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Comments and Controversies

Mesmerising mirror neurons

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ABSTRACT

Mirror neurons have been hailed as the key to understanding social cognition. I argue that three currents of thought—relating to evolution, atomism and telepathy—have magnified the perceived importance of mirror neurons. When they are understood to be a product of associative learning, rather than an adaptation for social cognition, mirror neurons are no longer mesmerising, but they continue to raise important questions about both the psychology of science and the neural bases of social cognition.

Mirror neurons respond when a monkey performs an action, such as grasping, and when the monkey passively observes a similar action performed by another agent. Since they were first discovered (Di Pellegrino et al., 1992) and given their evocative name (Gallese et al., 1996) many types of mirror neurons have been identified—"audiovisual" (Keysers et al., 2003), "communicative" (Ferrari et al., 2003), "tool-responding" (Ferrari et al., 2005), "peripersonal" and "extrapersonal" mirror neurons (Caggiano et al., 2009). But they are all "mesmerising" mirror neurons—cells that intrigue both specialists and nonspecialists, celebrated as a "revolution" in understanding social behaviour (Iacoboni, 2008) and "the driving force behind the 'great leap forward' in human evolution" (Ramachandran, 2008). Why? What is so mesmerising about mirror neurons? Three currents of thought may contribute:

Evolution—Scientific debate about the evolutionary origins and consequences of mirror neurons implies that they are an adaptation for social cognition (Rizzolatti and Arbib, 1998; Rizzolatti and Craighero, 2004); that they emerged in a common ancestor of extant monkeys and humans, and were favoured by natural selection because they facilitate social interaction. It is widely believed that hyper-sociality is what makes humans "special," the key to understanding why it is we, and not the members of any other species, who dominate the world with our language, artefacts and institutions (Emery et al., 2008). Therefore, in the light of this "adaptation hypothesis," mirror neurons emerge as an evolutionary foundation of human uniqueness.

Atomism—Mirror neurons are small and apparently indivisible; they combine sensory and motor properties in a single, simple unit. From ancient Greece to particle physics, there is a long tradition in which "atoms" of this kind are understood to be the building blocks of reality. This tradition makes it tempting to believe that simple, tidy mirror neurons can explain the messy complexities of the social world—including political strife, drug addiction, pornography and responses to media violence (Bocher et al. 2001; Iacoboni 2008). In this respect, mirror neurons are unlike other "smart" neurons, such as complex cells (Hubel and Wiesel, 1962), place cells (O'Keefe and Dostrovsky, 1971), and multisensory neurons (Stein et al., 1976). Compared with these, very little is known about the development of mirror neurons, or about the computations they perform—individually and in networks. Consequently, while other smart neurons are usually understood to be components—important parts of a complex system, which both need and yield explanation—mirror neurons are at risk of being viewed as atoms—primitive entities whose very existence explains a range of cognitive and behavioural phenomena.

Telepathy—Mirror neurons are said to mediate a "pre-conceptual and pre-linguistic form of understanding," which can "overcome all linguistic and cultural barriers" (Rizzolatti and Sinigaglia, 2008). I observe your action and—without inferences or a word being spoken—mirror neurons put me in the very same state that produced your action, and enable me to understand your intention. That kind of effortless, wordless communication sounds a lot like telepathy, and ancient links between mirrors, oracles and divination (e.g. Orofino, 1994) may further pump the intuition (Dennett, 1984) that, through mirror neurons, we can see directly into the minds of others.

These currents of thought may exaggerate the importance of mirror neurons but, provided that the adaptation hypothesis is correct, they are not wholly misleading. If mirror neurons are an adaptation, and more "advanced" in humans than in monkeys, they may well play a major role in explaining the evolutionary origins and online control of human social cognition. However, recent research suggests that, rather than being an adaptation, mirror neurons are produced by associative learning.

The "associative hypothesis" (Heyes, 2001, 2010) suggests that mirror neurons are formed in the course of individual development and via the same learning process that produces Pavlovian conditioning (Schultz and Dickinson, 2000). The individual starts life with visual neurons that respond to action observation, and a distinct set of motor neurons that discharge during action execution. Some of the

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motor neurons become mirror neurons if the individual gets experience in which observation and execution of similar actions are correlated—when they occur relatively close together in time, and one predicts the other. This kind of experience, which forges strong links between visual and motor neurons coding similar actions, is common when human children watch themselves acting, directly or using a mirror; when they are imitated by others; and when they take part in the kind of synchronous activities involved in sports and dance training (Heyes, 2005; Ray and Heyes, in press).

The associative hypothesis is consistent with research showing that the mirror neuron systems of musicians and dancers are different from those of other people (Haslinger et al., 2005; D'Ausilio et al., 2006; Calvo-Merino et al., 2006), and that monkeys acquire "tool responding" mirror neurons through experience (Ferrari et al., 2005). Direct support for the associative hypothesis comes from experiments showing that correlated experience of observing and executing different actions can put the mirror neuron system into reverse (Catmur et al., 2007). For example, the mirror neuron system is usually more responsive to hand than foot movements, but watching foot movements while performing hand movements, and vice versa, can reverse this dominance relationship (Catmur et al., 2008). This research does not merely show that the development of the mirror neuron system can be influenced by experience. That would be consistent with both the associative and the adaptation hypotheses. Rather, exactly as the associative account predicts, it shows that the development of the mirror neuron system is not "buffered" against the effects of experience, and that it can be readily transformed, rather than deformed, by sensorimotor learning (Heyes, 2010).

If the associative hypothesis is correct, mirror neurons did not evolve in any standard, biological sense. The mechanism that produces mirror neurons, associative learning, must have evolved, but since it is present in many species, and operates on a wide range of inputs, there is no reason to believe that associative learning is an adaptation for the production of mirror neurons. Similarly, evolution has provided the motor neurons that become mirror neurons, and the neuroanatomical potential for these to be connected with visual neurons, but it has not selectively established links between visual and motor neurons coding the same action. Therefore, it should be possible to "teach" mirror neurons; for example, to induce the development of mirror neurons in mice by giving them correlated experience of observing and executing the same action.

When mirror neurons are viewed as products of associative learning, they no longer have the appearance of unsplitable atoms. They start out as motor neurons, derive their visuomotor matching properties from connections with other, visual neurons, and they can lose those properties—they can be split—by experience in which observation of one action is correlated with execution of a different action. In everyday life, experience of this kind comes from coordinated instrumental action (e.g. you release an object and I grasp it; Newman-Norlund et al., 2007; Van Schie et al., 2008) and social control behaviour (e.g. you dominate and I submit; Tiedens and Fragale, 2003). Therefore, if the associative hypothesis is correct, the same process that produces mirror neurons will produce "counter-mirror neurons" in the same areas of the brain. During action observation, these neurons activate in me the opposite state, the opposite intention, from the one that is driving your behaviour—and that does not look anything like telepathy.

If mirror neurons come from associative learning, they could still contribute to social cognition. Some evolutionary byproducts are functionless (e.g. the whiteness of bones), but others are useful (e.g. reading). The neural mechanisms involved in reading did not evolve for that "purpose," but through explicit training they are made to fulfill an important function (Turkeltaub et al., 2003). We do not deliberately train children "to mirror" in the way we train them to read. Therefore it is unlikely that mirror neurons underwrite a whole, important cognitive function, such as action understanding, imitation and/or speech. However, as recent studies suggest, they may be recruited in the course of development to make some contribution to each of these faculties (Catmur et al., 2009; Mahon, 2008; Pobric and Hamilton, 2006; Scott et al., 2009). The priorities for future research are to find out more about the associative processes that build mirror neurons—for example, do they depend on predictive relationships, or are they purely "Hebbian" (Cook et al., in press; Hickok, 2009; Keysers and Perrett, 2004)? Also to subject hypotheses about the function of mirror neurons to rigorous experimental evaluation. When mirror neurons are understood to come from associative learning, they are no longer mesmerising, but they continue to raise important questions about both the psychology of science and the neural bases of social cognition.

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