follows her back to a diurnal refuge where they mate, often repeatedly, throughout the next day [10,11].

Some weta were tagged with small, 0.4 g radiotransmitters, which enabled individual insects reliably to be relocated and their movements tracked over successive days (Figure 1). To measure reproductive success, the investigators took advantage of the fact that weta, like many other invertebrates, transfer sperm from males to females in small packages called spermatophores [12]. Female giant weta eject the emptied spermatophores after mating, which then fall to the ground or sometimes remain stuck to their bodies. As a result, by relocating a radiotagged male paired with a female in their refuge before the couple emerge at night, a count of the ejected spermatophores in the refuge served as an indicator of the amount of sperm transferred by that particular male while mating during the day. Using their unique combination of individual mobility data, insemination success and body size information, Kelly et al. [9] clearly showed that those males that were more mobile were also more successful in finding and inseminating females. Importantly, they linked increased mobility with longer legs and smaller bodies in males, whereas no phenotypic traits were found to be associated with either mobility or insemination success in females.

In addition to finding evidence for sexual selection favouring smaller, longer legged males, Kelly et al. [9] tested a related hypothesis about the underlying intensity of selection. It has been suggested that the intensity of sexual selection is weaker in species exhibiting female-biased as opposed to male-biased dimorphism [13,14]. To test this, the authors used a statistical measure of the strength of sexual selection known as the 'opportunity for sexual selection' (I_{mates}) [2]. In the case of the giant weta, because males mate with only a single female per day, this statistic reduces simply to the proportion of mated to unmated males that were observed by the investigators while sampling the insects for the study. They found that the intensity of sexual selection on giant weta males was similar to that found in another co-occurring weta species under sexual selection (*Hemideina crassidens*), characterised by male-biased dimorphism in mandibular

tusks used in male–male competition for mates [15]. Thus, weta join other recent studies in birds and mammals [16,17] suggesting that the intensity of sexual selection for female-biased dimorphism can equal that observed in male-biased species.

By directly linking small male body size with increased mobility and mating success, these findings provide field-based support for the sexual selection mobility hypothesis in the giant weta. This work also raises the possibility that similar selection pressures may play a widespread role in the evolution of female-biased sexual size dimorphism in many other species. The ability to radiotrack and reliably relocate individual insects was a critical component of this and other recent studies (for example [18,19]). Indeed, as individual-based tracking technologies such as radiotelemetry become increasingly applicable to smaller animals like insects [20] we can expect further innovative field studies that move beyond descriptions of individual movement patterns to test general hypotheses about underlying behavioural, ecological and evolutionary processes.

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Human Cortex: Reflections of Mirror Neurons

Claims to have identified mirror neurons in human cortex have been controversial. A recent study has applied an fMRI adaptation protocol to the problem and come up with novel evidence for the existence of movement-selective mirror neurons in human cortex.

Ilan Dinstein

In 1996, Gallese et al. [1] discovered that about 10% of neurons in ventral premotor area F5 of the macaque monkey responded not only when the monkey executed a particular movement — as expected in this

cortical motor area — but also when the monkey observed the experimenter performing that same movement. These cells were named 'mirror neurons' because their activity in the brain of the motionless observing monkey seemed to mirror that of motor neurons active in the person actually executing the movement. Two years later, Fogassi et al. [2] reported that similar movement-selective mirror neurons also exist in the inferorior parietal lobule of the macaque and established the concept of a 'mirror system' composed of these two cortical areas. Over the past ten years, many functional magnetic resonance imaging (fMRI) studies have attempted to isolate the activity of mirror neurons in the human cortex, yet this task has proven to be very difficult. In this issue of *Current Biology*, Chong et al. [3] report evidence of mirror neuron responses in the right inferior parietal lobule of human cortex.

The discovery of mirror neurons generated much excitement about their possible role in mechanisms of movement and action perception. When we observe someone performing an action, such as waving their hand hello, how do we instantaneously understand that their intention is to greet us? According to the 'simulation theory' [4], we covertly and unconsciously simulate ourselves performing the movement, access our own associated intentions and goals for that particular movement, and assign them to the person we are observing. Mirror neurons have been proposed as the physiological mechanism that enables a critical step in this process: precise visual to motor mapping [5–7]. According to the theory, whenever you observe someone performing a movement, particular movement-selective mirror neurons embedded in your motor system are activated, enabling you to simulate yourself performing that movement, and access your own associated intentions and goals (probably through activity of other brain areas, including the limbic system). Taken a step further, mirror neurons can be thought of as a sensory-motor gateway for forming an internal representation of the observed person's state and intents based on their body language, facial expressions, actions, and so on.

Note, however, that for this mechanism to work properly, it is critical that the observed movement be
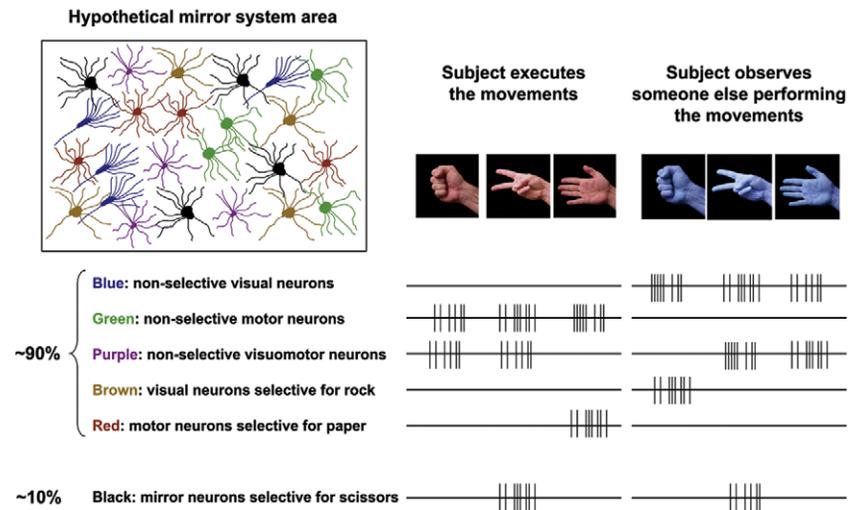

Figure 1. Caricature of neural subpopulations that exist in 'mirror system' areas along with their expected spiking activity during execution and observation of different movements.

Blue, green and purple subpopulations are non-selective and respond to any movement type. Brown neurons respond selectively to one observed movement. Red neurons respond selectively to one executed movement. Black neurons are mirror neurons that respond selectively to the same movement whether executed or observed. Mirror neurons make up about 10% of neurons in monkey areas F5 [2] and inferior parietal lobule [15].

mapped onto the particular neural circuits used to execute that exact same movement, otherwise you will assign improper intentions to the person you are observing. Movement selectivity, responding to only one movement and not to others during both execution and observation (Figure 1, black), is, therefore, a crucial feature of mirror neurons. It is important to emphasize this issue of movement selectivity, because the vast majority of neurons in both monkey 'mirror system' areas are not mirror neurons. Rather, these areas are rich with vision-only and motor-only neurons, as well as non-selective visuomotor neurons (Figure 1) which may respond when observing or executing movements, but are not necessarily important for movement perception — they may, for example, be neurons that respond during execution of any movement (Figure 1, green).

Many recent studies have searched for the human correlate of the monkey 'mirror system' and tried to isolate mirror neuron responses using non-invasive imaging techniques. Most fMRI studies have pointed to two cortical areas; the anterior intraparietal area and the ventral premotor area. These areas have been suggested as candidate 'mirror system' areas, because they resemble the anatomical location of monkey inferior parietal

lobule and F5 areas, and because they respond when subjects passively observe others performing movements, actively execute movements themselves, or imitate movements made by others (Figure 2A). The logic behind these experimental protocols is that mirror neurons are expected to respond during movement execution as well as during movement observation; hence cortical areas that exhibit responses during both tasks are likely to contain mirror neurons.

While this logic seems solid, these protocols are actually very limited in their ability to isolate mirror neuron activity. The problem, as mentioned above, is that the vast majority of neurons active during movement execution and movement observation are not mirror neurons (Figure 1). Because the fMRI technique measures the average neural response across a very large neural population located within each voxel — a unit of brain volume typically 3 x 3 x 3 mm^3 — it is difficult to separate the relative contribution of different neural subpopulations to the measured fMRI response. So when a study reports that a particular brain area exhibited an fMRI response both during the execution of a movement and during the observation of a movement, it does not necessarily mean that a single population of mirror neurons generated
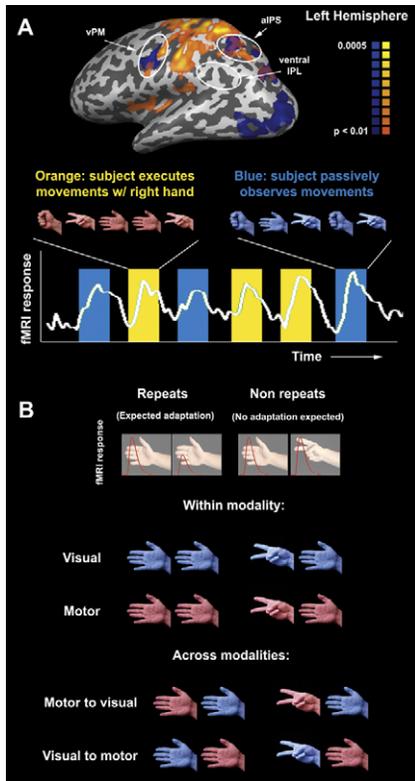
Figure 2. Mirror system fMRI experiments.
(A) Example of a common movement observation and execution experiment (unpublished data collected in our lab). Subjects were asked to execute or observe movements in separate blocks. Average results from six subjects are displayed on an inflated left hemisphere. Orange: cortical areas that exhibited larger fMRI responses during movement execution than rest. Blue: cortical areas that exhibited larger fMRI responses during movement observation than rest. Note that there is an overlap of both effects in anterior intraparietal sulcus and ventral premotor area, which have been suggested as the candidate human 'mirror system'. (B) Example of an adaptation experiment protocol. Subjects are asked to observe and execute movements in different orders such that movements are either repeated or not. Cortical areas containing mirror neurons are expected to exhibit decreased fMRI responses when movements are repeated in comparison to when they are alternated both within and across modalities.

both responses. Such a response could be generated by separate visual and motor neural populations co-existing in the same voxels. Even more importantly, such responses could be generated by neural populations that are not movement-selective at all (Figure 1, blue and green). Fortunately, through the use of fMRI adaptation protocols it may be possible to circumvent these resolution limitations.

The fMRI adaptation technique, also called repetition suppression, takes advantage of the common observation that most sensory neurons adapt/habituate when their preferred stimulus is presented repeatedly [8,9]. Cortical areas containing neurons selective for a particular stimulus attribute are, therefore, expected to exhibit reduced fMRI responses when the preferred stimulus is repeated in comparison to when it is alternated with non-preferred stimuli. This method has been used extensively to study the selectivity of visual system neurons for different low level visual stimuli (for example, [10,11]). Mirror neurons, if they adapt like sensory neurons, may be expected to adapt when the same movement is repeatedly observed, repeatedly executed, observed and then executed, or executed and then observed (cross-modal adaptation, Figure 2B). By comparing cortical responses to movement repeats versus non-repeats, it may be possible to assess movement selectivity within each modality (visual and motor) as well as across the modalities (visual to motor and motor to visual). Note that cross-modal adaptation is the critical signature of mirror neurons since visual adaptation may also be generated by movement-selective visual neurons (Figure 1, brown) and motor adaptation may be generated by movement-selective motor neurons (Figure 1, red).

Three studies [12–14] have recently used adaptation protocols to localize neural populations selective for particular observed and/or executed movements. Two of these studies [13,14] showed that anterior intraparietal sulcus exhibited visual adaptation when subjects repeatedly observed the same grasping movements regardless of the object type being grasped. In the third study [12], a group of us used a combined visual and motor adaptation protocol to show that anterior intraparietal sulcus and ventral premotor areas exhibited both visual and motor adaptation during repeated movement observation and repeated movement execution, respectively. In our study, however, we did not find any evidence of cross-modal adaptation anywhere in the brain. Chong et al. [3] report that they have successfully found such cross-modal adaptation in right inferiorior parietal lobule.

In their study, Chong et al. [3] asked subjects to execute several different hand movements and then observe video clips of either the same set of movements (repeats) or a set of entirely different movements (non-repeats). They report that an area in the ventral portion of right inferior parietal lobule exhibited reduced fMRI responses when subjects observed previously executed movements and interpret this as evidence for the existence of movement-selective mirror neurons exhibiting cross-modal adaptation. While this is a very exciting result, and possibly the first demonstration of movement-selective mirror neuron activity in humans, it is somewhat inconsistent with previous studies. First, ventral inferior parietal lobule, in contrast to more dorsal area anterior intraparietal area, does not respond that strongly during movement execution and observation (Figure 2A) and did not exhibit visual or motor (within modality) adaptation in our study [12]. Secondly, given that subjects executed movements with their right hand, it is surprising that cross-modal adaptation was found only in the ipsilateral right hemisphere. In the monkey, mirror neurons respond to the contralateral hand executing the movements [2,15].

Nonetheless, the fact that Chong et al. [3] report the same cross-modal adaptation effect from two separate subject groups scanned on different scanners and in different countries shows that it is a robust finding. Future mirror system studies would do well to adopt varied adaptation protocols and test whether the area reported by Chong et al. [3] as well as the more commonly reported anterior intraparietal sulcus and ventral premotor areas exhibit adaptation under different experimental conditions. Given the limitations of non-invasive imaging, adaptation protocols are proving to be useful tools for characterizing movement-selective cortical responses, which may underlie our ability to perceive the actions and intentions of others.

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Planar Cell Polarity: A Bridge Too Far?

The mechanisms of planar cell polarity are being revealed by genetic analysis. Recent studies have provided new insights into interactions between three proteins involved in planar cell polarity: Flamingo, Frizzled and Van Gogh.

Peter A. Lawrence[1,2], Gary Struhl[3] and José Casal[1]

We now understand much of how cells know where they are in an embryo, but little of how they know their orientation, anterior from posterior, distal from proximal. Yet we believe that many, perhaps all, epithelial cells are polarised in the plane of the sheet — that they exhibit planar cell polarity, and that this polarity is vital. Planar cell polarity is not used primarily to *make* structures but more to *orient* them, making its study conceptually difficult. But, genetics is the right approach and *Drosophila* has proved the model of choice — particularly as the genes identified in the fly are conserved in other animals, including vertebrates [1–3]. In the 60s it was argued that pervasive gradients are set up in the main axes of the body; it was suggested that the slope of a gradient could specify the polarity of cells [4,5]. This viewpoint is still very much alive and these gradients are now being identified with the help of genetics. There is now a resurgence of interest in the mechanisms of planar cell polarity: three new papers [6–8] (one in this issue of *Current Biology* [7]) report the use of both genetics and molecular techniques to get to one of the two hearts of the matter.

Drosophila cells make oriented structures; examples are hairs and bristles on the wing and abdomen. In the 80s, pioneers such as Adler and Gubb found genes whose mutants altered these polarities [9,10]. Early on *frizzled* (*fz*) was identified; and, significantly, it was found that clones of *fz*⁻ cells repolarised neighbouring wild-type cells so that they point their hairs towards cells with lower Fz activity [9,10]. It helps to think of the *fz*⁻ cells as *sending* and the wild-type cells as *receiving* polarising information [11]. Many different genetic mosaics can be made in *Drosophila* and, for example, each gene can be tested to see if it is needed in the sending, in the receiving cells or in both. This repolarisation assay has proved an incisive aid in the analysis of planar cell polarity.

The first working models used a small group of genes: *prickle* (*pk*), *fz*, *Van Gogh* (*Vang*) (also called *strabismus*, *stbm*) and *dishevelled* (*dsh*). In the 90s it was found that, just before polarised structures are formed, some of these proteins become localised to one or other ends of the cell [12]. It was suggested that some small initial bias (unknown) is amplified by interactions and feedback between these four proteins to polarise each cell; propagation from cell to cell would be driven by interactions across the intercellular space [13]. This model was simulated in a powerful computer [14] and became popular; however, complex computers are no match for simple experiments and the model looked feeble when it was found (in repolarisation assays) that *pk* and *dsh* are dispensable in *both* sending and receiving cells and so, for this central process, could be ignored [11,15–17]. The model suffered further blows when we found that a cell completely lacking *fz* could be repolarised [11] and that protein localisation itself appeared to be dispensable for repolarisation [11,16].

Flamingo (*fmi*, also known as *starry night* or *stan*), was largely left out of these models. In our assays, however, it was the only gene needed in *both* sending and receiving cells and, because its protein product is able to form homodimers from one cell to the next [18], we placed it at the centre of a new model [11]. In our model, the Fmi homodimers act as intercellular bridges. We suggested that, using Fmi to compare its neighbours, each cell points its hair towards the neighbour with the lowest level of Fz activity, and that there is an intercellular feedback via Fmi, which brings the level of Fz activity in one cell towards an average of its neighbours. We argued that Fmi–Fmi homodimers act asymmetrically to convey the level of Fz activity in the sending cell to Vang in the receiving cell. Because information is actually going in both directions — in the wild-type, each cell will both send and receive — it follows Fmi can act in two ways in the same cell depending on whether it sends (with Fz) or receives (with Vang) (Figure 1). A more detailed version of this model was elaborated subsequently [2] and another similar one simulated *in silico* [19].

Chen *et al.* [6] recently reported the results of similar experiments to ours [11] but, instead of monitoring hairs, they mostly looked at localisation of the proteins, a concordant indicator of polarity. They reached the same