

# Neural and Computational Mechanisms of Action Processing: Interaction between Visual and Motor Representations

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Action recognition has received enormous interest in the field of neuroscience over the last two decades. In spite of this interest, the knowledge in terms of fundamental neural mechanisms that provide constraints for underlying computations remains rather limited. This fact stands in contrast with a wide variety of speculative theories about how action recognition might work. This review focuses on new fundamental electrophysiological results in monkeys, which provide constraints for the detailed underlying computations. In addition, we review models for action recognition and processing that have concrete mathematical implementations, as opposed to conceptual models. We think that only such implemented models can be meaningfully linked quantitatively to physiological data and have a potential to narrow down the many possible computational explanations for action recognition. In addition, only concrete implementations allow judging whether postulated computational concepts have a feasible implementation in terms of realistic neural circuits.

## Introduction

Action recognition and its relationship to other cognitive functions have been one of the core topics in cognitive neuroscience over the last decade (Keysers, 2011; Keysers and Perrett, 2004; Rizzolatti and Fogassi, 2014; Rizzolatti et al., 2001; Schütz-Bosbach and Prinz, 2007). The discovery of *mirror neurons* in the premotor cortex of the monkey (Gallese et al., 1996; Rizzolatti et al., 1996) has initiated a wide interest in the neuroscience community for action processing and understanding, with implications in many other disciplines of neuroscience, including social neuroscience, motor control, body- and self-representation, body motion perception, and emotion processing. At the same time, action processing and understanding in biological systems have become topics of high interest in other disciplines outside neuroscience. This includes, for example, computer vision, robotics (e.g., Demiris and Hayes, 2002; Schaal et al., 2003), and philosophy (e.g., Petit, 1999; Sinigaglia, 2013). In spite of the outstanding interest for this topic, the number of publications on the electrophysiological basis of action recognition that provide *precise constraints* for the underlying neural and computational mechanisms is still rather limited (compare, e.g., Kilner and Lemon, 2013).

This lack of strongly constraining data, combined with the vivid interest in the problem of action recognition and understanding, motivated the development of a broad spectrum of partly extremely speculative theoretical accounts of action processing. Many of these theories have never been concretely implemented and have served only as frameworks for conceptual discussions. However, considering the complexity of the underlying neural and dynamical processes and the high dimensionality of the underlying visual and motor patterns, the establishment of valid theories without the help of concretely implemented models is

very difficult. Likewise, it is almost impossible to falsify such conceptual accounts by comparing them with specific experimental results in a conclusive manner.

Action-selective neurons are found in a number of brain structures, including the *superior temporal sulcus* (STS), the parietal, the premotor, and the motor cortex. We will briefly review here mainly the recent relevant results, focusing especially on a number of novel studies on mirror neurons. Much more detailed information about previous studies and other action-selective neurons without mirror properties can be found in other reviews (Nelissen et al., 2011; Puce and Perrett, 2003; Rizzolatti and Fogassi, 2014; Rizzolatti et al., 2001).

Early studies on mirror neurons (Gallese et al., 1996; Rizzolatti et al., 1996) reported that the responses of some mirror neurons to visual stimulus might depend on specific characteristics and modalities of the visual stimulation. However, only recent neurophysiological studies have studied these aspects systematically. They have investigated how spatial parameters of observed actions influence the activity of mirror neurons, including the distance of the action from the observer as well as the perspective or stimulus view, i.e., from which direction the action is observed. Moreover, these studies show that the mirror neuron discharge intensity is influenced by the value that is associated with objects on which the action is performed. We think that such parametrically well-controlled studies of the different aspects that influence the activity of action-selective neurons, and especially of mirror neurons, are absolutely essential for the development of solid computational theories of action perception in the primate cortex. In addition, the work of Lemon and his co-workers (see Kraskov et al., 2014) showed that the mirror mechanism is not limited to parieto-frontal circuit but also includes pyramidal tract neurons originating from areas F5 and F1 (primary motor cortex).

As a step toward a deepening of the understanding of the biologically relevant neuro-computational mechanisms of action recognition, we also provide an overview of the existing computational and neural models that are implemented in a sufficiently concrete manner to allow meaningful comparisons with such experimental data.

This overview of the existing work reveals several gaps in terms of critical experiments that might help to decide between different computational accounts, as well as between the available theoretical frameworks, all of which fail to capture some essential properties of the neural data. We hope that this analysis will help to set the goals for future research in experimental as well as in theoretical neuroscience.

### Preliminary Remark: Different Classes of Actions

Before reviewing neurophysiological data on action recognition and discussing related models, it is important to stress that actions made by other individuals fall into *two main categories*. One category is constituted by actions that are present in the motor repertoire of the observers, and the other by actions that are extraneous to their motor abilities. The processing of these two different classes of actions involves partially different neural substrates. Both categories of actions activate visual action-selective areas located in the superior temporal sulcus (STS), while they differ with respect to the involvement of motor structures. To give an example, the observation of biting done by a dog, a monkey, or a human being activates the same cortical parieto-frontal network in human observers. In contrast, the observation of a dog that barks activates visual but not motor areas (Buccino et al., 2004).

A psychological explanation of these findings has been proposed by Jeannerod. He suggested that “mere visual perception, without involvement of the motor system, would only provide a description of the visible aspects of the movements of the agent, but it would not give precise information about the intrinsic components of the observed action, which are critical for understanding what the action is about, what is its goal, and how to reproduce it.” This implies that perception of actions without motor involvement is in some sense incomplete. Others have interpreted the motor activation triggered by others’ actions in a more mechanistic way, suggesting that the motor activation of the parieto-frontal network results in a “direct recognition” of the observed action through the similarity between the observed and the executed action, not requiring additional complex inference processes (direct matching hypothesis) (Rizzolatti et al., 2014). A more recent interpretation is that motor activation during action observation represents a prediction triggered by the observed stimuli, which is necessary to disambiguate the sensory representations emerging during action observation (Kilner et al., 2007; Kilner, 2011; Wilson and Knoblich, 2005). Conceptually, this view minimizes, in part, the role of motor system in action processing, while stressing instead interactions between visual and motor areas for action understanding.

Another important distinction from a theoretical point of view is the one between *transitive* actions, which are directed toward goal objects, and *non-transitive* ones without such goal objects. It turns out (see ‘Example-based visual recognition models’) that

the processing of transitive actions is computationally more difficult. It requires not only the recognition of the effector movement (e.g., the moving hand) but also a processing of the relationship between the effector and the goal object (e.g., whether hand and object match spatially, or if the correct type of grip is applied to a specific object). This necessitates additional computational mechanisms that relate the movements of the effector to the properties of goal objects (e.g., Oztop et al., 2004).

### Electrophysiological Results

Due to space limitations, the following review of electrophysiological results focuses on a few recently established novel aspects of mirror neurons, and properties of action-selective neurons that likely provide input to the classical mirror neurons system. An overview of the anatomy of the action observation system is given in Figure 1. With respect to a more elaborate treatment of previous results on the mirror neuron and action processing system, we refer to several previous reviews (Puce and Perrett, 2003; Rizzolatti and Craighero, 2004; Rizzolatti and Fogassi, 2014).

#### Basic Motor Properties of Canonical and Mirror Neurons

Area F5 contains two main types of neurons responding to visual stimuli: canonical neurons and mirror neurons. *Canonical neurons* are neurons that respond to the presentation of three-dimensional objects. Typically, there is congruence between the size of the objects that trigger the neuron and the type of grip encoded by that neuron (Murata et al., 1997). More recently, Fluet et al. (2010) recorded canonical neuron activity in monkeys, instructed by an external context cue to grasp a handle with a precision grip or a power grip. In addition, object orientation was varied. The neurons showed a context-dependent grasp planning activity after cue presentation and a motor grasp-related activity during movement execution.

Contrasting with this class of neurons, mirror neurons are a specific set of neurons originally described in area F5 in the premotor cortex of the monkey. As all other types of neurons in area F5, mirror neurons discharge during *goal-directed* actions such as grasping, holding, and placing. Their main characteristic is that they respond to the observation of actions done by others. This property differentiates them not only from mere motor neurons, but also from canonical neurons. The relative proportion of these neuron types was investigated in a recent study in which a large number of neurons of F5 were recorded using multi-electrode linear arrays. The study reported that out of 479 recorded grasping neurons, 221 were purely motor neurons, 197 were mirror neurons, including 60 that also responded to object presentation, and, finally, 46 were canonical neurons (Bonini et al., 2014).

Mirror neurons are also present in monkey parietal areas connected with area F5 (see below). Their properties appear to be similar to those of mirror neurons in area F5. However, detailed comparative studies that assess possible differences between the functional properties of parietal and premotor mirror neurons have still to be undertaken.

In humans, mirror neurons were recorded in mesial motor areas and the hippocampus (Mukamel et al., 2010). The recordings were made in surgical patients with drug-resistant epilepsy. The type of electrodes used (large linear electrodes with low

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