

Empathy

*Philosophical and Psychological
Perspectives*

EDITED BY

Amy Coplan and Peter Goldie

OXFORD
UNIVERSITY PRESS

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Within Each Other: Neural Mechanisms for Empathy in the Primate Brain

Marco Iacoboni

4.1 Introduction

Empathy is commonly defined as the ability to understand and share the feelings of another. It is obviously a very complex ability. What are the neurophysiological mechanisms that underlie empathy? For years, nobody dared to investigate this issue. The main reasons were two. First, the study of the brain mechanisms associated with emotion and emotional understanding is relatively recent. Until approximately 20 years ago, the study of the neural systems associated with higher functions was focused exclusively on 'cold' cognitive processes. The dominant metaphor was 'the mind as a computer.' The study of emotions—especially complex social emotions—clearly did not fit in the prevalent paradigm. Second, even after emotions became a popular topic in cognitive neuroscience, mostly thanks to the influential work of Antonio Damasio, the neural mechanisms of empathy remained largely unexplored. This was likely due to the perceived complexity of empathy. Indeed, the complexity of a phenomenon is generally considered an obstacle for the study of its neural correlates, especially in single cell recordings. While neurophysiologists are able to study brain activity at its most exquisite spatial and temporal resolution, that is, the spiking activity of single cells, they also tend to study this activity in relation with relatively simple phenomena, such as the perception of individual sensory stimuli or the planning and execution of relatively simple actions. For this reason, neurophysiological data on empathy were virtually nonexistent until a few years ago. In recent years, however, a new wave of studies has investigated the links between empathic behavior and brain activity. The recent studies have been inspired by the discovery of mirror neurons in the macaque brain. These cells, which I describe in detail in the next section of the chapter, have *physiological properties* that are ideal to facilitate empathy. Indeed, the properties of mirror neurons seem to map extremely well onto emotional contagion, a phenomenon studied for decades by psychologists (Hatfield et al. (1994)). Most

scholars would probably agree that mirror neurons are likely critical neural elements for the relatively simple forms of empathic resonance that are observed in emotional contagion. However, most scholars would also argue that mirror neurons cannot account for more cognitively complex forms of empathy. In this chapter, I will argue instead that there are many different kinds of mirror neurons, and that they are also much more widely distributed in the primate brain than previously thought. The rich variety of mirroring responses and their diffuse anatomical localization suggest that neural mirroring may be a fundamental building block of empathy, even in its more complex forms.

In the next three sections of this chapter, I will review the single cell recordings on mirror neurons in macaques, the brain imaging data in humans that suggest links between activity in the human mirror neuron system and empathic behavior, and finally a set of unique data on single cell recordings in the human brain that demonstrate mirroring response in individual human neurons. In the final section of the chapter, I will discuss the theoretical implications of these empirical findings.

4.2 Mirror Neurons in the Macaque Brain

The first peer-reviewed scientific report on mirror neurons was published in 1992 (di Pellegrino et al. (1992)). This very short paper was followed four years later by a much more detailed report in which the term *mirror neurons* was used for the first time (Gallese et al. (1996)). The cells described in these two papers were recorded from the anterior sector of the ventral premotor cortex of *Macaca Nemestrina*. The anterior sector of the ventral premotor cortex in macaques is called area F5, and contains neurons with quite interesting motor properties (Rizzolatti et al. (1988)). The F5 motor neurons fire in relation with specific goal-oriented actions, rather than with individual movements. For instance, several F5 neurons fire during grasping actions, others during holding actions, and others during tearing actions. Interestingly, the same neuron may fire for a grasping action with the left hand *and* for a grasping action with the right hand. This firing pattern demonstrates that the firing of the cell does not occur in relation with the contraction of a specific set of muscles. Indeed, the same neuron will not fire for a different kind of action, say, scratching the head, which also involves the contraction of finger muscles used during grasping. Motor neurons in F5 show specificity of responses in relation with the *type* of grasp. Some cells discharge only during *precision grip* (opposition of thumb and index to grasp very small objects), others only during *finger prehension* (all fingers grasp a relatively small object), and others only during *whole hand prehension* (the whole hand grasps a big object). Taken together, these properties suggest that F5 motor neurons form a vocabulary of goal-oriented actions (Rizzolatti et al. (1988)), that is, as the vocabulary is the body of words of a language, the actions coded by F5 neurons seem to represent the body of actions that can achieve specific goals.

Approximately 20 to 25% of F5 motor neurons have also amazing *visual properties*. These cells fire also when the monkey is completely still and is just watching somebody

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else making a goal-oriented action. It is as if the monkey is watching her own actions reflected by a mirror. This is why these cells are called mirror neurons. Mirror neurons are defined exclusively on the basis of their physiological properties. They are cells that are specialized for actions, and that discharge in association with motor and perceptual aspects of actions. There are two main categories of mirror neurons: strictly congruent mirror neurons and broadly congruent mirror neurons. Strictly congruent mirror neurons discharge for the same action both when the monkey is performing it and when the monkey is simply observing it performed by somebody else. Broadly congruent mirror neurons, in contrast, fire not only for the same action, but also for different actions that achieve the same goal both when the monkey is performing the action and when the monkey is simply observing it performed by somebody else (Gallese et al. (1996)). The properties of mirror neurons suggest that these cells map the actions of others onto the motor repertoires of the observer, thereby providing an internal simulation of the actions of other individuals in the observer.

Further studies demonstrated that mirror neurons discharge also when the observed action is partially occluded (Umiltà et al. (2001)) and when the monkey does not see the action at all, but simply listens to sounds typically associated with the action (for instance, the sound of breaking a peanut) (Kohler et al. (2002)). These data suggest that mirror neurons are multimodal cells that can provide a fairly abstract representation of the actions of other individuals. How abstract? A recent experiment has addressed this question (Fogassi et al. (2005)). The single cell recordings of this recent study were performed in area PF/PFG, an area in the anterior sector of the inferior parietal cortex. This sector of the inferior parietal cortex is anatomically connected with area F5 in the ventral premotor cortex (Rizzolatti & Luppino (2001)). Parietal motor neurons in PF/PFG were recorded when the monkeys were performing grasping actions associated with different outcomes, eating or placing. In some trials the monkey was allowed to grasp food and eat it, while in others the monkey was rewarded with food only after the animal had successfully completed the trial by grasping the food and placing it in a container. While of parietal motor neurons fired equivalently for grasping to eat and for grasping to place, the remaining demonstrated differential discharges during the grasping action associated with different outcomes. Approximately $\frac{3}{4}$ of these cells discharged more vigorously for grasping to eat, while $\frac{1}{4}$ discharged more vigorously for grasping to place. Note that the neuronal discharges were measured during grasping, that is, *before* the monkey would eat or place the food in the container.

After this necessary testing of the motor properties of the parietal cells, the experimenters tested the mirror properties of the same pool of cells. In some trials, the monkey simply watched an experimenter grasping a piece of food and eating it. In some other trials, the monkey watched the experimenter grasping the food and placing it in a container. The visual cue that signaled the outcome of the grasping action was the presence of the container. If the container was present, the experimenter placed the food in it. If the container was not present, the experimenter ate the food. A subset of motor parietal neurons displayed mirror properties, that is, they discharged when the

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monkey simply observed the experimenter's grasping action. The discharge of these parietal mirror neurons during grasping observation mirrored the discharge previously measured during grasping execution. Cells that discharged equivalently for executed grasping actions associated with different outcomes, also discharged equivalently when the monkey simply observed grasping actions associated with different outcomes. For these mirror parietal cells, a grasp is a grasp, regardless of the outcome associated with it. Cells that discharged more when the monkey grasped to eat, also discharged more when the monkey watched the experimenter grasping to eat (the outcome was cued by the absence of the container). Also, cells that discharged more when the monkey grasped to place, also discharged more when the monkey watched the experimenter grasping to place (here the outcome was cued by the presence of the container). The preferential discharge for the same grasping action associated with different outcomes suggest that these mirror neurons do not simply code the action, but also the intention associated with it. In less mentalistic terms one could say that these cells predict the outcome of the observed grasping action, the action or actions that follow the grasp. This is evidence for a rather abstract and sophisticated coding of the observed grasp. The grasp is coded by these cells as embedded in a chain of concatenated and coordinated actions.

Mirror neurons do not simply code hand and hand-to-mouth actions. Both the ventral premotor and the inferior parietal cortex contain mirror neurons that code for mouth actions only. Two main types of actions are mirrored by these cells: ingestive and communicative actions. A recent depth electrode study demonstrated the mirroring properties of single cells in ventral premotor cortex for biting and sucking, and for lip-smacking, a communicative facial gesture with positive social valence (Ferrari et al. (2003)). The evidence that communicative facial gestures can be mirrored at the level of individual premotor neurons is theoretically important. It suggests that the evolutionary antecedents of empathy are based on relatively simple mechanisms of contagion and motor resonance.

4.3 Neural Systems with Mirroring Properties in the Human Brain

The single unit recordings in macaques described in the previous section have inspired a series of studies on humans. A common aspect of all these studies is that they cannot measure brain activity at the exquisite resolution of a single cell, as in the depth electrode studies in macaques. The neuroscience methods applied to the study of the human brain typically provide measures of *ensemble* neural activity, the activity of a large number of brain cells working together. Obviously, none of these techniques can definitely prove that the ensemble neural activity with mirroring properties truly represents the activity in concert of many mirror neurons. In principle, a neuronal ensemble may be activated during both action execution and action observation even

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