

THE ROLE OF MIRROR NEURONS IN OBSERVATIONAL MOTOR LEARNING: AN INTEGRATIVE REVIEW

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ABSTRACT

Mirror neurons were discovered in the early 1990's in the premotor cortex of the rhesus macaque. These special, visuo-motor neurons discharge action potentials when executing an action, as well as during the observation of the performance of a similar action. During an observational motor learning protocol, learners acquire new motor patterns based on the visual information presented by an execution model. In order to do so, learners have to transform the observed visual information into motor commands (visuo-motor transformation). Studies show that observational motor learning may improve action perception and motor execution. Moreover, action perception and action execution interact in a mutual and bi-directional fashion (visuo-motor and motor-visual interaction), suggesting that perception and action share common neural mechanisms. Mirror neurons have been proposed as the neurophysiological basis of the visuo-motor and motor-visual transformation processes, and may play a role in the perceptual and motor improvements induced by observational motor learning.

Key Words: mirror neurons, observational motor learning, internal models, visuo-motor experience

RESUMEN

Las neuronas espejo fueron descubiertas a comienzos de los años 90 en la corteza premotora de macaco Rhesus. Las neuronas espejo son un tipo especial de neuronas visuo-motoras que se activan tanto cuando alguien ejecuta una acción, como cuando observa a otra persona ejecutando una acción similar. Durante un protocolo de aprendizaje motor por observación el aprendiz adquiere nuevos patrones de movimiento a partir de la información visual presentada por un modelo de ejecución. Para lograrlo, el aprendiz ha de transformar la información visual observada en comandos motores (transformación visuo-motora). Se ha demostrado que mejoras perceptivas y motoras se pueden lograr a través del aprendizaje motor por observación. Además, la percepción de acciones y la ejecución de acciones presentan una interacción mutua y bi-direccional (interacción visuo-motora y motora-visual). Esto sugiere que percepción y ejecución de acciones comparten ciertos mecanismos neurales. Ya que las neuronas espejo se activan tanto cuando alguien observa una acción como cuando la ejecuta, se las ha propuesto como la base neurofisiológica de los procesos de transformación visuo-motora y motora-visual. Por lo tanto, las neuronas espejo podrían dar explicación a las mejoras logradas mediante aprendizaje motor por observación tanto a nivel perceptivo como motor.

Palabras clave: neuronas espejo, aprendizaje motor por observación, modelos internos, experiencia visuo-motora

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Submitted: 15/06/2014

Accepted: 30/06/2014

INTRODUCTION

Action demonstration is a method extensively used by coaches to teach athletes how to perform new motor tasks (Bandura, 1986; McCullagh & Weiss, 2001). During action demonstration, learners are presented with a model that shows them how to execute the action they wish to learn (Al-Abood, Davids, & Bennett, 2001; Buchanan & Dean, 2010; Hodges & Williams, 2007; Rohbanfar & Proteau, 2011; Sheffield, 1961). Thus, it is necessary for learners to transform the observed visual information into motor commands that allow them to perform the action correctly (visuo-motor transformation) (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995; Rizzolatti, Luppino, & Matelli, 1998; Vogt & Thomaschke, 2007). Observational motor learning is the process that underlies learning of a motor action based on the information presented by an execution model (Hodges, Williams, Hayes, & Breslin, 2007; Maslovat, Hodges, Krigolson, & Handy, 2010). Studies have demonstrated that observational motor learning improves motor performance (e.g.: achievement of better outcomes) (Hayes, Ashford, & Bennett, 2008; Hayes, Hodges, Scott, Horn, & Williams, 2006; Horn, Williams, Hayes, Hodges, & Scott, 2007). Interestingly, observational motor learning has been also shown to improve learner's perceptual ability (e.g., more accurate action discrimination) (Lago-Rodríguez, Lopez-Alonso, & Fernandez-del-Olmo, 2013).

Since the beginning of the XXth century it has been repeatedly suggested that action perception and action execution share common neural structures. In a seminal study, Eidelberg reported the first indirect behavioural evidence for the activation of the motor system during action observation. The experimenter reported that subjects tend to imitate the action performed by an experimenter, although they had been previously asked to perform a different action (Eidelberg, 1929). Eidelberg named this phenomenon "spontaneous imitation". In line with Eidelberg's findings, several theories have later proposed the motor system to be actively involved in the perception of actions performed by others (e.g.: common-coding theory) (Prinz 1997); theory of mental simulation (Jeannerod, 2001, 2006)). This led to the proposal that while observing others performing an action, the observer activates motor structures that mirrors the observed action (Prinz, 1997; Viviani & Stucchi, 1992).

The discovery in non-human primates of a population of special type of visuo-motor neurons that discharges action potentials (becomes activated) both when a monkey observes and executes an action has given a neurophysiological support for the notion of a common neural representation for action execution and action observation (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). These so-called mirror neurons have been proposed as the neurophysiological basis

for observational motor learning because this pool of neurons mediates the transformation of visual information (e.g.: movement pattern presented by an execution model) into motor commands. Such a transformation occurs through the activation of motor programs that resemble the observed action (Hodges et al., 2007; Maslovat et al., 2010). Moreover, mirror neurons may account for the interaction between executed and perceived actions (motor-visual interaction) because these neurons code sensory consequences associated with the executed action, which can interact with online perceptual processes (Craighero, Bello, Fadiga, & Rizzolatti, 2002; Vogt & Thomaschke, 2007).

In this paper we review evidence that humans can learn to execute an action through observational motor learning. Furthermore, we report studies that have reported improvements in individuals' perceptual ability resulting from observational motor learning. Although, several recent reviews have been published about this topic (e.g. Cook, Bird, Catmur, Press & Heyes 2014), the current review specifically focus on athletic performance. Since mirror neurons might form a common neural mechanism for action execution and action perception, we finally argue that mirror neurons could be at the neurophysiological basis of the motor and perceptual benefits resulting from observational motor learning.

Observational motor learning

During action demonstration, athletes are presented with an execution model demonstrating the performance of an action (Bandura, 1986; McCullagh & Weiss, 2001). This process has been referred to as observational motor learning, in which action observation and action executions are combined in order to acquire new motor patterns (Hodges et al., 2007; Maslovat, Hodges, Krigolson, & Handy, 2010).

Observational motor learning can be achieved in two ways: observational learning and observational practice (Vogt & Thomaschke, 2007). During observational practice, individuals learn by performing the motor task they just observed. In contrast, observational learning consists of a mix of observation and physical practice during the entire or a part of the practice period (for details, see Vogt & Thomaschke, 2007). Interestingly, observational learning could be easily implemented as a dyad practice, where two learners work together, interspersing one's own physical practice with observation of their peer's action execution (Wulf, Shea, & Lewthwaite, 2010). Therefore, dyad practice could potentially be more effective than observational practice and physical practice, since with the same amount of time and half of the resources (e.g.: number of balls in a basketball training session), learners can achieve similar, or even higher levels of performance (Sanchez-Ku & Arthur W, 2000;

Shea, Wulf, & Whitacre, 1999; Shebilske, Regian, Arthur Jr, & Jordan, 1992). Nevertheless, in order to select the most efficient observational motor learning program, it is essential to accurately characterize the action that is to be learned (Figure 1). Every action is formed by a group of movements (movement pattern) (Howard, Ingram, & Wolpert, 2011). These movements can be oriented to an object-transitive actions, in which case there would be an interaction between a biological effector and the manipulated object (e.g.: throwing a ball in order to score, for instance, in handball or basketball), or non-object-oriented intransitive actions (e.g.: gymnastic and athletic actions, dance or stereotyped movements) (Króliczak & Frey, 2009; Liepelt, Prinz, & Brass, 2010; Press, Bird, Walsh, & Heyes, 2008). We may further classify actions based on the characteristics of their movement pattern. Then we can also differentiate between spatial characteristics (C. M. Heyes & Foster, 2002), temporal properties (Badets, Blandin, & Shea, 2006), coordination patterns (inter or intra limbs) (Hodges & Franks, 2000), and execution strategies (i.e. movement patterns that result in the achievement of the desired objective) (Buchanan & Dean, 2010; Lago-Rodríguez et al., 2013).

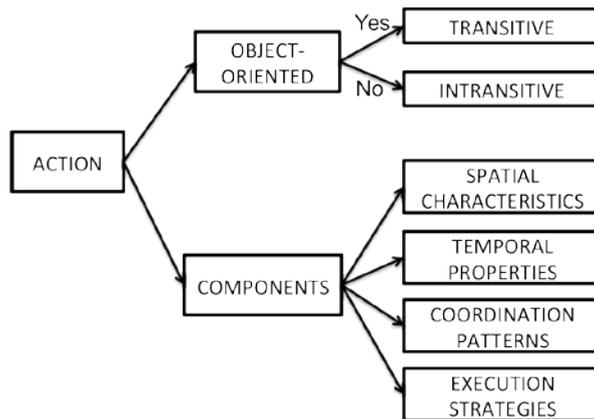


FIGURE 1: Actions can be classified based on either the relationship with an object, or on the movement components. These action characteristics would determine which observational motor learning program should be used.

Performance improvements resulting from observational motor learning

Several studies have evaluated performance benefits of observational motor learning during acquisition of sport skills, for instance in climbing (Boschker & Bakker, 2002), dart throwing (Al-Abood, Davids, Bennett, Ashford, & Martinez Marin, 2001; Al-Abood, Davids, & Bennett, 2001), cricket (Breslin, Hodges, Williams, Curran, & Kremer, 2005), baseball (Horn, Williams, Hayes, Hodges, & Scott, 2007), bowling (Hayes, Hodges, Scott, Horn, & Williams, 2006,

2007), football (Horn, Williams, & Scott, 2002; Horn, Williams, Scott, & Hodges, 2005; Janelle, Champenoy, Coombes, & Mousseau, 2003), free-weight lifting (McCullagh & Meyer, 1997; Ram, Riggs, Skaling, Landers, & McCullagh, 2007), and volleyball (Barzouka, Bergeles, & Hatziharistos, 2007; Weeks & Anderson, 2000).

Differences in performance improvements resulting from observational motor learning and physical practice have been extensively studied for both transitive and intransitive actions. It should be noted that for transitive actions the objective is to correctly manipulate an object in order to achieve an outcome (e.g., perform a movement pattern during a free-basketball throw that scores points). Interestingly, the same outcome may be achieved through a variety of movement patterns (e.g.: a free-basketball throw can be executed by a down-up arm movement or an arm extension movement) (Buchanan & Dean, 2010). Importantly, one of these movement patterns (execution strategies) leads to a more efficient performance (e.g.: accomplishing the goal at the lowest cost) (Al-Abood, Davids, Bennett, et al., 2001; Al-Abood, Davids, & Bennett, 2001). Conversely, motor patterns for intransitive actions are stereotyped (e.g.: gymnastic movements), and thus only one execution strategy results in the “ideal” performance. This suggests that to learn an intransitive action through observational motor learning athletes would have to replicate the observed movement pattern (action imitation) (C. Heyes, 2001).

Studies have demonstrated that observing an execution model of an intransitive action during the acquisition period allows learners to accurately replicate the spatial (C. M. Heyes & Foster, 2002) and temporal (Badets, Blandin, & Shea, 2006) characteristics of the movement, as well as its inter-limb coordination patterns (Black & Wright, 2000; Buchanan & Dean, 2010; Hodges & Franks, 2000). Moreover, the ability to imitate intransitive actions is determined by previous visuo-motor experience. For example, musicians are able to better reproduce complex finger movements that make up sign language when compared with non-musicians (Spilka, Steele, & Penhune, 2010).

Several studies have found performance benefits as a result of observational motor learning during acquisition of transitive actions, for instance: throwing darts (Al-Abood, Davids, Bennett, et al., 2001; Al-Abood, Davids, & Bennett, 2001), bowling (Hayes et al., 2006), and juggling (Hayes, Ashford, & Bennett, 2008). Recently, we compared performance benefits resulting from physical practice and observational motor learning (both observational learning and observational practice) (Lago-Rodríguez et al., 2013). Participants were asked to hit a ball towards a bull-eye by abduction of the index finger (figure 2). Therefore, only one execution strategy was possible. Results showed that after 100 trials of practice, observational motor learning

and physical practice lead to equivalent levels of motor performance. In line with previous hypotheses, these results suggest that for transitive actions, observing an execution model may have additional benefits compared with physical practice, only when the action to be learned presents more than one execution strategy (Buchanan & Dean, 2010).



FIGURE 2: Scheme of the experimental set up used in Lago-Rodríguez et al. (2013). Participants were asked to hit a ball by an abduction of the right index finger while their hand was attached to the table in a fixed position.

In summary, findings suggest that for intransitive actions, observing an execution model teaches learners “how” to perform an action. Conversely, for transitive actions the execution model teaches learners “what” movement pattern should be used to achieve the action outcome more efficiently (e.g.: making a free throw in basketball).

Perceptual improvements resulting from observational motor learning

Humans perform actions in response to external stimuli. This is especially important for accurate performance in sports (e.g., act in response to an opponent and peers’ actions). Our actions are greatly affected by how accurately we perceive external stimuli and predict their outcome (e.g.: while driving a car). When observing actions performed by others, we can measure the observers’ perceptual ability by asking them to predict or estimate the unseen outcome of the observed action (Yarrow, Brown, & Krakauer, 2009).

Motor expertise is thought to determine perceptual ability because there is a mutual and bi-directional interaction between action perception and action execution (Vogt & Thomaschke, 2007). This is supported by studies showing higher perceptual ability in high-level athletes. High-performance basketball players show earlier and more accurate predictions of the result of an observed free basketball throw action, when compared with basketball coaches, basketball journalists, and naïve subjects (Aglioti, Cesari, Romani, & Urgesi, 2008). Expert cricket batsmen use visual information occurring before and

after the bowler releases the ball in order to predict its future trajectory (Land & McLeod, 2000; Mann, Abernethy, & Farrow, 2010). More specifically, batsmen process information about the relation of the bowling arm and hand, primarily at the end of the throwing action (Müller, Abernethy, & Farrow, 2006). Expertise vs. novice athletes anticipate ball trajectories based on the opponent's movement kinematics more accurately in tennis (Goulet, Bard, & Fleury, 1989; Williams, Ward, Knowles, & Smeeton, 2002), squash (Abernethy, 1990), volleyball (Starkes, Edwards, Dissanayake, & Dunn, 1995), and football (Savelsbergh, Williams, Van der Kamp, & Ward, 2002).

We have recently demonstrated that subjects improve their ability to estimate the unseen outcome of an observed action after having observed an execution model during the training period but not after just having practiced physically (Lago-Rodríguez et al., 2013). Thus, observational motor learning results in perceptual improvements that cannot be achieved through physical practice alone. These results are in line with studies showing that subjects are able to perceive more accurately those stimuli that share some characteristics with previously performed actions (Miall et al., 2006; Schubo, Prinz, & Aschersleben, 2004; Stoet & Hommel, 2002; Zwickel, Grosjean, & Prinz, 2007).

Interestingly, a recent study showed improvements of participants' perceptual ability after observation of an execution model, with no physical practice (Maslovat et al., 2010). Subjects were asked either to perform or to observe a bimanual coordination pattern. Results showed that physical practice resulted in better motor performance compared with observation or no practice. Surprisingly, when subjects were asked to discriminate between bimanual coordination patterns, subjects from the observation and physical practice groups showed similar levels of performance, in both cases higher than the control group that had no practice. The authors concluded that observation of an execution model leads to perceptual improvements without improvements on physical performance (Maslovat et al., 2010). Thus, observational motor learning has greater benefit than observation alone, as it improves both perceptual and motor performance (Lago-Rodríguez et al., 2013).

In summary, expert compared with novice athletes predict earlier and more accurately the outcome of sport-specific observed actions. This suggests that continuous exposure to visual and motor practice can improve perception of the practiced action. Furthermore, improvements in the ability to perceive others' action can be achieved through observational motor learning, where action observation and action execution are combined. This learning method, which improves motor performance, may be a valuable training tool in sports, where both motor and perceptual ability determine final performance.

Mirror Neurons

The discovery of a special type of visuo-motor neurons in non-human primates in the early 1990's (for a recent review see Rizzolatti & Fogassi, 2014) that becomes activated both when a monkey observes and executes an action has given a neurophysiological support for the notion of a common neural representation for action execution and action observation (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). These brain cells were named Mirror Neurons due to their special activation properties (Rizzolatti & Craighero, 2004).

First indirect evidence of mirror neurons in humans was discovered by Fadiga and colleagues (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995). In this study transcranial magnetic stimulation (TMS) was applied over the primary motor cortex (M1) while participants observed actions made by others. Direct evidence of mirror neurons in the human brain was demonstrated 15 years later (Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) by recording extracellular neuronal activity from intracranial depth electrodes of epileptic patients. In this study subjects were asked to observe and execute reaching movements and facial expressions. Results showed that a significant proportion of neurons in the supplementary motor area (SMA) fired both when subjects observed and executed similar actions.

Mirror neurons have been studied in the human brain, using functional magnetic resonance imaging (fMRI) (Logothetis, 2008) and transcranial magnetic stimulation (Rossi et al., 2009). In fMRI studies participants are asked to observe and execute similar actions while inside the scanner. This allows experimenters to locate brain areas that increase their activity during both tasks (Buccino et al., 2004; Grezes, Armony, Rowe, & Passingham, 2003). In line with evidence from studies in non-human primates, a recent meta-analysis of fMRI studies in humans showed that the inferior parietal lobule, inferior frontal gyrus, and the adjacent ventral premotor cortex have mirror properties (Molenberghs, Cunnington, & Mattingley, 2012). These areas form the so-called mirror neuron system (MNS) (Craighero, Metta, Sandini, & Fadiga, 2007) or the action-observation network (AON) (Kilner, 2011). Interestingly, mirror activation has been also observed in the primary motor cortex (Nojima, Mima, Koganemaru, Thabit, Fukuyama & Kawamata 2012) primary visual cortex, the cerebellum and parts of the limbic system (Molenberghs, Cunnington, & Mattingley, 2012).

TMS is another technique used for the study of mirror neurons. Unlike the low temporal resolution of fMRI in the order of seconds (Logothetis, 2008), TMS allows experimenters to measure brain activity with higher temporal

resolution –in the order of milliseconds- (Walsh & Rushworth, 1999). In TMS studies, activity of the motor system is measured indirectly using motor-evoked potentials (MEPs), which are muscle responses evoked by a single TMS pulse applied over the primary motor cortex (M1)(Hallett, 2007). Under identical conditions, increased cortical excitability results in higher MEPs (Ziemann, Lonnecker, Steinhoff, & Paulus, 1996). Assuming that mirror neurons activate motor programs that resemble the observed action, then TMS applied over M1 would result in higher MEPs when subjects observe an action, compared with control conditions (Fadiga, Craighero, & Olivier, 2005). This non-invasive stimulation technique can be used to study patterns of brain activity modulation for different observed actions, as well as the temporal gradient of this activity modulation as a function of the observed motor pattern (Gangitano, Mottaghy, & Pascual-Leone, 2004; Lago & Fernandez-del-Olmo, 2011; Senna, Bolognini, & Maravita, 2014). These studies show that the human motor system modulates its activity during action observation, both at the cortical (Fadiga et al., 1995; Strafella & Paus, 2000) and corticospinal level (Borroni, Montagna, Cerri, & Baldissera, 2005; Montagna, Cerri, Borroni, & Baldissera, 2005). Interestingly, modulation of the activity in the motor system during action observation resembles temporal properties of the observed action (Borroni, Montagna, Cerri, & Baldissera, 2008; Gangitano, Mottaghy, & Pascual-Leone, 2001; Gangitano et al., 2004; Lago & Fernandez-del-Olmo, 2011). Furthermore, the type of observed action determines the modulation of the motor system during action observation (Brighina, La Bua, Oliveri, Piazza, & Fierro, 2000; Enticott Peter G. , 2010). Evidence suggests that mirror neurons initially map observed transitive actions based on their objective, and later specify the muscles that are to be involved in the observed movement pattern (Lago & Fernandez-del-Olmo, 2011; Lepage, Tremblay, & Theoret, 2010).

The MNS has been proposed to have several functions. One is to help us understand the goal pursued by the observed individual's action, and thus, infer an individual's intentions (Ferrari & Rizzolatti, 2014; Rizzolatti & Fogassi, 2014; Rizzolatti & Sinigaglia, 2010). Second, the MNS allows the observer to acquire a new motor pattern based on an observed execution model, by activating a “mirrored” motor pattern in the observer (e.g.: observational motor learning) (Cattaneo & Rizzolatti, 2009; Fabbri-Destro & Rizzolatti, 2008). Finally, recent reviews suggest a putative role for the MNS in facilitating the neural adaptations to strength training and possibly augmenting inter-limb transfer (Howatson, Zult, Farthing, Zijdwind & Hortobágyi 2013; Zult, Howatson, Kádár, Farthing & Hortobágyi 2014). Still, the function of mirror neurons remains controversial (for a discussion on mirror neurons' function see (Hickok &

Hauser, 2010; Rizzolatti & Fogassi, 2014) and more studies need be conducted in order to disentangle the function of mirror neurons in the human brain.

Mirror neurons and visuo-motor experience

The observer's visuo-motor experience determines the extent to which the MNS is activated during action observation. The MNS becomes active when the observer has previous experience regarding the observed action (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005; Calvo-Merino, Grezes, Glaser, Passingham, & Haggard, 2006; Kim et al., 2011). For example, professional basketball players show greater M1 activity in response to an observed free throw compared with control subjects (Aglioti et al., 2008). Moreover, MNS activity increases after physical practice when subjects watch the motor acts they are learning (Cross, Hamilton, & Grafton, 2006), as well as when subjects combine action observation with action execution (Sakamoto, Muraoka, Mizuguchi, & Kanosue, 2009). Recent findings from our lab showed that performance of an observational learning protocol leads to significant increments of M1 excitability when observing others performing the practiced tasks (Lago-Rodríguez et al., 2013). However, we failed to find differences in the activity of cortico-cortical connectivities that have been described as part of the MNS (vPM-M1 and PPC-M1) (Koch et al., 2010; Lago & Fernandez-del-Olmo 2011).

Motor and perceptual resonance mechanisms

The MNS is thought to activate the so-called motor resonance mechanism (Buccino et al., 2001), the mechanism associated with the link between perception and action: during action observation, the motor resonance mechanism activates motor programs that resemble the observed action in the observer's motor repertoire (Rizzolatti & Craighero, 2004). To learn an action from an observed execution model, the observer needs to transform the presented visual information into motor commands (visuo-motor transformation) (Rizzolatti, Cattaneo, Fabbri-Destro, & Rozzi, 2014). The motor resonance mechanism has been proposed as the neural basis of the visuo-motor transformation process, since it activates mirroring motor patterns (Fabbri-Destro & Rizzolatti, 2008). This supports the notion that mirror neurons allow humans to execute new motor patterns based on the visual information presented by an execution model (C. Heyes, 2001; Vogt, 2002). Therefore, mirror neurons may be the neural basis of observational motor learning, eliciting motor programs that resemble the observed action by activating the motor resonance mechanism (Cattaneo & Rizzolatti, 2009).

When action execution and action observation happen at the same time, there is an interaction between the two processes (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Craighero et al., 2002). The motor resonance mechanism might explain the influence that perception exerts over action, since it activates motor programs similar to the observed motor pattern. However, this mechanism does not account for the interaction between action execution and action perception. An alternative mechanism has been proposed by Schutz-Bosbach & Prinz, suggesting the existence of a perceptual resonance mechanism, which would activate a perceptual copy of the executed motor commands (Schutz-Bosbach & Prinz, 2007). Interestingly, this mechanism becomes active when someone is asked to predict the unseen outcome of an observed action (Canal-Bruland & Williams, 2010).

Both motor and the perceptual resonance mechanisms become active during the performance of an observational motor learning protocol, the former during action observation and the later during action execution. Thus, mirror neurons may be the neurophysiological basis of observational motor learning (Cattaneo & Rizzolatti, 2009; Fabbri-Destro & Rizzolatti, 2008) and may play a role in both the motor and perceptual performance benefits achieved by observational motor learning (Lago-Rodríguez et al., 2013).

Motor and perceptual resonance mechanisms as internal models

Motor and perceptual resonance mechanisms share similarities with the theory of internal models proposed by Wolpert et al. (Miall & Wolpert, 1996; Wolpert, 1997; Wolpert, Ghahramani, & Jordan, 1995). Inverse models generate motor commands that lead to a desired trajectory (Jordan, 1996). Conversely, forward models have been suggested to predict sensory consequences of a desired motor command (Miall & Wolpert, 1996). Thus, the motor resonance mechanism may work as an inverse model, which activates motor programs that mirror the observed action. The perceptual resonance mechanism on the other hand resembles a forward model, which triggers sensory consequences associated with the observed action. To activate sensory consequences, the perceptual resonance mechanism uses motor commands triggered by the motor resonance mechanism. Interestingly, the cerebellum has been proposed as the generator of both inverse and forward models (Wolpert, Miall, & Kawato, 1998), and has been described as part of the MNS (Molenberghs et al., 2012). This supports the notion of the cerebellum as a part of a “mirror” loop during action observation (Miall, 2003).

Studies of the MNS have reported MEP suppression during the observation of a needle entering body parts of another person (Avenanti, Bueti, Galati, & Aglioti, 2005; Avenanti, Minio-Paluello, Sforza, & Aglioti, 2009; Fecteau,

Pascual-Leone, & Theoret, 2008), and MEP facilitation during the observation of bio-mechanically impossible movements (Avenanti, Bolognini, Maravita, & Aglioti, 2007; Romani, Cesari, Urgesi, Facchini, & Aglioti, 2005). This modulation was specific to those muscles that were observed to be painfully stimulated (Avenanti, Minio-Paluello, Bufalari, & Aglioti, 2006; Avenanti et al., 2009). Moreover, cortico-cortical connectivity between the ventral premotor cortex (PMv) and the primary motor cortex (M1) is modulated during observation of grasping actions according to the type of observed action (Lago et al., 2010). In this study PMv-M1 connectivity was modulated when subjects observed a naturalistic grasping action, but not when the observed grasping action was performed towards a noxious object (e.g.: soldering iron). Altogether, these results suggest that the activation of mirror neurons during action observation is modulated by potential afferences elicited in the observer by the observed action (Avenanti et al., 2007; Lago et al., 2010). One possible explanation is that by activating forward models within the cerebellum (Miall, 2003), the perceptual resonance mechanism predicts sensory consequences of the observed action based on motor commands triggered by the motor resonance mechanism.

Furthermore, activation of forward models during action observation could account for higher anticipatory skills described in expert athletes for sport-specific actions (Abernethy, 1990; Goulet et al., 1989; Müller et al., 2006; Savelsbergh et al., 2002; Williams et al., 2002). This means that action-specific sensory consequences predicted by forward models are available for cognitive processes that are independent from motor control (Miall et al., 2006), for instance to predict future states of the observed action. Moreover visuo-motor experience (e.g.: observational motor learning) results in more accurate motor commands. Thus, it is likely that improved motor programs after observational motor learning leads to more accurate sensory predictions by forward models, based on motor programs activated by the motor resonance mechanism. This is in line with evidence showing that the ability to predict the outcome of an observed dart throwing action is higher when observers are presented with their own movement pattern (Knoblich & Flach, 2001), since predicted sensory consequences are based on the same motor commands that the subject is observing.

CONCLUSIONS

In conclusion, mirror neurons code both executed and observed actions by activating the motor- and perceptual-resonance mechanism. Thus, mirror neurons could play a role in the motor and perceptual improvements achieved by observational motor learning. Motor- and perceptual-resonance

mechanisms may rely on the activation of inverse and forward models, respectively. Based on the critical role that the cerebellum has in generating internal models, future studies should evaluate potential involvement of cortico-cerebellar loops in observational motor learning, as well as possible modulations of these brain pathways as a result of observational motor learning. In addition, it is also possible that some of the properties that distinguish expert sports people from beginners, such as a better anticipatory skills, rely on a higher specialization/activation of the mirror neuron system.

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