

mirror neurons

When tasks are simple, the extent to which they occupy working memory resources determines whether mind-wandering occurs. As task complexity increases, however, mind-wandering is suppressed not simply by working memory involvement, because a task such as reading a dry expository text requires more resources than does reading an intriguing fiction story. Instead, mind-wandering is suppressed when we engage in a task which absorbs us in the experience of task-completion. We have suggested that the influences of factors like absorption or structure on mind-wandering, provides evidence that certain situations provide a cognitive *affordance* which help to anchor attention in the current context (Smallwood and Schooler 2006). The notion of an affordance emphasizes that certain situations provide the individual with the opportunity to focus on the here and now and that, if motivated to do so, can be used to temporarily escape from our own private thoughts and experiences. Considering our last visit to the cinema, for instance, it is obvious that the skill of the director and the effectiveness of the actors, rather than the amount of working memory load, determined whether the film afforded absorption or encouraged mind-wandering.

3. The neurophysiology of mind-wandering

The relative dearth of research on mind-wandering means that few studies have directly examined the neuropsychological concomitants of mind-wandering. Studies have documented that physiological activity (such as heart rate and skin conductance) is elevated during periods of mind-wandering. This physiological activity reflects the fact that during mind-wandering our attention is often drawn to our own current concerns—topics which are more emotionally arousing than the dry and relatively uninteresting cognitive situations in which these studies take place (see Smallwood and Schooler 2006).

One important implication of understanding the neuropsychological substrates of mind-wandering is that it provides a novel method for understanding brain activity that is unconstrained by the external environment. Research has documented that when deprived of external stimulation the brain recruits a network of discrete areas which are commonly referred to as the *default network* (Raichle et al. 2001). One plausible reason why this phenomenon occurs is because when resting participants can indulge in private thought, an activity which shares the same lack of environmental constraint as is involved in mind-wandering. Researchers have recently documented that situations that lead to task-induced deactivations in the default network correspond to the same situations in which mind-wandering is reduced. Indeed, a recent *functional brain imaging study

using fMRI (Mason et al. 2007) found that under circumstances when practice on a task had reduced the need for attentional supervision there was enhanced default network activation.

In the future, it may be possible to use changes in the activity of the default network, or other indirect measures of mind-wandering including response time, physiological activation, or evoked response to task stimuli (Smallwood et al. 2008), to reveal mind-wandering unfolding in real time. Methodologically, this would revolutionize the study of mind-wandering by enabling the empirical examination of these private experiences without bringing them to the attention of the participant, and thereby prematurely terminating the episode.

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minimally conscious state. See ACUTE BRAIN DAMAGE

mirror neurons. In the mid 1990s a new class of premotor neurons was discovered in the rostral sector of the macaque monkey's ventral premotor cortex, known as area F5. These neurons discharge not only

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when the monkey executes goal-related hand actions like grasping objects, but also when observing other individuals (monkeys or humans) executing similar actions. These neurons were called *mirror neurons* (Gallese et al. 1996). Neurons with similar properties were later discovered in a sector of the posterior parietal cortex reciprocally connected with area F5.

Action observation causes in the observer the automatic activation of the same neural mechanism triggered by action execution. 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 of meaning for the observer—into an account that the individual is able to understand. It was proposed that this mechanism could be at the basis of a direct form of action understanding. If mirror neurons really mediate action understanding, their activity should reflect the meaning of the observed action, not its visual features.

1. Mirror neurons in monkeys
2. Mirror neuron systems in humans

1. Mirror neurons in monkeys

Typically, mirror neurons in monkeys 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 (see Rizzolatti and Craighero 2004).

Prompted by these considerations, two series of experiments were carried out in which the monkey had no access to the visual features that normally activate mirror neurons. The first experiments tested whether the mental representation of an action triggers F5 mirror neurons, the second whether the monkeys are able to recognize actions from their sound. The results of these experiments provided positive answers to both questions, by showing that what drives the discharge of mirror neuron is not the pictorial description of an action, but rather the goal of the action, or to use a more mentalistic term, the motor idea of that action (see Rizzolatti and Craighero 2004).

In the most lateral part of area F5 a population of mirror neurons related to the execution/observation of mouth actions was described (see Rizzolatti and Craighero 2004). Most of these neurons discharge when the monkey executes and observes transitive, object-related ingestive actions, such as grasping, biting, or licking. However, a small percentage of mouth-related mirror neurons discharge during the ob-

servation of intransitive, communicative facial actions performed by the experimenter in front of the monkey (*communicative mirror neurons*). Macaque monkeys seem to have an initial capacity to control and emit 'voluntarily' social signals mediated by the frontal lobe. Most interestingly, this capacity develops in a cortical area—area F5—that in humans became Brodmann's area 44, a key area for verbal communication.

More recently the role of parietal mirror neurons in intention understanding has been unveiled. Fogassi et al. (2005) described a class of parietal mirror neurons whose discharge during the observation of an act (e.g. grasping an object), is conditioned by the type of not yet observed subsequent act (e.g. bringing the object to the mouth) specifying the overall action intention. This study shows that parietal mirror neurons, in addition to recognizing the goal of the observed motor act, allow the observing monkey to predict the agent's next action, henceforth its overall intention. This neural mechanism could scaffold more sophisticated mind reading abilities, as those characterizing our species (Gallese 2006, 2007).

2. Mirror neuron systems in humans

Several studies using different experimental methodologies and techniques have demonstrated that a mirror neuron system matching action perception and execution also exists in the human brain (for reviews see Gallese et al. 2004, Rizzolatti and Craighero 2004). During action observation there is a strong activation of premotor and posterior parietal areas, the likely human homologue of the monkey areas in which mirror neurons were originally described. The mirror neuron system for actions in humans is somatotopically organized, with distinct cortical regions within the premotor and posterior parietal cortices being activated by the observation/execution of mouth-, hand-, and foot-related actions.

The mirror neuron system for actions in humans is directly involved in imitation, in the perception of communicative actions, and in the detection of action intentions (see Gallese 2006). Furthermore, the premotor cortex containing the mirror system for action is involved in processing action-related sentences (see Gallese 2007), suggesting that mirror neurons together with other parts of the sensorimotor system could play a relevant role in language semantics (Gallese and Lakoff 2005, Gallese 2007).

Mirror neuron systems also underpin our capacity to *empathize. When we perceive others expressing a given emotion such as disgust, the same brain areas are activated as when we subjectively experience the same emotion. Similar direct matching mechanisms have been described for the perception of pain and

mirror test

touch (see Gallese et al. 2004, Gallese 2006). These results taken together suggest that our capacity to empathize with others is mediated by embodied simulation mechanisms; that is, by the activation of the same neural circuits underpinning our own emotional and sensory experiences (see Gallese et al. 2004, Gallese 2006). Recent studies suggest that these mechanisms could be deficient in individuals affected by *autistic spectrum disorders (see Gallese 2006).

The discovery of mirror neurons opens new exciting perspectives in a variety of different fields in social cognitive neuroscience, like our understanding of language, ethics and aesthetics (see Freedberg and Gallese 2007).

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mirror test. The mirror test is employed to examine an individual's ability to recognize itself in a mirror. It has been used as a test for self-recognition in primates and other non-human species, developmentally in humans and primates, and in clinical populations. Though proponents of this test argue that positive self-recognition indicates the presence of self-awareness, this idea is still debated.

Testing for self-recognition using a mirror has a long and rich history. The earliest published report was in 1828, when J. Grant presented a looking glass to orangutans and monkeys. Grant noted that neither species appeared to self-recognize; the monkeys appeared surprised and the orangutans did not express any noticeable emotional reaction. Charles Darwin also tested non-human primates in 1872 when he too examined the reaction of orangutans. They also failed to exhibit

self-recognition. Darwin is also thought to be the first researcher to formally employ a mirror to determine when human children develop self-recognition and self-awareness. Though his studies of children (he tested his own) originated in 1839, he did not publish his findings until 1877. A number of other prominent researchers employed mirrors to test for self-recognition including Wilhelm Preyer in the 1880s and Wolfgang Kohler in the 1920s (see Keenan et al. 2003).

However, the first formalized experimental tests of mirror recognition did not occur until the late 1960s when the *mirror-mark test* was introduced by Gordon G. Gallup, Jr. (Gallup 1970). The mirror-mark test (typically referred to as the mirror test) introduced sterner controls and a true dependent variable in testing for self-recognition. The test involves four distinct phases. First, the individual is exposed to a mirror to establish baseline recognition and familiarity. Second, the individual is placed under anaesthesia and a mark is placed on the body in an area only observable via the mirror (e.g. the individual's forehead). The anaesthesia is used in order to eliminate all other cues that would alert the individual to the presence of the mark and therefore influence the direction of attention once in front of the mirror. The mark is meant to be viewed as a novel stimulus discriminated on the basis of prior knowledge. The last phase of the testing involves re-introducing the animal to the mirror and observing mark-directed responses. If the individual touches the mark while in front of the mirror, it is considered to have self-recognition. A number of controls are normally put in place, such as replications of the procedure and only counting movements to the mark while in front of the mirror. Gallup's initial examinations involved the testing of monkeys and chimpanzees. To most people's surprise, it was found that chimpanzees actually 'passed' the test while monkeys did not. His data provided the first solid evidence that humans are not the only species to self-recognize.

Through extensive testing, it has been found that chimpanzees do possess self-recognition abilities; on average about 50% pass the mirror test. Orangutans, contrary to the earlier historical accounts, also pass the test. Monkeys, regardless of species or length of exposure, do not demonstrate self-recognition (one report of tamarins passing has failed to replicate). These data suggest a clean phylogenetic trend such that the closest relatives to humans (the apes) self-recognize, while our more distant relatives the monkeys do not. Unfortunately, the results for gorillas, who are genetically more related to humans than orangutans, are puzzling. Gorillas do not pass the mirror-test on a consistent basis, and only anecdotal reports exist of them passing (for review, see Parker et al. 1994).