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Review

From monkey mirror neurons to primate behaviours: possible 'direct' and 'indirect' pathways

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The discovery of mirror neurons (MNs), deemed to be at the basis of action understanding, could constitute the potential solution to the 'correspondence problem' between one's own and others' action that is crucial for of imitative behaviours. However, it is still to be clarified whether, and how, several imitative phenomena, differing in terms of complexity and cognitive effort, could be explained within a unified framework based on MNs. Here we propose that MNs could differently contribute to distinct imitative behaviours by means of two anatomo-functional pathways, subjected to changes during development. A 'direct mirror pathway', directly influencing the descending motor output, would be responsible for neonatal and automatic imitation. This proposal is corroborated by some new behavioural evidences provided here. During development, the increased control of voluntary movements and the capacity to efficiently suppress automatic motor activation during action observation assign to the core MNs regions essentially perceptuo-cognitive functions. These functions would be exploited by an 'indirect mirror pathway' from the core regions of the MN system to prefrontal cortex. This latter would play a key role in parsing, storing and organizing motor representations, allowing the emergence of more efficient and complex imitative behaviours such as response facilitation and true imitation.

Keywords: imitation; motor cognition; development

1. INTRODUCTION

One of the most important advances of our knowledge about the primate cerebral cortex is that perceptual and motor processes often share a common code. This view is now widely accepted, despite the classical and very influential theoretical grounding of electrophysiological brain research (Woolsey *et al.* 1952; Evarts 1968) supporting the idea that perceptual and motor functions are anatomically segregated in the cerebral cortex.

The discovery in the monkey premotor cortex of neurons having not only motor, but also somatosensory and visual responses (Gentilucci *et al.* 1983, 1988; Rizzolatti *et al.* 1988; Graziano *et al.* 1994, 1999; Fogassi *et al.* 1996, 1999) showed that the motor cortex has both sensory and motor properties and that it can also play a role in cognitive functions (Rizzolatti *et al.* 2002; Jeannerod 2006). Particularly intriguing is the discovery of a peculiar class of ventral premotor (PMv) neurons, called mirror neurons (MNs) (di Pellegrino *et al.* 1992; Gallese *et al.* 1996; Rizzolatti *et al.* 1996*a*,*b*), that discharge during both observation and execution of a motor act. In other words, the observer's motor representation 'resonates' while observing another agent performing a correspondent act. Subsequent studies revealed the existence of a mirror system also in humans (Fadiga *et al.* 1995; Grafton *et al.* 1996; Rizzolatti *et al.* 1996*a*,*b*; Hari *et al.* 1998; Iacoboni *et al.* 1999, 2001; Nishitani & Hari 2000, 2002; Buccino *et al.* 2001; Decety *et al.* 2002; Koski *et al.* 2002, 2003; Grezes *et al.* 2003). These findings challenged the classical view of segregated sensory and motor functions, indicating that perception and action can share the same neuronal substrates. More importantly, this discovery attracted the attention of scientists from many disciplines because of its possible implications in explaining different aspects of primate social cognition.

One of the first proposals on the role of MNs was that they serve action understanding and imitation (Jeannerod 1994; Rizzolatti *et al.* 2001). The former hypothesis, despite some exception (Brass *et al.* 2007; Csibra 2007; Csibra & Gergely 2007), has been generally accepted, while the latter has not yet found a general consensus because of the widely accepted view

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One contribution of 13 to a Theme Issue 'Evolution, development and intentional control of imitation'.

that monkeys do not imitate (Visalberghi & Fragaszy 1990). However, the term ‘imitation’ is frequently used to refer to several behavioural phenomena requiring different degrees of cognitive processing (Visalberghi & Fragaszy 1990; Byrne & Russon 1998), very likely subserved by different neurophysiological mechanisms. Following this view, despite the lack of evidence about ‘true imitation’ in monkeys, several different imitative behaviours are nonetheless shared by most primate species and even by other non-primate animals (Zentall 2006). Imitative behaviours rely on the capacity of an observer to translate some aspects of the other agent’s behaviour into motor programmes enabling him/her to reproduce the observed movements (Byrne 2003). This so-called ‘correspondence problem’ between one’s own and others’ movement (Heyes 2001; Brass & Heyes 2005) can be solved by the automatic activation in the observer’s brain of the motor representations corresponding to the observed movements.

In this article, we will argue that the MN system constitutes the grounding substrate of all imitative behaviours, since it allows those basic forms of automatic recognition of others’ acts and motor intentions that are crucial for copying them. We propose that MNs could differently contribute to distinct imitative behaviours, either directly influencing the motor output through a ‘direct pathway’ or working together with other cortical structures exploiting their properties through an ‘indirect pathway’. We will also provide new behavioural evidence that early forms of imitation in newborns can rely on a direct pathway. Finally, we will attempt to outline a model in which the relative contribution of the two distinct pathways (direct and indirect) could account for the role of the MN system in imitative behaviours through a developmental perspective.

2. WHAT MIRROR NEURONS CAN TELL US ABOUT MONKEY UNDERSTANDING OF THE SOCIAL WORLD

MNs have been initially found in the ventral premotor area F5 (di Pellegrino *et al.* 1992; Gallese *et al.* 1996; Rizzolatti *et al.* 1996*a*,*b*; Ferrari *et al.* 2003) and subsequently in the inferior parietal lobule (IPL) (Gallese *et al.* 2002; Fogassi *et al.* 2005; Rozzi *et al.* 2008) of the macaque monkey. The main feature of these neurons is that they discharge both when the monkey performs a motor act (e.g. grasping an object) and when it observes the same, or a similar act, performed by an experimenter or another monkey (figure 1). Interestingly, they do not respond when the monkey observes similar biological movements mimicked in the absence of a target. These findings suggest that their discharge is not related to simple body parts displacements, but codes the goal of the observed or executed motor acts.

The possibility of matching the visual description of a goal-directed act with its cortical motor representation could allow extraction of important information about others’ action. In fact, about one-third of premotor MNs (‘strictly congruent MNs’) matched the observed act both in terms of its motor goal (e.g. grasping) and of *how* it is achieved (i.e. grasping with the whole hand or with a precision grip). The majority (‘broadly congruent MNs’) instead showed a broader selectivity for the type of grip during action observation when compared with execution (Gallese *et al.* 1996; Rizzolatti & Craighero 2004), suggesting that one of their main functions is to allow the observer to understand *what* has been done, that is, the overall goal of others’ acts. This property is not limited to hand actions because in the lateral part of the ventral premotor cortex MNs have been described to respond during the observation and execution of goal-directed and even communicative mouth actions (Ferrari *et al.* 2003).

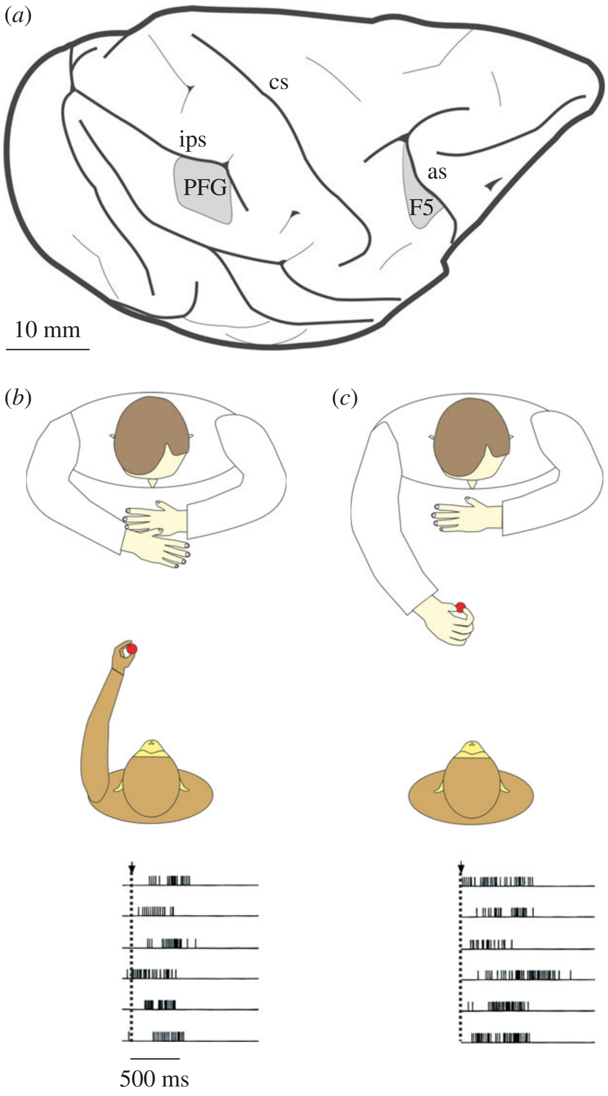

Figure 1. Example of a MN responding during observation and execution of a grasping action. (*a*) Lateral view of the monkey brain. Shaded areas correspond to the ventral premotor area F5 and the inferior parietal area PFG in which MNs have been found. In (*b*) and (*c*), on the top is depicted the experimental condition, on the bottom the neuron discharge. (*b*) The monkey grasps the food. Six trials are shown for each condition. (*c*) The experimenter grasps the food in front of the observing monkey. Every little bar indicates a single action potential. Arrows indicate the grasping onset. Modified from di Pellegrino *et al.* (1992).

The hypothesis that MNs play a key role in action understanding has obtained strong support from a

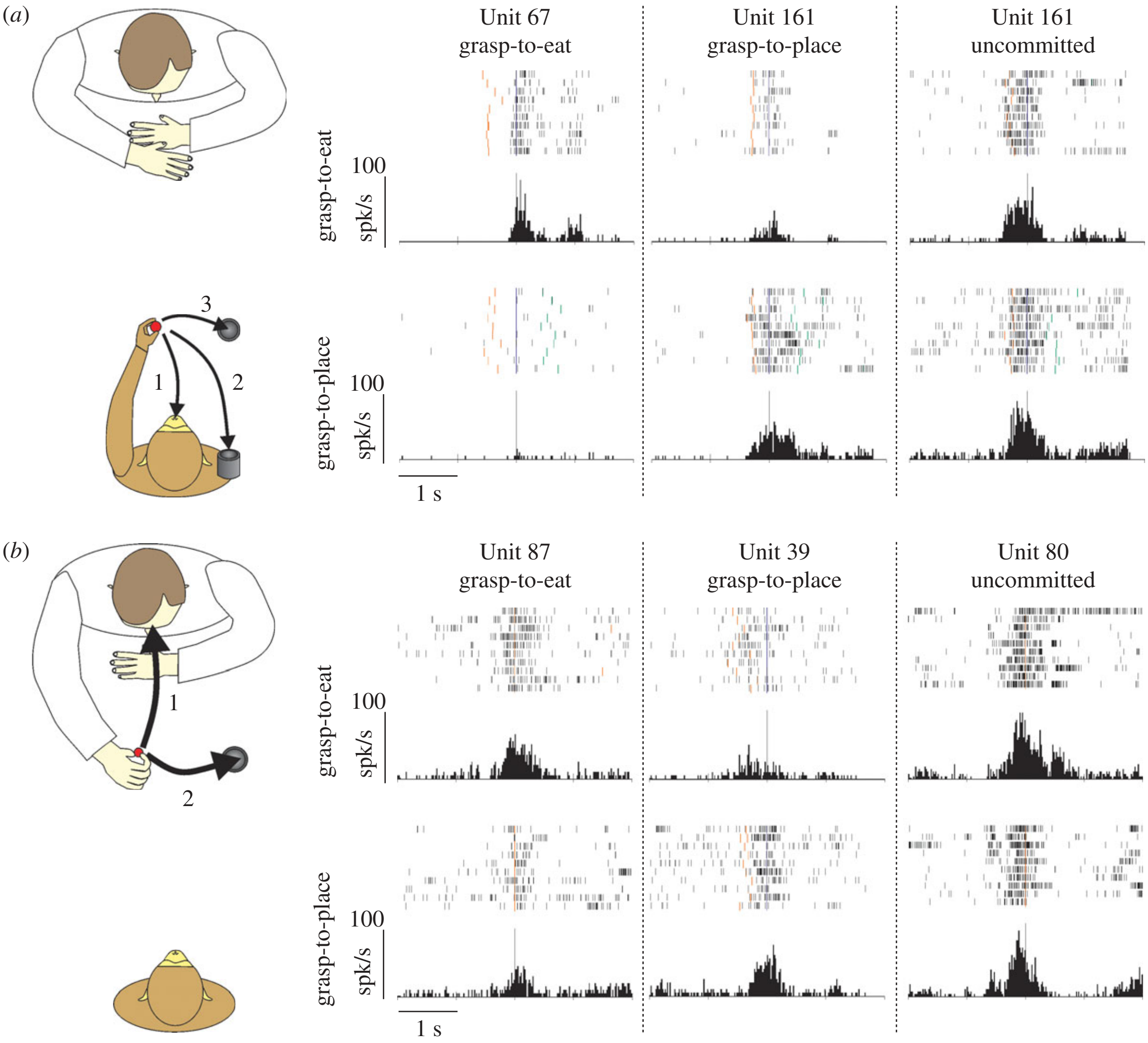

Figure 2. Examples of neurons recorded with the motor and the visual task. (*a*) The paradigm used for the motor task and examples of three IPL motor neurons recorded during grasp-to-eat (1) and grasp-to-place (2, 3). Rasters and histograms are synchronized with the moment when the monkey touched the object to be grasped. Red bars: monkey releases the hand from the starting position. Green bars: monkey touches the container. Abscissa: time, bin = 20 ms; ordinate: discharge frequency in spikes per second (spk/s). (*b*) The paradigm used for the visual task and examples of three IPL mirror neurons recorded during the observation of grasp-to-eat (1) and grasp-to-place (2) done by an experimenter. Rasters and histograms are synchronized with the moment when the experimenter touched the object to be grasped. Conventions as in figure (*a*). Modified from Fogassi *et al.* (2005).

neurophysiological study showing that F5 MNs are activated also when the final part of the observed act, that is, the hand–object interaction, is hidden behind a screen and can therefore only be inferred (Umiltà *et al.* 2001). Interestingly, the discharge was absent when the monkey knew that no object was behind the screen ('mimicked hidden action'), suggesting that when prior contextual information is available, a motor representation can be internally generated despite the absence of a full visual description of the action. In another study, it has been shown that a particular class of F5 MNs, called 'audio-visual MNs', discharges not only during execution and observation of a noisy act (i.e. breaking a peanut), but also by simply listening to the sound produced by that act (Kohler *et al.* 2002), suggesting that the motor representation of an act can be triggered simply by its corresponding auditory consequence.

Goal coding by F5 neurons has been recently re-assessed by Umiltà *et al.* (2008) in macaques. In this study, monkeys were trained to use two different types of tool pliers requiring opposite pattern of finger movements (opening–closure or vice versa) in order to grasp pieces of food. Interestingly, motor neurons in area F5 discharged during the attainment of the goal (grasping the object) independently from both the effector used (i.e. the hand or the pliers) and the sequential pattern of movements performed. Moreover, MNs in these trained monkeys responded to the observation of grasping performed not only with the hand, but also with the pliers. This finding demonstrates that motor learning, besides modifying F5 neuron motor properties, can also affect how MNs generalize their visual response based on the expanded motor knowledge.

The possibility for MNs to code also motor goals that are related to acts outside of monkeys' motor repertoire has been recently described (Ferrari *et al.* 2005). A number of MNs specifically firing during the observation of acts made with tools (a stick or pliers) were found after several months of visual exposure to an experimenter using these tools. When tested for the use of the observed tool, monkeys were not able to use it. It has been suggested that the prolonged visual experience promotes the establishment of an association between the tool and the experimenter's hand. According to the authors' interpretation, visual inputs related to stimuli with similar motion (i.e. a moving hand and a tool moved by the hand) and directed to the same target object would access F5 MNs having a specific motor response (usually grasping with both the hand and the mouth), but still uncommitted on the visual side. Thus, the synaptic competition between visual afferences related to tools and biological effectors is solved by the dominance of one of these inputs (in this case, a tool). These types of MNs can be very relevant from an ethological point of view because they may reveal that the behaviours of monkeys that have acquired new skills can be somehow understood by other naive monkeys as goal-directed, through the activation of representations of motor acts aimed at the same goal.

Although a wide consensus does exist as far as MNs properties are concerned, criticisms have been raised about their putative role in action understanding (Brass *et al.* 2007; Csibra 2007; Csibra & Gergely 2007). Their alternative proposal states that action understanding could be the cause rather than the consequence of MNs' activation. In this view, other regions lacking mirror properties would be responsible for integrating contextual information, providing action and intention understanding by means of inferential processes. Subsequently, these 'non-mirror' regions would activate MNs resulting in a top-down-generated emulation process in which 'action mirroring does not follow but anticipates ongoing actions and enables *predictive tracking* and *action coordination with others*' (Csibra 2007). This perspective appears to us untenable for several reasons. First, it is difficult to understand why it would be necessary to activate one's own motor representation, when others' behaviour has been already interpreted and fully understood by higher order inferential mechanisms. Second, the suggestion of MNs' involvement in predictive tracking leads to the hypothesis that MNs' visual discharge is anticipated with respect to the motor discharge, because its motor content should be predictively activated. This is in contrast to the observation that visual and motor timing of discharge tightly correspond, as is shown in several works on MNs (Gallese *et al.* 1996; Kohler *et al.* 2002; Ferrari *et al.* 2003; Fogassi *et al.* 2005). Third, the hypothesis that MNs provide the substrate for predictive emulation of observed action by means of its reconstruction at a low (kinematic) level (Csibra 2007) does not reconcile with the empirical data in the monkey showing that in the great majority of MNs the visual discharge is more unspecific than the motor discharge. For example, a MN can activate when the monkey *observes* a grasping motor act, independently of whether this consists of a precision grip or a power grasp, while it activates only for precision grip during motor execution (Gallese *et al.* 1996; Rizzolatti *et al.* 1996*a*,*b*; Ferrari *et al.* 2005). All these considerations appear to us more coherent with the view that MNs directly code the goal of observed and executed motor acts (e.g. 'grasping').

We do not deny the existence of neuronal substrates possibly responsible for specific 'inferential processes', expecially when novel or implausible actions are investigated by means of functional magnetic resonance imaging (fMRI) in humans (Brass *et al.* 2007). However, even in this case, the MN system is activated in the different conditions encoding the goal of the observed act (Kilner & Frith 2008), that is, 'switching on the light with the leg', since it is the same in all conditions. The subtraction between conditions simply eliminates this activation, so that this procedure correctly identifies the brain areas likely involved in the inferential processes in which the subject has to come out with a reason 'why an individual is switching on the light in such a bizarre way'. That is an essentially different concept from that of 'motor goal' we are focusing on.

Beyond coding the goal of motor acts, recent neurophysiological findings show that MNs could also enable the monkey to infer others' motor intentions, that is, predicting *why* an individual is doing something. In a series of experiments (Fogassi *et al.* 2005, 2007), neuronal activity was recorded from inferior parietal and ventral premotor grasping MNs while the monkey executed a motor task and observed the same task performed by an experimenter. The task consisted of two basic conditions: grasping a piece of food, or an object, either to eat (in the case of food) or to place (in the case of the object). Thus, the first part of the task (grasping the target) was identical in the two conditions. In spite of this, the results showed that the great majority of both parietal and premotor MNs discharged differently during both execution (figure 2*a*) and observation (figure 2*b*) of a grasping act according to the goal of the action in which the act was embedded. This finding indicates that the action goal could be coded well before the beginning of the subsequent motor act specifying that action (either eating or placing). This may not be surprising during execution because the monkey knows in advance the goal of its own action. However, because in the case of the visual task the preference for the action goal was present already during the initial phase of the observed action, it has been suggested that these MNs could provide the neural basis for a simple mechanism for understanding others' intentions. Contextual information and previous experience of the observer with other individuals acting in that context might provide sufficient clues to activate the correct motor representation of the impending action.

A recent study (Caggiano *et al.* 2009) suggests that MNs not only provide an individual with a basic neural mechanism for understanding others' actions, but they could also play a role in social interaction. In fact, this work shows that part of ventral premotor MNs discharged stronger when an experimenter grasped a piece of food within the monkey's peripersonal operant space than when he grasped the same piece of food in the extrapersonal far space. Other neurons behaved in the opposite way, coding others' actions only when performed in the extrapersonal space. Interestingly, when the monkey's operant space was limited by a barrier, extrapersonal MNs started discharging strongly also within the peripersonal space, despite the fact that the distance between the experimenter's action and the monkey has not changed. Taken together, these data suggest that MNs could code other's actions within different operative spaces, probably related to the possibility to socially interact with others.

(a) *Behavioural evidence of action recognition in monkeys and other primates*

The discovery of MNs has provided evidence of a neuronal mechanism in the monkey brain which allows recognition and immediate understanding of others' motor acts and actions. However, the question is whether there is any behavioural evidence that monkeys are actually able to recognize others' actions. The most convincing demonstration of action recognition in monkeys would show that they can *voluntarily* imitate.

The general failure of these attempts has been partially overcome by using a different experimental approach, classically employed in child development studies (Nadel 2002). Instead of requiring monkeys to explicitly repeat a series of actions or gestures shown by an experimenter, we evaluated monkeys response when facing two human experimenters, one imitating the monkeys' object-directed actions (imitator) while the other performed temporally contingent but structurally different object-directed actions (non-imitator; Paukner *et al.* 2005). Results clearly show that macaques gazed more frequently at the imitator than at the non-imitator, thus suggesting that they recognized when they were being imitated. Similar results have been recently obtained in capuchin monkeys (Paukner *et al.* unpublished data). Although indirectly, these data show that monkeys are able to detect contingencies in the social environment structurally matching their own motor behaviour and not simply based on temporal synchronies. Further recent experiments (Rochat *et al.* 2008) employing a preferential looking paradigm have shown that macaque monkeys can recognize efficiently performed actions, but only when they are directed to achieve goals that have become familiar through previous experience.

In addition, it has recently been shown (Lyons *et al.* 2006) that capuchins are able to infer the location of hidden food by observing a human experimenter performing two different actions: (i) to look at and attempt to reach a container in a purposeful manner or (ii) to handle the same container but displaying no goal-directed movement. Capuchins were then required to choose one of the two containers, and they chose the one handled by the experimenter in a purposeful way, showing not only the ability to recognize other's actions, but also the capacity to discriminate between intentional and accidental ones.

Although using different paradigms, chimpanzees and other apes have also been shown to possess a similar imitation recognition capacity (Nielsen *et al.* 2005; Haun & Call 2008). Taken together, these findings show that the ability to match one's own behaviour with that of others is a feature shared by several non-human primate species, very likely relying on a common neural matching mechanism.

3. FROM MIRROR NEURONS TO BEHAVIOUR: 'DIRECT' AND 'INDIRECT' PATHWAYS

The sensorimotor properties of MNs point to an important aspect of the motor system: its capacity to activate motor representations of an action not only while performing it, but also when observing it being performed by another individual. This 'direct matching' of the visual description of other's action with one's own motor repertoire would permit translation of the observed action into the correspondent motor plan (Jeannerod 1994; Rizzolatti *et al.* 2001), thus rendering MNs the potential solution for the 'correspondence problem' between one's own and other's movement deemed to be at the basis of imitative behaviours (Heyes 2001; Brass & Heyes 2005). However, it must be clarified how and to which extent the activity of the MN system could contribute to different imitative behaviours.

Here we argue that MNs can exert an influence on the motor output through two distinct anatomo-functional pathways (figure 3). On the one hand, a direct parieto-premotor pathway underlies others' action understanding and exerts a direct influence on the motor output *during* action observation (figure 3*a*). On the other hand, an indirect pathway (figure 3*b*) linking parietal and premotor areas with ventro-lateral prefrontal cortex (see Tanji & Hoshi 2008) could exploit the sensory-motor representations provided by the mirror regions of the direct pathway for more complex cognitive and behavioural functions, such as those required for delayed imitative behaviours.

(a) *The direct mirror pathway*

Probably, the most convincing phenomenon that seems to imply a direct influence of MNs on behaviour is neonatal imitation (Ferrari *et al.* 2006; Lepage & Théoret 2007). First demonstrated in humans (Meltzoff & Moore 1977, 1983), it has been subsequently shown in apes (Myowa 1996; Myowa-Yamakoshi *et al.* 2004) and monkeys (Ferrari *et al.* 2006).

In both humans and monkeys, neonatal imitation typically involves effectors (tongue and mouth) that the neonate has never had the possibility to visually access. Thus, the main open question concerns how does the infant translate the observed movement into a correspondent motor programme. We hypothesized that this phenomenon can rely on a mirror mechanism present at birth and capable of matching some facial features with an internal motor representation of these features already present at birth (Ferrari *et al.* 2006). In fact, foetuses in the womb often perform tongue and mouth movements (De Vries *et al.* 1984; D'Elia *et al.* 2001; Hata *et al.* 2005) similar to those shown in neonatal imitation experiments.

The existence of an MN system already functioning in the first stages of postnatal development has also been investigated in human infants by means of electroencephalography (EEG). Similar to adults, six-month-old infants showed a desynchronization of

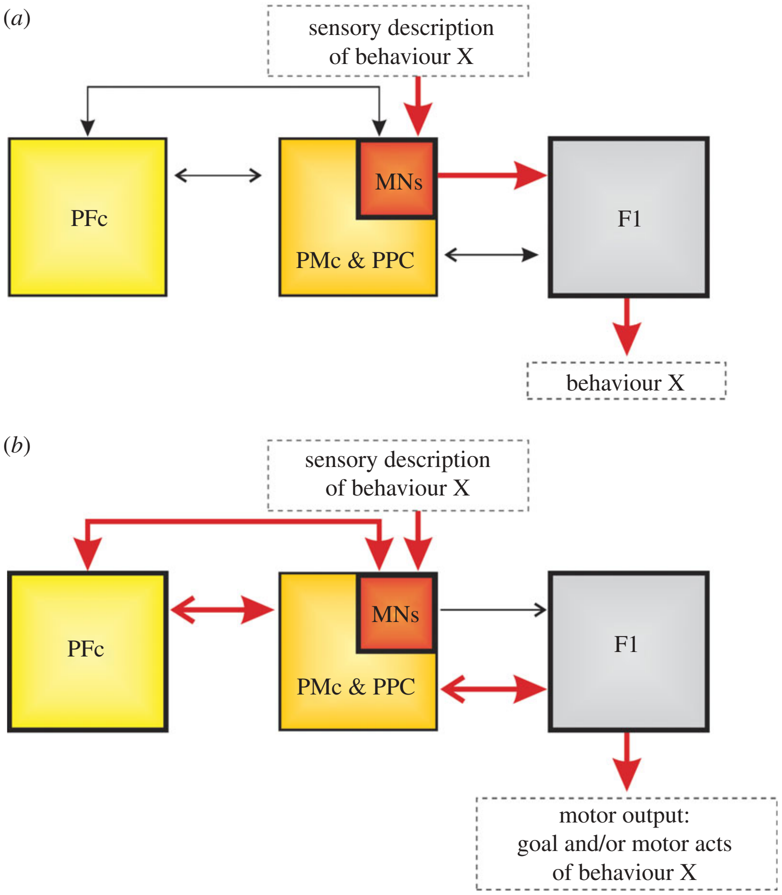

Figure 3. Schematic view of the direct and indirect mirror pathways described in the text. Each box represents an area or an anatomo-functional circuit. In the case of MNs, the box refers to the circuit including both F5 and PFG cortical areas. In the case of motor neurons, the box labelled ‘PMc & PPC’ refers to both premotor and posterior parietal regions included in the cortical motor system. The anatomical connections and the weight of the information flow are depicted by the thickness of the arrows. (*a*) *Direct mirror pathway.* The red arrows indicate that the visual information is activating the mirror areas and that the activation of these areas have their main output on the descending motor pathways involving mainly the primary motor cortex (F1). Note that the anatomical connections between prefrontal cortical and motor and mirror areas exist although they are not fully functional (Fuster 2002). (*b*) *Indirect mirror pathway.* The activation of the mirror system has a reduced or suppressed direct influence on the primary motor cortex (black thin arrow). Its activation instead provides information (red thick arrows) about action goals and motor acts to prefrontal cortical areas (PFc) that in turn integrate it with motivational and contextual factors in order to select, organize and/or keep active the actions correspondent to the observed ones, in terms of general goal and/or the motor patterns.

the mu rhythm (a rhythm correlated to sensorimotor activation) during the observation of goal-directed movements (Shimada & Hiraki 2006; Lepage & Théoret 2007; Nyström 2008), possibly as a result of early MNs activity. More recently, we explored EEG responses to facial gestures in one-week-old infant macaques who showed significant suppression of an alpha rhythm (falling between 3 and 5 Hz frequency band in infant macaques) when compared with control stimuli (Ferrari *et al.* 2008). As this inhibition seems to reflect the activation of areas recorded in the central-parietal motor regions, although preliminary, this finding would indicate that the MN system is selectively sensitive to biologically meaningful stimuli already at a very early age.

In a previous study, we investigated the imitative capacity of infant macaques showing that they could imitate two basic facial gestures, namely, tongue protrusion and lip-smacking (figure 4*a*,*b*). In particular, we demonstrated that infant macaques increased the frequency of mouth movements when observing similar movements performed by the experimenter, and this effect was significantly higher than when observing other biological (i.e. eye blink or hand opening) and non-biological (i.e. rotating disc) movements (Ferrari *et al.* 2006).

Here we explored more in depth whether the neonatal imitative response could result from a direct activation of MNs by investigating the latencies of mouth opening when infant macaques observed mouth movements when compared with non-biological disc movements. We hypothesized that viewing the movement of a natural effector (i.e. the mouth) should directly activate corresponding motor programmes within a time interval that is compatible with that of MNs discharge (i.e. within few hundreds of milliseconds from the observed agent movement onset). Furthermore, we expected that a non-biological effector should have been less effective in triggering such responses.

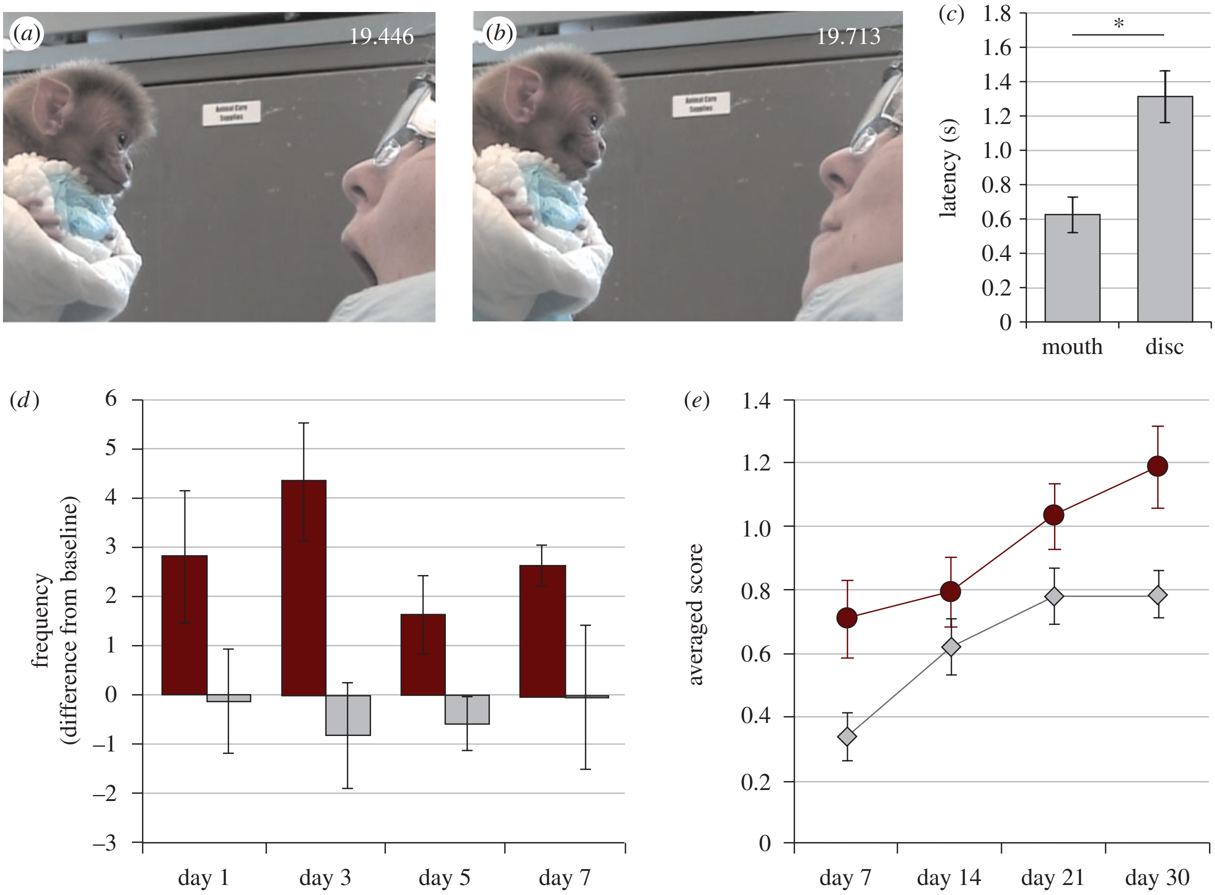

Figure 4. Neonatal imitation of tongue protrusion in a 3-day-old rhesus macaque. The two pictures are taken from a tape. (*a*) The gesture made by the model (open mouth) is depicted. (*b*) Picture taken about 270 ms after the first one. The gesture made by the model was repeated seven to eight times in a period of 20 s. (*c*) Latency of 1–8-day-old infant macaques to mouth opening in the MO and DISC conditions. $^*p<0.05$. (*d*) Averaged scores (difference in frequency between stimulus period and baseline) ± s.e.m. of infant macaques responding to lip-smacking gesture tested on different postpartum days. Infant macaques have been categorized into two groups, imitators and non-imitators, according to their consistent imitative lip-smacking response towards the model on different testing days. Modified from Ferrari *et al.* (in press). Black bars, imitators; grey bars, non-imitators. (*e*) The frequency scores of infant macaques reaching and grasping obtained during neurobehavioural assessment in the first month of life. Infants have been assigned to one of the two categories (imitators/non-imitators) according to their consistent imitative responses to lip-smacking during the first week of life. Modified from Ferrari *et al.* (in press). Black circles, imitators; grey diamonds, non-imitators.

We considered 21 infant macaques already employed in the previous study (see Ferrari *et al.* 2006 for details about methods). In the present investigation, we re-analysed the data by taking into account only two experimental conditions: mouth opening (MO, opening and closing the mouth, either at low or high frequency, about seven or 20 openings/20 s), or rotation disc (DISC, a 15 cm diameter plastic disc with a red and black cross painted on it, rotated 90° clock- and anti-clockwise, about seven rotations/20 s). Videotapes (30 Hz sampling rate) were digitally analysed by one coder not blind to the experimental conditions. The infant latency to mouth opening has been considered as the time lag between the stimulus movement onset (both in MO and DISC condition) and the beginning of the infant mouth opening. As a criterion for the analysis, we chose only those trials in which the monkey oriented and looked at the stimulus for 5 s before the stimulus movement onset.

The results show that 12 of the infants tested in the first week of life imitated mouth opening in the stimulus period and nine of them responded also with mouth opening in the DISC condition (Ferrari *et al.* 2006). We recorded a total of 44 mouth responses in the MO condition and 27 in the DISC condition. The great majority of infant mouth responses began before the end of the moving stimulus in the MO but not in the DISC condition (30/44 in MO and 9/27 in DISC, $p<0.007$, Fisher's exact probability test, two-tailed). Furthermore, the latency of mouth opening was much shorter in MO than in the DISC condition ($t=-3.93$, $p<0.001$, two-tailed; see figure 4*c*).

Overall, these findings show that infants' motor behaviours can be facilitated by the ongoing observation of a corresponding behaviour. Moreover, they suggest that neonatal imitative responses, when present, have timing features that are compatible with a direct effect of a MN system already active and directly linked with descending motor pathways, leading to the overt display of the corresponding behaviour. These responses are, however, not always triggered in all animals, suggesting that there are additional factors affecting the hypothesized MN system influences on behaviour. A possible explanation comes from a recent study evidencing the existence of a relationship between the consistency of imitative skills in the first week of life (figure 4*d*) and the subsequent development of manual skills (Ferrari *et al.* in press). In particular, reaching–grasping abilities appear earlier in imitators when compared with non-imitators (figure 4*e*), probably reflecting a different degree of maturation of cortical motor areas. In addition, although speculatively, the correlation between 'being imitator' and 'being skilful hand-users' might be accounted for not only by this anatomo-functional basis, but also by early social factors. In fact, at the evolutionary origin of neonatal imitative responses, there was most likely the necessity to automatically establish, and subsequently sustain, the relation with the caregiver, typically the mother (Ferrari *et al.* 2006).

It is interesting to note that neonatal imitation usually disappears in humans and chimpanzees at about two to three months of age (one week in monkeys), very likely following the development of cortical organization and motor control allowing the inhibition of unwanted movements (Held & Bauer 1967; Bauer & Held 1975; Abravanel & Sigafoos 1984; Ferrari *et al.* in press). Interestingly, at an older age (about nine months of age), intentional forms of imitation, including imitation learning, appear in humans (Meltzoff 1988) but not in monkeys. It is well known that several neural circuits are formed in early development by transient connectivity pattern that do not persist in adulthood or undergo deep reorganization by means of 'pruning' or 'dieback' of inappropriate or non-functional connections (O'Leary 1992; Armand *et al.* 1996). A similar developmental pattern could be hypothesized for explaining the disappearance of neonatal imitation phenomena. In this view, it is plausible that in a basic MN circuit existing at birth, a biological visual input to its core regions directly facilitates the motor output, giving rise to an overt replica of the observed gesture, usually constituted by simple motor patterns. This system would constitute an early functioning 'mirror direct pathway' from sensory representation of the outside social world to prewired cortical motor representations, still lacking fully inhibitory control.

It is also important to emphasize the fact that this direct pathway is fully functional in adults and this has been recently demonstrated by studies on cortico-spinal excitability in humans, where the observation of simple hand movements and actions induced specific subliminal muscle activations as measured with H-reflexes and transcranial magnetic stimulation (Borroni *et al.* 2005, 2008). Interestingly, during observation, motor pathways are subliminally modulated reproducing the motor commands needed to execute the observed movement with high temporal fidelity. Although most of the effects owing to MNs activation in adult primates are suppressed, there are examples in which it is still possible to observe behavioural outcomes directly linked to action observation such as, for example, in the cases of the so-called 'automatic imitation' (Brass *et al.* 2001). Besides laboratory conditions, it has been recently reported in orang-utans in natural context that automatic imitation of facial expressions of play (referred by these authors as facial mimicry) during the observation of conspecifics' similar displays occurs within a second or less (Davila Ross *et al.* 2008). As this behaviour and its function are widespread among primates, it is very likely that it could also be present in monkeys and humans. Other examples suggest the presence of pure visuo-motor facilitation, such as the synchronous behaviours displayed by young chimpanzees observing skilled individuals performing nut-cracking actions (Marshall-Pescini & Whiten 2008). These types of behaviours, although not well investigated, are probably very common among primates and even other taxa. For example, flocks of birds and herds of mammals tend to synchronize their movements during antipredatory responses or feeding activities. This synchronization could rely on automatic motor resonance systems. Doing the same things at the same time has often undoubted advantages for survival as it helps group cohesiveness, increases defensive opportunities against predator and tunes individuals in similar activities (Coussi-Korbel & Fragaszy 1995).

However, in natural contexts, it is usually necessary to inhibit the automatic tendency to overtly reproduce the observed behaviour. This may be one of the reasons why even such very basic types of sensory-motor matching processes, at least in humans, may be subject to flexible changes owing to learning processes (Heyes *et al.* 2005). Recent studies provided also evidence of a dedicated neuronal system responsible for inhibiting the automatic tendency to reproduce others' observed movements (Brass *et al.* 2005; Brass & Haggard 2007; Bien *et al.* in press), a phenomenon that would be a great obstacle in everyday social interaction.

In summary, the direct mirror pathway produces uninhibited motor resonance phenomena such as neonatal imitation, the functional meaning of which is probably that of promoting intersubjective exchanges between mother and infant, favouring the early development of sensory-motor skills and social interaction abilities. Its early disappearance is probably related to an increased voluntary motor control that would allow infants to exploit the representations coded by the MN system to respond in a more adequate and flexible modality to the complex solicitations of the social environment and to better control intentional communication. The maintenance of some simple imitative behaviours in adulthood suggests that the MN system could still directly affect the motor output, enabling individuals of many animal species to coordinate their social activity.

(b) *The indirect mirror pathway*

The behavioural responses that are delayed in time with respect to the observed behaviour can hardly be explained based on the sole activity of MNs. In fact, MNs are active within a short time window depending on the timing of the observed action, and their response is crucial to provide an immediate recognition and automatic understanding of the observed motor events. How then can MNs mediate delayed behavioural responses?

First of all, it must be considered that there are several distinct forms of imitative responses that are delayed in time, and they can be distinguished based on both the complexity of the observed behaviour and on its presence in the observer's motor repertoire. Contagion (Thorpe 1963), response facilitation (Byrne 1994), emulation (Nagell *et al.* 1993) and true imitation (Thorpe 1963; Tomasello & Call 1997) constitute the best-studied categories. Furthermore, we propose that besides requiring a basic form of recognition and understanding of the observed behaviour such as those provided by MNs, all these imitative phenomena rely on additional neural systems working together with the 'core' MNs brain regions.

Essentially, in all primates species including humans, the observation of familiar actions that are already part of the observer's motor repertoire can increase the frequency of re-enactment of the same actions (Voelkl & Huber 2000, 2007; Anderson *et al.* 2004; Ferrari *et al.* 2005, 2006; Paukner & Anderson 2006; Ferrari & Fogassi in press). This phenomenon has been called response facilitation (Byrne 1994; Byrne & Russon 1998; Miklosi 1999). Crucially, the 'facilitated response' matches the observed one in terms of motor goal but not necessarily in terms of motor pattern, even though the same effectors are generally involved. Response facilitation has been reported in many primate species such as capuchin monkeys (Visalberghi & Addessi 2000; Dindo *et al.* 2009), macaques (Ferrari *et al.* 2005) and human children (Addessi *et al.* 2005). Most of the experiments explored feeding behaviours because their presence and huge variability in terms of motor patterns in all primate species provide the opportunity to study them in both natural and laboratory conditions. In these studies, the observation of conspecifics eating food triggers eating behaviour in the observer and can influence the acceptance of novel foods (Visalberghi & Addessi 2000; Addessi *et al.* 2005), the latency (Dindo *et al.* 2009) or the effector used (Voelkl & Huber 2000, 2007) to successfully solve a novel foraging task. Interestingly, eating behaviour in macaques can be facilitated by simply listening to a conspecific eating (Ferrari *et al.* 2005), with no visual access to the copied behaviour. Therefore, the facilitation effect can exploit different sensory modalities and could depend on the activation of representations of actions shared by the observer and the agent. These specific actions would therefore be enhanced and lead to increases in the probability of being performed by the observer.

As described in the previous section, monkeys' MNs can provide an abstract representation of an observed act in terms of its goal even though the sensory description of the action is only partial, such as when the hand–object interaction is hidden (Umiltà *et al.* 2001) or when only the acoustic feedback of the executed act is available (Kohler *et al.* 2002). MNs' activation very likely constitutes the neural basis of most of the cases of contagion or response facilitation. However, this cannot be the only one mechanism, since the observer's feeding behaviour is usually delayed in time with respect to the sensory information related to the others' action, but MNs' discharge is not. Therefore, MNs' motor representation of others' behaviour can turn into a corresponding behaviour whenever other cortical areas involved in planning and integration of motivational and contextual factors are driven by the activation of the MN system.

The neuronal motor representations of behaviour so far reviewed are completely available to the observer in terms of both action goals and the motor acts required to achieve those goals. However, it often happens that in primate social groups, an individual observes a conspecific obtaining a clear advantage when adopting a specific behaviour, possibly acquired through individual learning. In these circumstances, it is obviously more relevant to be able to reproduce the environmental results caused by the other's action rather than to precisely copy the details of his/her movements. In other terms, the observer could focus on the overall goal of the action, thus 'emulating' it rather than truly imitating the specific movement pattern or technique (Nagell *et al.* 1993; Call & Tomasello 1995). Emulating others' actions requires therefore, first of all, the capacity to extract from the observed scene the goal of the motor acts and actions performed by others. As described above, the properties of different classes of MNs (Gallese *et al.* 1996; Umiltà *et al.* 2001; Fogassi *et al.* 2005) can underpin this capacity even though the motor organization of the observer, in some cases, does not match in its motor details the one displayed by the observed agent (Ferrari *et al.* 2005).

Given the time lag between action observation and execution, copying can occur only if other brain structures, anatomically connected with the MNs system, are involved. We propose that delayed imitative phenomena can rely on the activity of prefrontal cortical regions. These regions should not only store the representation of others' goals, but also extract the means–ends relationships necessary for organizing one's own motor repertoire, and their relevance should be higher whenever the most complex forms of imitative behaviours are considered.

The most complex form of imitative behaviour is undoubtedly true imitation (Thorpe 1963). It is mastered by humans but its presence among other primate is still debated (Tomasello & Call 1997; Call *et al.* 2005; Buttelmann *et al.* 2007; Whiten 1998). This capacity allows an observer not only to recognize and copy the goal of others' actions, but also to rapidly acquire the form and the sequence of the observed motor pattern, reproducing them with high fidelity. According to many authors, the single motor elements or their complex organization do not yet belong to the observer motor repertoire, thus resulting in an overall novel action (Tomasello & Call 1997; Visalberghi & Fragaszy 2002).

Brain imaging studies carried out in the last decade, targeting the issue of the neural bases of imitation (Iacoboni 2009), show that the MN system is activated when subjects are required to observe and imitate simple finger movements (Iacoboni *et al.* 1999; Koski *et al.* 2002), goal-related motor acts (Nishitani & Hari 2000) or complex action sequences (Buccino *et al.* 2004; Vogt *et al.* 2007). Recent fMRI experiments in humans (Buccino *et al.* 2004; Vogt *et al.* 2007) studied brain activation when subjects imitated an action outside their own motor repertoire (i.e. playing a guitar chord). Results show activation of the parieto-frontal MN system (the inferior parietal lobule, the dorsal part of PMv and the *pars opercularis* of the inferior frontal gyrus) in all the three phases of the task, namely: observation of the model playing guitar chords, pause in which the observer had to remember the observed chords in order to subsequently reproduce them and actual imitation of the observed chords. Interestingly, during the pause event, there was a strong activation of the middle frontal cortex (area 46) and of areas of the anterior mesial wall. These findings have been interpreted as the need to recruit cortical areas that have the role to decompose the actions into their basic motor elements and then subsequently recombining them into a new action matching the observed one not only in terms of action goal, but also of the specific motor patterns (Vogt *et al.* 2007). Thus, the possible involvement of prefrontal cortices in imitation could be that of (i) parsing the behaviour and reconstructing it in a novel sequence; (ii) maintaining motor programmes active after the visual information is not available anymore; and (iii) removing the inhibition from specific neuronal motor representations to let the action programme run.

The existence of this form of inhibitory control on the motor system is also revealed by studies on patients with frontal lesions (Lhermitte *et al.* 1986; Brass *et al.* 2003). In fact, patients suffering from this condition tend to spontaneously imitate body gestures even in the cases in which they are explicitly requested to inhibit their behaviour. The echopraxic condition owing to prefrontal lesions has been attributed to the lack of inhibitory command to the motor areas, thus supporting the view of the critical function of the prefrontal cortex in controlling the initiation and volitional aspects of behaviour. This is also in line with recent findings provided by brain imaging and transcranial magnetic stimulation studies in healthy humans, suggesting that medial inferior frontal cortex prevents automatic imitation from occurring by inhibiting the right premotor cortex (Bien *et al.* in press).

4. CONCLUSIONS

Several authors have acknowledged the importance of distinguishing different levels among imitative processes (Byrne & Russon 1998; Rizzolatti *et al.* 1999, 2001; Visalberghi & Fragaszy 2002; Byrne 2003, 2005; Meltzoff & Decety 2003; Brass & Heyes 2005; Iacoboni 2009). In our view, the monkey MN system represents an important starting point to understand the possible links between one's own and others' behaviour based on its general properties and neuroanatomical connections.

The MN system could be at the core of a neural network that enables the monkey to understand actions and goals and to copy others' acts and action goals when they are already present in its motor repertoire. Some behaviours, such as neonatal imitation or automatic imitation in adults, could be triggered by MNs' activity because of their direct influence on the motor output (direct mirror pathway).

Other behaviours are indirectly affected by MNs through the involvement of other brain structures to which MN regions are connected. We identify these brain structures as prefrontal cortical regions, which integrate motivational and contextual factors in order to select and organize actions that match the observed ones in terms of motor goal, action goal or, in humans and possibly apes, even motor pattern (indirect mirror pathway).

The relative contribution of these two pathways to imitative behaviours in the course of ontogeny and phylogeny depends on the developmental stage of the cortical regions involved in these pathways, and thus on the possibilities of organization and control of intentional motor behaviour.

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