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Mirror Neurons

Cristina Becchio¹

¹University Medical Center Hamburg-Eppendorf

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Mirror neurons are a class of neurons that respond when an individual performs a motor act (such as grasping) and when that individual observes another performing the same act, suggesting a direct link between action and perception. Initially discovered in macaques and later identified in humans, these neurons have been posited as fundamental to action understanding and social cognition. Their discovery has inspired hypotheses regarding the mechanisms underlying empathy, imitation, and language and reshaped cognitive scientists' view of the motor system.

History

Visuomotor neurons that fire both when an individual performs a motor act (such as grasping) and when it observes another individual performing the same act were first identified in the area F5 of the ventral premotor cortex of macaques ([di Pellegrino et al., 1992](#)). The term *mirror neurons*, introduced a few years later ([Rizzolatti et al., 1996](#)), emphasizes the distinctive dual activation properties of these neurons. Subsequent studies in nonhuman primates revealed mirror neurons in other areas, including the inferior parietal lobule and the dorsal premotor and primary motor cortices. In humans, the first evidence of a mirror response came from a transcranial magnetic stimulation study, which showed that observing an action selectively increased excitability in the muscles involved in performing that action ([Fadiga et al., 1995](#)). Direct evidence of mirror neuron activity was later obtained through single-neuron recordings in neurosurgical patients, revealing activation during both the execution and observation of hand-grasping actions and facial emotional expressions ([Mukamel et al., 2010](#)).

Core concepts

Early studies identified two primary types of mirror neurons based on the specificity (i.e., congruency) of their response ([Gallese et al., 1996](#)). Strictly congruent mirror neurons respond selectively to the execution and observation of the same motor act (e.g., grasping an object with a precision grip using the thumb and the index finger). In contrast, broadly congruent mirror neurons respond during the execution of one motor act (e.g., precision grip) and the observation of similar, but not identical, acts (e.g., power grip performed using the whole hand or grasping with the mouth).

Subsequent research expanded the understanding of mirror neuron responses by revealing additional properties ([Kilner & Lemon, 2013](#); [Bonini et al., 2022](#)). While early studies suggested that mirror neurons do not respond to tool use ([Rizzolatti et al., 1996](#)), later findings demonstrated that extensive tool-use training can induce mirror neuron activation in response to grasping actions performed with tools ([Rochat et al., 2010](#)).

Mirror neurons show a preference for live over video-recorded actions, with a lower proportion of neurons responding to video-recorded actions than live actions ([Caggiano et al., 2011](#); [Caggiano et al., 2013](#)). Some mirror neurons, known as auditory mirror neurons, respond to the execution of an action and to its associated sound, such as the cracking of a nut ([Kohler et al., 2002](#)). Mirror neurons can also fire

in response to partially or entirely occluded actions, supporting their role in action prediction ([Umiltà et al., 2001](#)). Additionally, they exhibit spatial preferences, with some neurons responding more strongly to actions in peripersonal space and others favoring extrapersonal space ([Caggiano et al., 2009](#)).

Many mirror neurons show selectivity for the viewpoint of an observed action, such as frontal, lateral, or overhead perspectives ([Caggiano et al., 2011](#)). Moreover, mirror neuron activity can be modulated by the reward associated with an observed action, with stronger activation elicited by actions involving a rewarded object ([Caggiano et al., 2012](#)). Finally, a subset of mirror neurons is tuned to the intention behind the observed act, responding stronger when the executed or observed motor act, for instance, grasping, is chained to eating (grasp-to-eat sequence) compared to when it is chained to placing (grasp-to-place sequence; [Bonini et al., 2010](#); [Fogassi et al., 2005](#)). This chain organization of motor acts, combined with the mirror mechanism, has been proposed to be fundamental for understanding others' intentions ([Rizzolatti & Sinigaglia, 2016](#)).

Questions, controversies, and new developments

The role of mirror neurons in intention understanding

One of the most debated claims about mirror neurons is their role in intention understanding. Mirror neurons have been proposed to enable intention understanding by transforming visual information into motor knowledge ([Gallese & Goldman, 1998](#); [Rizzolatti & Craighero, 2004](#); [Rizzolatti & Sinigaglia, 2016](#)). However, a major critique of this view, known as the one-to-many problem, argues that the same movement pattern (kinematics) can correspond to multiple intentions, challenging the notion that simulating observed kinematics provides access to the agent's intention ([Jacob & Jeannerod, 2005](#); [Kilner, 2011](#)). However, a recent development suggests that intention information is encoded in movement kinematics ([Patri et al., 2020](#)) and can be used to drive the selection of the most probable motor chain (e.g., grasp-to-place), allowing the observer to link the observed act to the agent's intention ([Soriano et al., 2018](#)).

Origins of mirror neurons

Mirror properties have been proposed to arise from sensorimotor associative learning, in which repeated simultaneous observation and execution of actions form visual-motor links ([Catmur et al., 2007](#)). Debate continues over whether genetic predispositions canalize (i.e., guide and shape) this learning process ([Cook et al., 2014](#); [Heyes & Catmur, 2022](#)).

“Broken mirror” hypothesis of autism

The *broken mirror hypothesis* posits that autism-related social deficits stem from impaired mirror neuron systems ([Iacoboni & Dapretto, 2006](#)). Early studies suggested differences in mirror neuron regions, but more recent research has not consistently supported this view ([Hamilton, 2013](#); [Heyes & Catmur, 2022](#)). Related theories propose that disruptions in chaining mechanisms, rather than mirror neurons themselves, may underlie intention understanding deficits in autism ([Cattaneo et al., 2007](#)) [see [Autism](#)].

Broader connections

Empathy and simulation

Observing actions may engage neural processes akin to those used for action planning, supporting simulation-based theories of empathy and mind reading ([Gallese & Goldman, 1998](#)) [see [Theory of Mind](#), [Social Cognitive Neuroscience](#)].

Language and music

Mirror neurons have been proposed as a neural basis for the evolution of the syntactic-like structure characterizing language and music ([Fadiga et al., 2009](#)).

Rehabilitation

Mirror neurons have inspired therapeutic approaches for motor recovery after stroke, with techniques such as action observation therapy leveraging mirror mechanisms to facilitate motor rehabilitation ([Small et al., 2010](#)).

Further reading

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