



Review article

Neural mechanisms of vocal imitation: The role of sleep replay in shaping mirror neurons



Nicolas Giret*, Jean-Marc Edeline, Catherine Del Negro

Neuroscience Paris-Saclay Institute, CNRS, Université Paris Sud, Université Paris Saclay, Orsay, France

ARTICLE INFO

Article history:

Received 18 November 2016
 Received in revised form 14 February 2017
 Accepted 20 February 2017
 Available online 11 March 2017

Keywords:

Imitation
 Learning
 Mirror neurons
 Neuronal reactivation
 Sensorimotor integration
 Offline processing
 Songbirds

ABSTRACT

Learning by imitation involves not only perceiving another individual's action to copy it, but also the formation of a memory trace in order to gradually establish a correspondence between the sensory and motor codes, which represent this action through sensorimotor experience. Memory and sensorimotor processes are closely intertwined. Mirror neurons, which fire both when the same action is performed or perceived, have received considerable attention in the context of imitation. An influential view of memory processes considers that the consolidation of newly acquired information or skills involves an active offline reprocessing of memories during sleep within the neuronal networks that were initially used for encoding. Here, we review the recent advances in the field of mirror neurons and offline processes in the songbird. We further propose a theoretical framework that could establish the neurobiological foundations of sensorimotor learning by imitation. We propose that the reactivation of neuronal assemblies during offline periods contributes to the integration of sensory feedback information and the establishment of sensorimotor mirroring activity at the neuronal level.

© 2017 Elsevier Ltd. All rights reserved.

Contents

1. Introduction.....	59
2. Mirror neurons as a neural substrate for imitative learning.....	59
2.1. Mirror neurons in non-human and human primates.....	59
2.2. Ontogeny of mirror neurons.....	60
3. Vocal behavior and mirror neurons in songbirds.....	60
3.1. Vocal learning in songbirds.....	60
3.2. Mirror neurons in songbirds.....	61
3.3. The auditory feedback processing.....	63
3.4. State-dependent modulation of auditory responses.....	63
4. Offline processes.....	64
4.1. Sleep and song learning.....	64
4.2. Reactivation of neuronal circuits during sleep.....	65
5. Toward a theoretical model of the shaping of mirror neurons through sleep replay.....	65
5.1. Causal relationship between sleep replay and mirror properties.....	65
5.2. Future research orientation.....	67
6. Concluding remarks.....	68
Acknowledgements.....	68
References.....	68

* Corresponding author at: Neuroscience Paris-Saclay Institute (Neuro-PSI), CNRS UMR 9197, Building 446, Université Paris Sud, Université Paris Saclay, Rue Claude Bernard, 91405 Orsay cedex, France.

E-mail addresses: nicolas.giret@u-psud.fr (N. Giret), jean-marc.edeline@u-psud.fr (J.-M. Edeline), catherine.del-negro@u-psud.fr (C. Del Negro).

1. Introduction

Observing other individuals when they interact with their environment, provides an unending opportunity to acquire new behaviors. Using information provided by others to guide the behavioral repertoire characterizes imitation. It thereby constitutes the foundation of language and speech acquisition. The ability to imitate others is not restricted to humans: it has been described in the entire animal kingdom, including the octopus (Fiorito and Scotto, 1992), parrots (Giret et al., 2009; Pepperberg, 2006), songbirds (Kroodsma and Miller, 1996; Marler and Slabbekoorn, 2004) or elephants (Poole et al., 2005). Among non-human primates, although early reports failed to demonstrate imitative abilities in the wild (Lyons et al., 2006; Visalberghi and Fragaszy, 2002), more recent studies have successfully described imitation in apes (Buttelmann et al., 2007; Call, 2001; Custance et al., 1995; Fuhrmann et al., 2014; Marshall-Pescini and Whiten, 2008), monkeys (Simpson et al., 2016) and marmosets (Voelkl and Huber, 2007; see for review Huber et al., 2009). Adopting a behavior exhibited by others instead of learning by individual experience is considered a key advantage of sociality and a major driving force for evolution (Boyd and Richerson, 2004; Gergely and Csibra, 2006). This ability is an important developmental milestone of the theory of mind (Korkmaz, 2011; Meltzoff and Decety, 2003). Importantly, depending on what the term “imitation” refers to, the underlying neural mechanisms could vary.

When a subject imitates an action that is already present in its motor repertoire, a mechanism that matches the sensory representation of this action with its motor representation is essential (Brass and Heyes, 2005; Iacoboni, 2009a; Iacoboni et al., 1999). When an individual has to perform a new action, acquires a new skill or merely adjusts an action present in the motor repertoire after observing the same action being done by another individual, additional mechanisms are needed for allowing the observer to compare observed and generated actions. Imitation learning thus requires practice by the observer and relies, at least in part, on sensorimotor experience, *i.e.* on the sensory feedback provided by the subject’s movements. Sensorimotor training would thus establish new sensorimotor matches or associations, *e.g.* between the sensory representation of an action and its motor representation. What the neural bases of this imitation process are, however, is still an open question. Mirror neurons, which fire when an individual performs or observes the same action, are often viewed as the missing link between the sensory and motor representations of the same action. We review in the following the recent discoveries on the mirror system and we propose how the template representation of an action might interact with the mirror neuron system in the context of imitation learning.

Here, we focus on studies that have described mirror neuron properties in monkeys, humans and songbirds. We review studies providing insights into the potential mechanisms underlying the establishment of mirror properties that have been described only in adults. We propose that the precise sensorimotor correspondence of mirror neurons arises from spontaneous offline reactivations, in particular during sleep or rest, of neural circuits involved in the execution of a behavior during the waking state.

2. Mirror neurons as a neural substrate for imitative learning

2.1. Mirror neurons in non-human and human primates

First discovered in the macaque brain, mirror neurons display similar patterns of activity when an individual observes or executes the same action (di Pellegrino et al., 1992; Gallese et al.,

1996). Mirror neurons thus have particular sensorimotor properties (Rizzolatti and Buccino, 2005; Rizzolatti and Craighero, 2004). They were first reported in the ventral premotor area F5 of rhesus macaques (di Pellegrino et al., 1992), and later in the parietal cortex (Fogassi et al., 2005; Fig. 1). More recently, mirror neurons were reported in the ventrolateral frontal cortex of common marmosets (Suzuki et al., 2015). These neurons fired both when the monkey performed a grasping movement and when it observed an experimenter performing the same movement (di Pellegrino et al., 1992; Gallese et al., 1996). Later reports investigated the properties of mirror neurons, using a screen that occluded the completion of the grasping action (Umiltà et al., 2001). Authors have suggested that mirror neurons provide a substrate for goal-directed behavior and thus for the understanding of an action (Gallese et al., 1996; Rizzolatti et al., 1996; Rizzolatti and Arbib, 1998; Rizzolatti and Craighero, 2004). Another study extended the mirror properties of neurons in the F5 area from actions involving the hand to those involving the mouth, related to ingestive and communicative functions (Ferrari et al., 2003). Interestingly, some neurons in the F5 area show auditory-motor mirroring properties: they are activated when the monkey hears the sound of an action, such as that of a peanut breaking, and when it performs the corresponding motor action, such as breaking a peanut (Kohler et al., 2002). As the F5 area is considered the homolog of the human inferior frontal gyrus, which includes Broca’s area, a brain area associated with language production (Broca, 1861a, 1861b; see also Dronkers et al., 2007; Fadiga et al., 2009), it has been suggested that mirror neurons play a role in speech and language processing (Kohler et al., 2002; Rizzolatti and Arbib, 1998).

In humans, indirect evidence reveals the existence of a so-called mirror neuron system (Fig. 1). Functional Magnetic Resonance Imaging (fMRI), which provides a quite indirect measure of neural activity, reveals the activation of a similar neural network, which includes the inferior frontal gyrus, containing the Broca’s area (Brodmann areas 44 and 45), the medial frontal gyrus, the insula, the cingulate gyrus, the temporal gyrus, the anterior parietal lobule, the postcentral gyrus and the precuneus during observation and execution of a motor act (Iacoboni et al., 1999; Kilner et al., 2009; Molenberghs et al., 2012). In humans involved in an imitation learning task, such as observing guitar chords played by a guitarist and then playing the chords, their inferior parietal lobule and inferior frontal gyrus were strongly activated during both conditions (Buccino et al., 2004; Higuchi et al., 2012; Vogt et al., 2007). Direct evidence of individual mirror neurons in the human brain have been provided by Mukamel and colleagues. They performed single neuron recordings while patients were observing or executing grasping actions and facial gestures. Recordings were conducted in brain regions surrounding the epileptic area, which did not include Broca’s area, and revealed mirror neurons in the supplementary motor area, the hippocampus, the parahippocampal gyrus and entorhinal cortex (Mukamel et al., 2010).

A few decades ago, the existence of links between speech perception and production was predicted by the motor theory of speech perception proposed by Liberman and colleagues (*e.g.* Liberman et al., 1967; Liberman and Mattingly, 1985). While the two first claims of this theory, *i.e.* speech is special and perceiving speech is perceiving gesture, remains controversial, the third claim, *i.e.* the motor system is recruited for perceiving speech, has been supported by several behavioral evidence within and outside of the communication domain (see for review Galantucci et al., 2006). The discovery of mirror neurons in the motor areas of the monkey brain has reinforced the view of the involvement of the motor system in general perception (Rizzolatti and Arbib, 1998). However, given the absence of any direct evidence of mirror neurons in the human Broca’s area, researchers have challenged the involvement of mirror neurons in language (Hickok, 2009; Lotto et al., 2009) that

Download English Version:

<https://daneshyari.com/en/article/5043554>

Download Persian Version:

<https://daneshyari.com/article/5043554>

[Daneshyari.com](https://daneshyari.com)