to as 'action-level imitation'[84,85]. With this term he indicates the copying of a behaviour that is not previously present in the motor repertoire of the observer. He suggests that such a behaviour can be imitated by dissecting the observed behaviour into a string of simpler sequential components that are already in the observer's repertoire. Specifically, the behaviour observed in another individual could be seen as a sequence of simple elements or, using our terminology, of motor acts. The system of mirror neurons would provide the neural basis for recognizing and segmenting 'motor actions' into strings of discrete elements, each of which is a motor act in the observer's repertoire. Using Byrne's words, the imitation of 'motor action' is "reading the letters of action by means of response facilitation, action by action"[84].

It is obvious that this proposal leaves open the issue of how the various motor acts are assembled to construct the new 'motor action' (for hypotheses on this point, see REFS 86–91). Yet, this 'mechanistic' theory of imitation opens new empirical possibilities, and could clarify why only humans and some other primates seem able to imitate in the proper sense.

A final aspect of imitation is the capacity to modify a motor act or a 'motor action' that is already in the motor repertoire of the observer, so that the new action becomes most similar to that made by the agent of the action. This capacity underlies many types of motor learning by imitation, from lifting a finger in a specific way to playing tennis. To express this type of imitation, a subject should have the capacity to generate a sensory copy of the produced action (motor act or 'motor action'), and to compare it with the action that has to be imitated. The idea that any time we generate an action we produce a sensory copy of it is consistent with forward models of different brain functions[92–95], and is the basis of the ideomotor theory of action[96–98].

The idea that there is an internal sensory copy of the executed action has far-reaching consequences for understanding how an observed action can be precisely imitated. If the motor representation of a voluntary action evokes an internal sensory anticipation of its consequences, imitation can be achieved by a mechanism that connects this internal, action-related representation with the representation of visually observed movements that have to be imitated, and a subsequent reactivation of the relevant motor representations. Preliminary brain-imaging experiments indicate that this mechanism might indeed exist in humans[99].

Conclusions

The mirror system seems to unify in the same neural mechanism a variety of phenomena that range from elementary behaviours, such as response facilitation, to higher cognitive functions, such as imitation learning and action understanding. In addition, the mirror system could underlie other fundamental cognitive functions that have not been dealt with in this article, such as language understanding[53] and mind reading[9,100–103]. Although we still lack a satisfactory comprehension of these higher capacities, and the precise role of the mirror system in these functions remains unknown, we think that the mirror system offers a new and very promising heuristic tool for their empirical investigation.

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Links

MIT ENCYCLOPEDIA OF COGNITIVE SCIENCES
Positron emission tomography | Motor control | Magnetic resonance imaging | Attribution theory | Perception of motion | Theory of mind

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CORRECTION

ACETYLCHOLINESTERASE — NEW ROLES FOR AN OLD ACTOR

Hermona Soreq & Shlomo Seidman

Nature Reviews Neuroscience **2**, 294–302 (2001)

In figure 4, the three messenger RNAs that encode acetylcholinesterase are missing exon 1. The correct version of the figure is printed below. This correction has been made to the online and PDF versions of the Perspective.

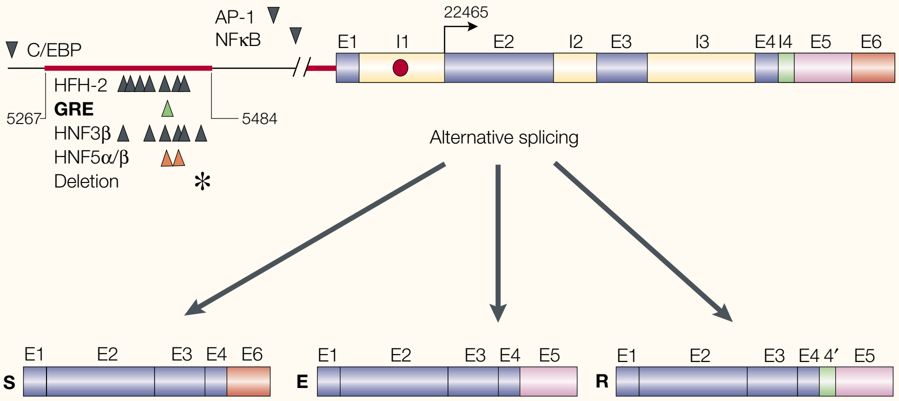

Figure 4 | **The human *ACHE* gene and its alternative messenger RNAs.** The core of human AChE is encoded by three exons and parts of additional regions encode the variant-specific carboxy-terminal sequences. Transcription begins at E1, and E2 encodes a leader sequence that does not appear in any mature protein. In addition to a proximal promoter (red line adjacent to E1), a distal enhancer region (more distal red line) is rich in potential regulatory sequences, some of which are shown as wedges. The transcriptional activation of *ACHE* by cortisol[58] is probably due to the distal glucocorticoid response element (GRE). A deletion mutation in this region disrupts one of two HNF3 (hepatocyte nuclear factor 3) binding sites, a factor that also activates transcription[60]. Intron 1 (I1) contains an enhancer sequence[56,57] indicated by a red dot. Nucleotide numbers are those of GeneBank cosmid AF002993. Normally, much more AChE-S than AChE-R mRNA is produced, but under stress or inhibition of AChE, alternative splicing produces much more of the AChE-R mRNA.

CORRECTION

ROLES OF SERINE/THREONINE PHOSPHATASES IN HIPPOCAMPAL SYNAPTIC PLASTICITY

Danny G. Winder & J. David Sweatt

Nature Reviews Neuroscience **2**, 461–474 (2001)

In the section 'Future directions', it is stated that autophosphorylated CaMKII binds to the NMDA receptor subunit NR2A. It should have stated that it binds to NR2B. A similar correction applies to figure 2 and its legend. These corrections have been made to the online and PDF versions of the Review.

CORRECTION

STEM CELL PLASTICITY — BUILDING THE BRAIN OF OUR DREAMS

Sally Temple

Nature Reviews Neuroscience **2**, 513–520 (2001)

In figure 1, some of the reference numbers were incorrect. In the top panel, only reference 18, instead of references 17 and 18, should have been cited under 'Multiple types; forebrain and midbrain'. In the same figure, reference 35 should be replaced with reference 38, reference 50 with reference 55, and reference 44 with reference 49. These corrections have been made to the online and PDF versions of the Perspective.

ERRATUM

RECRUITMENT & EVENTS

Because of an advertising production error, the *Recruitment & Events* page of the July issues of *Nature Neuroscience* and *Nature Reviews Neuroscience* implied incorrectly that the Burnham Institute in La Jolla, California, and the Center for Neuroscience at the University of California, Davis are recruiting new directors. In fact, neither position is open. The new Director for the Center for Neuroscience and Aging at The Burnham Institute is Stuart A. Lipton, and the Scientific Director of the Institute is John Reed. The Director of the Center for Neuroscience at the University of California, Davis is Edward Jones. We apologize to all concerned for any confusion or embarrassment that this error may have caused.