



## Action Observation and Execution Network: An Extended View

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**Abstract.** The mirror mechanism is a basic mechanism that transforms sensory representations of others' behaviours into one's own motor or visceromotor representations concerning that behaviour. In this review, we examine the different functions of the mirror mechanism according to its location in the brain, with particular emphasis on recent data concerning the prefrontal cortex and the emotional centres.

**Keywords:** mirror mechanism, action understanding, emotion, prefrontal cortex

### 1 Introduction

For many years, the action execution-observation network has been considered mostly formed by reciprocally connected premotor and parietal areas. In particular, in the monkey, the parietal area PFG and the premotor area F5 were reputed the crucial areas of this network. Functionally, the basic operation of the neurons belonging to these areas was thought to involve a transformation of visual representations of actions into motor representations of the same actions. This transformation was named the Mirror Mechanism. The role attributed to this transformation was that to provide a detailed understanding of others' actions.

In the last few years, evidence was provided that indicates that the action observation network is not limited to the aforementioned areas, but is much more extended and involves additional parietal areas, such as the anterior intraparietal area (AIP), second somatosensory area, primary motor cortex, mesial premotor area F6 and ventral prefrontal areas 46 and 12.

The aim of this review is to describe these new nodes of the circuit, with particular emphasis to their functional role in action execution and observation. We will

first review the anatomy and physiology of the action execution and observation system in the monkey, and then we will compare the anatomical and functional properties of these nodes with those of the human action execution and observation circuit. Finally, we will discuss some emotional centres that have recently been thought to comprise of neurons described endowed with the mirror mechanism.

### 2 Anatomical Organization of the Action Execution-Observation Network in the Monkey

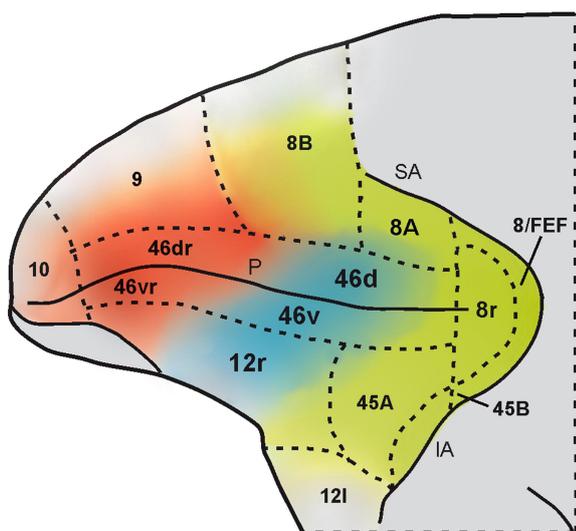
#### 2.1 The Anatomy of the Premotor Nodes of the Action Execution-Observation Network

Fig. 1 shows the architectonic parcellation of the monkey frontal cortex. Among the areas constituting the agranular frontal cortex, the crucial node of the action execution-observation network is area F5. Luppino and co-workers showed that this area is architectonically not homogeneous, but consists of three sub-areas (Belmalih et al., 2009): F5 anterior (F5a), F5 posterior (F5p) and F5 convexity (F5c). Their location is shown in Fig. 1. F5p and F5a are located on the posterior bank of the inferior arcuate sulcus whilst F5c lies on the cortical convexity. Of these sub-areas, F5c and F5p have an agranular structure, while F5a appears to be a transition area towards the prefrontal cortex (Belmalih et al., 2009).

Connectional studies support this architectonic subdivision. In fact, F5c and F5p are strongly connected with the inferior parietal lobule (IPL), and in particular with areas AIP, PF, PFG and the SII-complex, as well as with the primary motor cortex. Area F5 – especially F5p – projects to the spinal cord. Although F5a, F5c and F5p all have connections with IPL, F5a is the only F5 sub-area connected with the ventrolateral prefrontal

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**Figure 2:** Lateral view of the monkey prefrontal cortex. Dashed lines indicate the architectonic borders. The coloured shadings delimit three groups of areas. Green: areas mostly connected to oculomotor cortical and subcortical centers (Gerbella, Belmalih, Borra, Rozzi & Luppino, 2010, 2013; Borra, Gerbella, Rozzi & Luppino, 2015; Borra, Ferroni et al., 2017); blue: areas mostly connected to skeletomotor cortical and subcortical centers (Borra, Gerbella, Rozzi & Luppino, 2011, 2014; Gerbella, Borra, Tonelli, Rozzi & Luppino, 2013, 2016; Borra, Ferroni et al., 2017); red: areas mostly showing intrinsic prefrontal connections (Borra, Gerbella, Rozzi & Luppino, 2011; Gerbella, Borra, Tonelli, Rozzi & Luppino, 2013; Borra, Ferroni et al., 2017).

Albeit, the intermediate strip of areas 12r and 46v is connected to areas forming the classically described action execution-observation network, each of them showing some specificity in their connections. Area 12r is connected with areas AIP and F5, particularly with F5a. In addition, it is also linked with the SII-complex and with the anterior part of the ventral bank of STS (Borra et al., 2011), possibly corresponding to area LB2, an area active during observation of hand grasping actions (Nelissen et al., 2011). Additional connections were also observed in the middle part of the insula. The adjacent area 46v shows a pattern of connections similar to that of area 12r, displaying connections with areas F5a and AIP, as well as with SII and the insula. In addition, it is strongly connected with area PFG, and to a lesser extent with area F6, cingulate motor area 24 and with the temporal lobe (Gerbella et al., 2013). Note that the connections of area 12r and 46v with the temporal lobe increase ventrally, suggesting a stronger role of ventral prefrontal areas in processing of object visual features. Conversely, the connections with the parietal and pre-motor areas increase dorsally, suggesting a major role for area 46v in controlling motor behaviour.

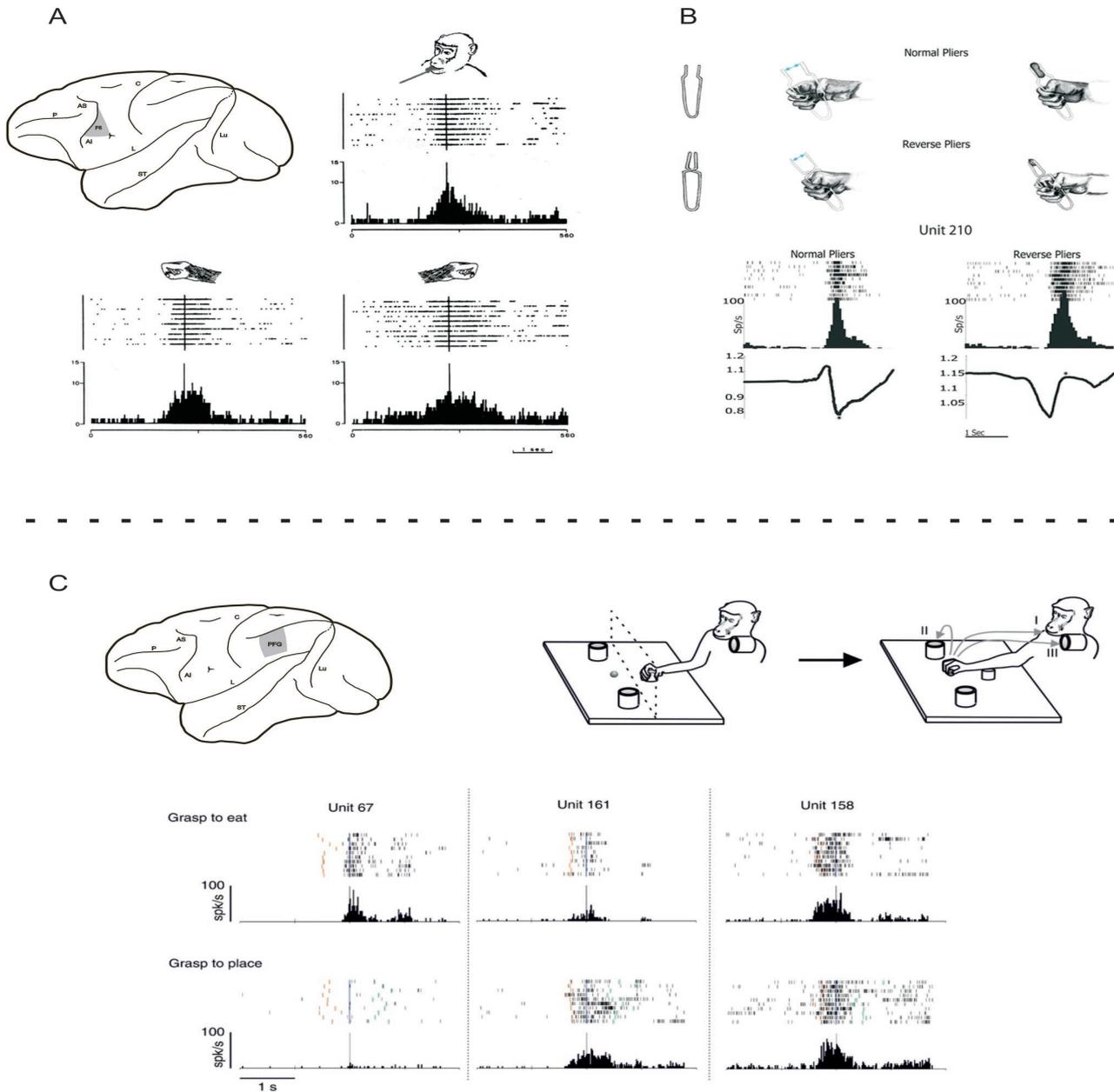
In conclusion, the prefrontal information reaches pre-motor action execution-observation areas through two main gateways: F5a, ventrally, and F6, dorsally.

### 3 Coding Motor Goals: The Vocabulary of Motor Acts

Single neuron studies revealed that most of F5 neurons code specific motor acts, rather than individual movements (Rizzolatti et al., 1988). F5 neurons were subdivided into various classes based on the effective motor act as the classification criterion. Neurons discharging for a specific motor act typically do not discharge during the execution of similar movements aimed at a different goal. For example, a neuron that discharges during finger movements for grasping an object does not discharge during similar movements aimed at scratching. On the other hand, F5 neurons typically discharge when the same goal is achieved by using different effectors (e.g. the right hand, the left hand or the mouth), and thus requiring completely different movements (Fig. 3A).

On this basis it has been proposed that F5 contains a “vocabulary” of motor acts (Rizzolatti et al., 1988). A further demonstration that F5 neurons encode motor acts has been provided by a study (Umiltà et al., 2008) in which the same motor goal (taking possession of food) was achieved by means of opposite movements. Monkeys grasped objects using “normal pliers”, which require hand closure in order to take possession of the object, and “reverse pliers”, that require hand opening to achieve the same goal (Fig. 3B). In both cases, the neural discharge encoded food grasping, regardless of whether it was achieved by closing the hand or by opening it. Similar to area F5, PFG neurons also typically code the goal of the motor acts rather than movements (Gallese et al., 2002; Fogassi et al., 2005; Rozzi et al., 2008).

Subsequent studies addressed the issue of how the intention of an action, i.e., the overarching goal of a series of motor acts, is encoded in both PFG and F5 neurons. With this aim, grasping neurons were recorded in two conditions: in one, the monkey grasped a piece of food and brought it to the mouth for eating, whilst in the other, it grasped an object or a piece of food to place it into a container (Fogassi et al., 2005; Bonini et al., 2010). Some neurons discharged stronger when the monkey grasped food to bring it to its mouth, while a weaker or absent response was observed when it grasped food to put it into a container (Fig. 3C). Other cells had an opposite behaviour (Fig. 3C). Interestingly, the difference in response in the two conditions was already present during grasping that was executed in exactly the same way. The differential activation of these neurons according to the overarching goal, represents the neural substrate of the acting individual intention.



**Figure 3:** Goal and intention encoding in areas F5 and PFG. **A:** Upper part, left: lateral view of the monkey brain showing the location of area F5, right and lower part: discharge of an F5 neuron active during grasping with the mouth, the right hand and the left hand. Conventions as in Fig. 6A. **B:** Example of an F5 neuron discharging during grasping with normal and reverse pliers. Upper part: Pliers and hand movements necessary for grasping with the two types of pliers. Lower part: Rasters and histograms of the neurons' discharge during grasping with pliers. The alignments are with the end of the grasping closure phase (asterisks). The traces below each histogram indicate the hand position, recorded with a potentiometer, expressed as function of the distance between the plier's handles. When the trace goes down, the hand closes, when it goes up, it opens. The values on the vertical axes indicate the voltage change measured with the potentiometer. Other conventions as in Fig. 6A. **C:** Example of a motor neuron in PFG modulated by action intention. Upper part left: lateral view of the monkey brain showing area PFG. Upper part right: paradigm used for the motor task. The monkey, starting from a fixed position, reaches and grasps a piece of food or an object, then it brings the food to the mouth and eats it (I, grasp-to-eat), or places it into a container (II/III, grasp-to-place). Lower part left: Activity of three IPL neurons during grasping in the two actions. Rasters and histograms are aligned 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. Modified from Rizzolatti et al. (1988) (**A**), Umiltà et al. (2008) (**B**) and Fogassi et al. (2005) (**C**).

## 4 Mirror Neurons and Action Understanding

Areas F5 and PFG contain a peculiar class of visuo-motor neurons, the mirror neurons. These neurons discharge, both when the monkey performs a goal-directed motor act and when it observes the same, or a similar, motor act performed by another individual (Fig. 4A; di Pellegrino, Fadiga, Fogassi, Gallese & Rizzolatti, 1992; Gallese, Fadiga, Fogassi & Rizzolatti, 1996; Rizzolatti, Fadiga, Gallese & Fogassi, 1996). Mirror neurons do not respond to object presentation. The observed hand motor acts more effective in eliciting mirror neurons discharge are grasping, manipulating and holding. The visual response of many mirror neurons is invariant with respect to visual aspects of the observed action. However, other mirror neurons show specificity for the direction of the hand movement (left or right), the space sector in which the observed motor act is presented (close or far), or the hand used by the observed agent (left or right) (Caggiano, Fogassi, Rizzolatti & Thier, 2009; Gallese et al., 1996). In terms of the location of the motor act presentation, it was found that half of mirror neurons sensitive to this parameter discharged stronger when the motor act was performed within the monkey's peripersonal space, while the other half responded better when the same motor act was performed in the extra-personal space. Interestingly, when the monkey's peripersonal space (defined as the space within which grasping is possible) was reduced by introducing a transparent barrier, and thus the space was no longer reachable, a set of extra-personal neurons started to discharge within the previously peripersonal space (Caggiano et al., 2009).

It has been proposed that the observation of a motor act done by others determines an automatic retrieval of a potential motor act from the "vocabulary" of the observer, thus enabling mirror neurons to encode the visual description of a goal directed act in motor terms, allowing the observer to understand what another individual is doing. The hypothesis that mirror neurons have an important role in the understanding of others' motor acts has been supported by various studies. In one study, it was shown that grasping mirror neurons discharge not only when the monkey observes a grasping motor act (effective visual stimulus), but also when it sees the agent's hand moving towards the target hidden by an opaque screen (Umiltà et al., 2001). The discharge was absent when the monkey knew that there was no object behind the screen. This finding suggests that mirror neurons use prior information to retrieve the motor representation of the observed motor act.

In another study, sensory information concerning the motor act was presented to the monkey in an acoustic and/or a visual format (Kohler et al., 2002). It was

found that a subset of mirror neurons, called "audio-visual mirror neurons", discharged not only during execution and observation of a motor act (e.g. breaking a peanut), but also by listening to the typical sound produced by that act. This indicates that a motor act is understood regardless of how the information reaches the mirror neurons.

Besides mirror neurons encoding hand motor acts, mouth mirror neurons have been also described. These neurons are mostly found in the lateral part of area F5. The majority of them respond to the observation and execution of ingestive motor acts such as biting, sucking and licking (Ferrari, Gallese, Rizzolatti & Fogassi, 2003; Ferrari, Gerbella, Coudé & Rozzi, 2017). They do not respond to object presentation or to mouth mimed motor acts.

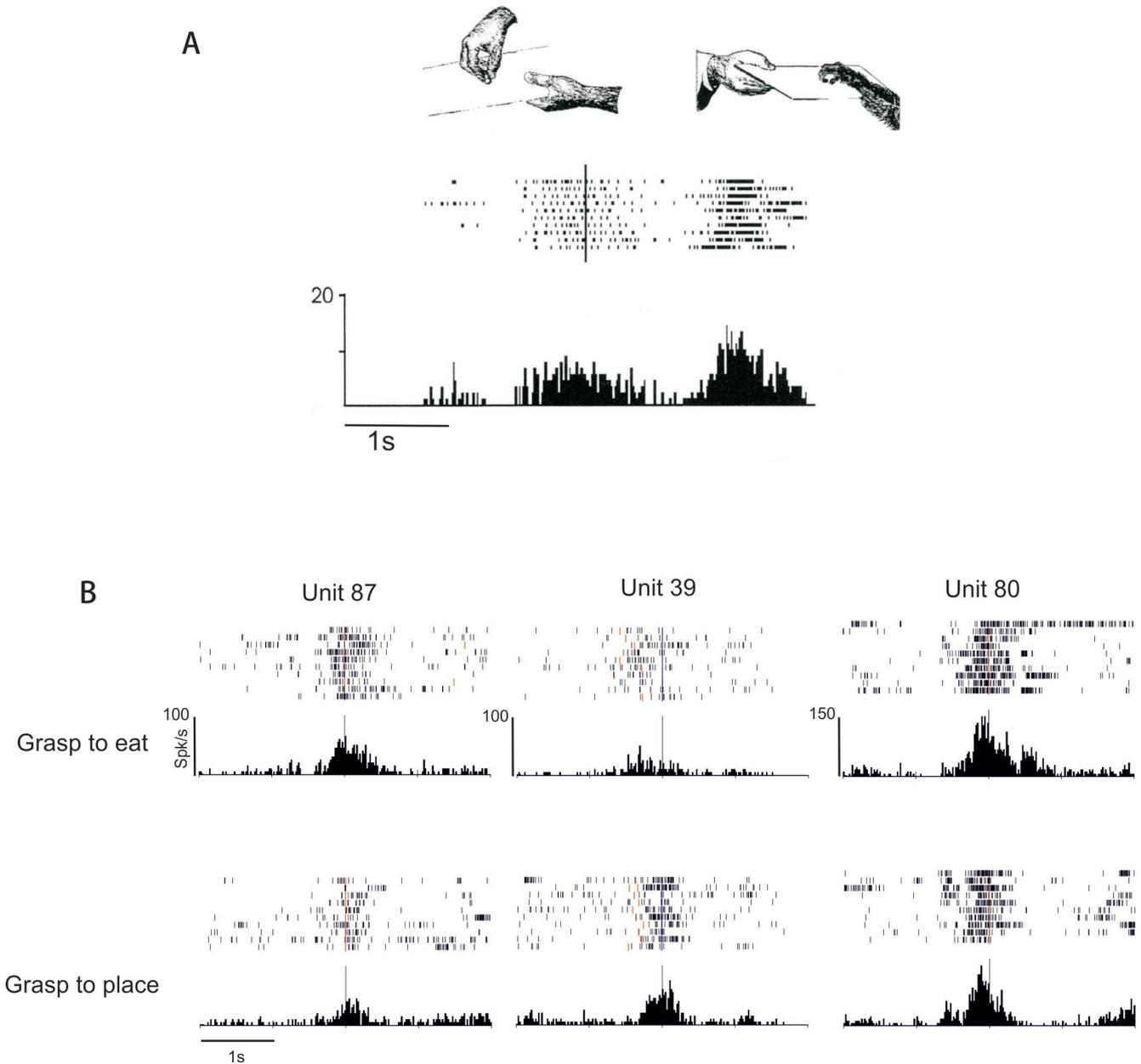
In the previous sections we showed that PFG grasping neurons discharge is modulated by the overarching action intention (Fogassi et al., 2005). For this purpose their activity was recorded while the monkey executed a motor task in which the same motor act (grasping) was embedded into two different actions (grasping to eat and grasping to place). The neurons were also tested with the monkey observing the same task, performed by an experimenter. Similar to the motor task outcome, in the visual task most mirror neurons also discharged differently during grasping, depending on overarching goal of the actions (Fig. 4B). Since in this case grasping was performed by the observed agent, it was suggested that the neuronal selectivity for the action goal during grasping observation activated the chain of motor neurons corresponding to a specific intention. Similar results were also obtained in area F5, where the same paradigm was applied (Bonini et al., 2010).

## 5 Mirror Neurons in Additional Nodes of the Action-Observation Network

### 5.1 Primary Motor Cortex

It has been recently addressed the issue of whether the output of premotor and motor cortex contains neurons endowed with mirror properties. Kraskov and collaborators (Kraskov, Dancause, Quallo, Shepherd & Lemon, 2009) have recently investigated the activity of corticospinal neurons (PTNs) located in both area F5 and F1, in order to address the issue regarding whether the output of premotor and motor cortex contains neurons endowed with mirror properties.

They found that about half of F5 cortico-spinal neurons responded to action observation. Interestingly, about 25% of these PTNs showed a suppression of their discharge when the monkey observed the experimenter grasping an object. The authors suggested that the suppression of the PTNs during grasping observation may play a role in inhibiting the movement of the observer



**Figure 4:** Mirror neurons. **A:** Example of an F5 mirror neuron. Left: Grasping observation. Right: Grasping execution. **B:** Examples of parietal mirror neurons modulated by action motor intention. Activity of three IPL neurons during grasping observation of two actions: grasp-to-eat, and grasp-to place. Rasters and histograms are aligned with the moment when the experimenter touched the object to be grasped. Red bars: experimenter grasps the object. Unit 87 is selective for observation of grasping to eat, while unit 39 is selective for observation of grasping to place. Unit 80 is not selective. Conventions as in Fig. 3. Modified from di Pellegrino, Fadiga, Fogassi, Gallese and Rizzolatti (1992) (A) and Fogassi et al. (2005) (B).

triggered by the observed action.

The same paradigm was applied to F1 PTNs (Kraskov et al., 2009). As in F5, about half of these neurons were modulated during action observation. The majority increased their discharge during action observation (“facilitation-type” mirror neurons), while some reduced or stopped their firing (“suppression-type” mirror neurons). A comparison of the properties of F1 and F5 PTNs

mirror neurons showed that the visual response in F1 was much weaker than in F5. Taken together these data indicate that the understanding of motor goals is not only the function of F5 mirror neurons, but rather of the activation of a complex motor pattern that involves corticospinal tract neurons, including those originating in F1.

## 5.2 Area F6 (Pre-SMA)

Several physiological investigations indicated that area F6 has a role in forwarding prefrontal signals to posterior premotor areas, allowing the transformation of potential actions into actual movements, by determining movement onset based on contextual and motivational information (Gerbella, Rozzi & Rizzolatti, 2017; Borra, Gerbella, Rozzi & Luppino, 2017). This idea is in line with the presence of strong F6 connections with prefrontal, cingulate and premotor areas (Luppino et al., 1993; Morecraft et al., 2012). Recent studies show that F6 also plays a role in social behaviour, forming part of a brain network dedicated to the processing of social interactions (Sliwa & Freiwald, 2017), as well as hosting neurons encoding others' actions (Yoshida, Saito, Iriki & Isoda, 2011, 2012; Livi et al., submitted). In particular, Isoda and co-workers (Yoshida et al., 2011) trained two monkeys to monitor each other's actions for adaptive behavioural planning. In each trial, one monkey was assigned the role of the actor and the other the role of the observer, inverting the role every two trials. They found that F6 and the adjacent cingulate motor cortex, besides containing neurons that discharge during monkey actions, also host neurons that fire during action execution and observation ("mirror" neurons), as well as neurons that fire during the observation of other's actions exclusively ("partner" neurons). In a subsequent experiment, Yoshida et al. (2012) used the same paradigm to analyse the neural activity during actor's error trials. They identified a set of neurons that showed a significant activity increase associated with errors of the monkey actor. Nearly half of these neurons showed activity changes consistent with general reward-omission signals, whereas the remaining neurons specifically responded to another's erroneous actions. These findings are in line with the recent demonstration of "other-predictive neurons" in the cingulate motor cortex (Haroush & Williams, 2015).

Similarly, a recent study (Livi et al., submitted) showed that area F6 hosts neurons selectively encoding objects when they are the target of monkey's grasping action (self-type), another agent's action (other-type), or both (mirror neurons or self-and-other type). This type of code strongly depends on the position of the object in the peripersonal space of both agent and observer. These findings suggests a novel, non-inferential "object-mirroring" mechanism, through which observers could accurately predict another's impending action by recruiting the same motor representation they would activate if they were to act upon the same object in the same context.

## 5.3 Area AIP

As described above, IPL mirror neurons were originally discovered in PFG (Fogassi et al., 2005; Gallese et al., 2002; Rozzi et al., 2008), but were more recently also found in AIP and in SII (Maeda, Ishida, Nakajima, Inase & Murata, 2015; Pani, Theys, Romero & Janssen, 2014; Hihara, Taoka, Tanaka & Iriki, 2015; Lanzilotto et al., submitted).

Although AIP is classically considered to be involved in the visuomotor transformations for grasping, recent data showed that it also contains mirror neurons.

In recent years, three independent studies described the presence of neurons in AIP that are sensitive to action observation (Maeda et al., 2015; Pani et al., 2014; Lanzilotto et al., submitted). In particular, they showed that a set of AIP neurons that are active during grasping execution, is also activated by the observation of a video of the same grasping action seen from a first-person perspective (Maeda et al., 2015; Pani et al., 2014). Interestingly, neural activation was also observed when the hand movement is visible, while object target of the action is not. Lanzilotto et al. (submitted) showed that AIP grasping neurons also activate during observation of other hand manipulative actions observed from a third-person perspective. Altogether, these data indicate that AIP mirror neurons play a crucial role in the visual control of own action and in action understanding.

## 5.4 Area SII

Classical neurophysiological studies performed in macaque monkeys have shown that the secondary somatosensory cortex (SII) is essentially engaged in the processing of somatosensory information. In contrast, subsequent human brain-imaging investigations have revealed the effects of visual and auditory stimuli on SII activity, suggesting the presence of multisensory integration in this region (Keysers et al., 2004; Gazzola & Keysers, 2009). Accordingly, recent deoxyglucose and electrophysiological experiments in monkeys showed that this region is active during manual action execution and observation, particularly when the viewpoint is a first-person perspective (Raos & Savaki, 2016; Ishida, Fornia, Grandi, Umiltà & Gallese, 2013; Hihara et al., 2015). In particular, Hihara and co-workers demonstrated that 30% of SII neurons respond to visual stimuli. About 1/3 of visual neurons respond to the observation of human action. These data and the anatomical connections of SII with many nodes of action observation and execution network (Gerbella, Rozzi & Rizzolatti, 2017; Borra, Gerbella, Rozzi & Luppino, 2017; Bruni et al., 2018) suggest that this region is involved in coding an observer-centred, haptic description of actions.

### 5.5 Ventrolateral Prefrontal Cortex

Social interactions deeply rely on the understanding of others' actions and the predictions of their outcomes. Thus, if the prefrontal cortex has a role in this type of interaction, one could predict the presence of neurons sensitive to others' actions. In recent years, it has been shown that this may be the case for arm actions. Nelissen, Luppino, Vanduffel, Rizzolatti and Orban (2005), in an fMRI monkey experiment, identified a VLPF activation during the observation of grasping actions contrasted with the observation of static controls or scrambled stimuli. The activated areas included areas 46, 45A, and 45B.

Concerning single-neuron studies, Tsunada and Sawaguchi (2012) recorded monkey VLPF neurons selectively activated during the observation of videos showing conspecifics grooming or mounting another monkey and not when the monkeys observed videos in which several conspecifics were present but not interacting. In a recent study, monkeys were trained to observe videos showing arm and hand movements and object motion during a VLPF neuronal activity recording (Simone, Bimbi, Rodà, Fogassi & Rozzi, 2017). Arm and hand movements included goal-directed actions performed by monkeys or humans (e.g., reaching-grasping of food/objects) and non-goal-directed movements performed by humans (e.g., extending an arm or pantomiming the grasping action). The main result was that in areas 12, 46 and 45A, there are neurons responding to the observation of arm movements. The observation of reaching-grasping actions was the most effective stimulus (Fig. 5A). To assess whether the neural discharge to action observation was dependent on visual information, a control task was carried out in which different parts of the actions, including the final goal, were obscured. The response of most of the tested neurons was unaffected by the obscuration (Fig. 5B). Thus, the interpretation of this effect was that these neurons code the goal of the action. This type coding is similar to that demonstrated for premotor mirror neurons. Interestingly, a portion of prefrontal action observation neurons, are mirror neurons, since they also discharged when the monkey performs a grasping action (Simone, Rozzi, Bimbi & Fogassi, 2015).

In addition, this study demonstrated that VLPF neurons can code other features of the observed action, such as the agent (human or monkey) or the perspective from which the action was observed (first- or third-person perspective). In fact, the most effective observed actions were those performed by a monkey, especially from the first-person perspective. A preference for this perspective was found also in mirror neurons of the ventral premotor area F5, which were recorded during monkeys' observation of videos depicting grasping actions

performed by another monkey from three different perspectives (Caggiano et al., 2011).

## 6 Further Nodes of the Action Execution-Observation Network: Indirect Evidence

In a recent study, neural tracers were injected in F5, in PFG/AIP or in both these regions hosting mirror neurons (Bruni et al., 2018). This study allowed the identification of all nodes of the network, including those in which mirror neurons has not been yet described (Fig. 6). For example, projections to both F5 and PFG/AIP sectors containing mirror neurons originate from limbic structures. In particular, connections were found with a portion of the insula where long-train microstimulation evokes forelimb movements (Jezzini, Caruana, Stoianov, Gallese & Rizzolatti, 2012). These projections may provide the action execution and observation network with information related to the internal states underlying executed and observed actions and their affective significance (vitality forms; Di Cesare, Di Gio, Marchi & Rizzolatti, 2015).

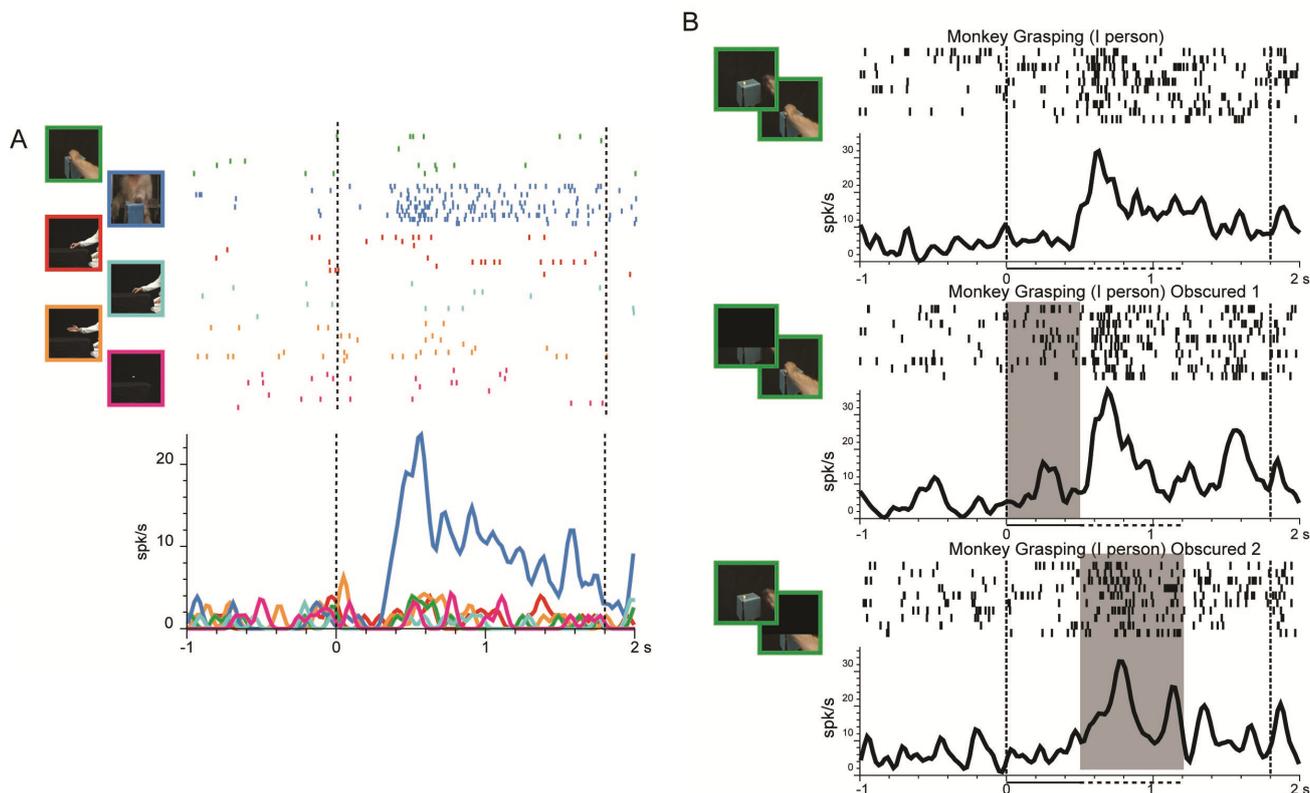
In addition, we identified subcortical connections with specific polysensory and sensory-motor thalamic nuclei (Central lateral, Mediodorsal, and Pulvinar) and with the mid-dorsal claustrum. Furthermore, different areas of the action execution-observation network (F5, PFG/AIP and 12r/46v) project to the same portion of the basal ganglia (Gerbella et al., 2016). The role in the mirror mechanism of these cortical and subcortical nodes has still to be elucidated.

## 7 The Mirror Mechanism in Humans

### 7.1 Goal-Directed Arm, Hand and Mouth Actions

The existence of the mirror mechanism in humans has been demonstrated by a large number of neurophysiological (EEG, MEG and TMS) and neuroimaging (PET and fMRI) studies (Rizzolatti & Craighero, 2004; Caspers, Zilles, Laird & Eickhoff, 2010; Grosbras, Beaton & Eickhoff, 2012; Molenberghs, Cunnington & Mattingley, 2012). These studies have shown that the mirror network mainly includes two regions: the dorsal part of the inferior parietal lobule, comprising the cortex located inside the intraparietal sulcus and the ventral premotor cortex, plus the caudal part of the inferior frontal gyrus (area 44). Additional areas, such as the dorsal premotor cortex and the superior parietal lobule, were also found to be active during action observation (Di Dio et al., 2013; Filimon, Nelson, Hagler & Sereno, 2007).

Similar to monkeys, there is clear evidence from fMRI studies that human mirror sectors encode the goal of motor acts. Gazzola and colleagues (Gazzola, Rizzo-

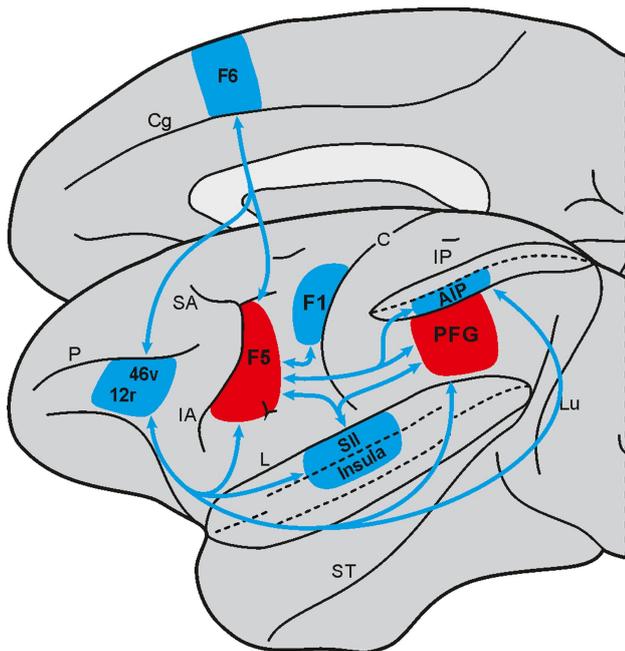


**Figure 5:** Prefrontal neurons responding to action observation. **A:** Neuron responding exclusively during the observation of a monkey grasping a piece of food from a third person perspective. **B:** Example of a neuron discharging during the observation of a monkey grasping an object from a first person perspective (Video Epoch 2), that, with respect to when the video is fully visible (top), does not change its discharge when either the first (middle) or second (bottom) video epoch is obscured. The activity is aligned on the beginning of the video presentation. Abscissae: time (s); Ordinates: firing rate (spikes/s). The shaded areas on rasters and histograms in **B** indicate the timing of obscuration. The horizontal lines under the x-axis indicate the duration of the first (continuous line) and second (dashed line) Video Epochs considered for statistics. Modified from Simone, Bimbi, Rodà, Fogassi and Rozzi (2017).

latti, Wicker & Keysers, 2007) presented volunteers with video-clips depicting either a human or a robot arm grasping objects. The results showed that the parieto-frontal mirror circuit was activated by both these types of stimuli. This observation was extended by Peeters and colleagues (Peeters et al., 2009). They investigated the cortical activations in response to the observation of motor acts performed by a human hand, a robot hand and a variety of tools in both humans and monkeys. Regardless of the type of effector used, the mirror circuit was activated in humans, as well as in monkeys. In humans, the observation of tool motor acts also activated a rostral sector of the left anterior supramarginal gyrus. Such activation was absent in monkeys, even when they observed actions made with the tools they have learned to use.

A series of experiments addressed the issue of the somatotopic organization of the areas endowed with the mirror mechanism (Buccino, Binkofski & Fink, 2001; Wheaton, Thompson, Syngeniotis, Abbott &

Puce, 2004; Wilson, Saygin, Sereno & Iacoboni, 2004; Sakreida, Schubotz, Wolfensteller & von Cramon, 2005; Shmuelof & Zohary, 2005; Ulloa & Pineda, 2007). These studies showed that the observed motor acts are encoded in the precentral gyrus according to a rough somatotopic organization similar to that of the classical motor physiology. A somatotopic organization was found to be also present in the inferior parietal lobule along to and within the intraparietal sulcus. The mouth is located rostrally, the hand in an intermediate position and the leg caudally (Buccino et al., 2001). A recent study by Jastorff, Begliomini, Fabbri-Destro, Rizzolatti and Orban (2010) tried to better define the general principles underlying the somatotopic organization in the parietal and frontal cortex. Four motor acts (grasping, dragging, dropping and pushing) performed with the mouth, hand and foot were presented to volunteers. The results confirmed the data from previous authors concerning the premotor cortex. As for the parietal lobe, they showed that different sectors of IPL were activated



**Figure 6:** Lateral and mesial views of the macaque brain showing the connections between the two main nodes (red) and the additional ones (blue) forming the extended object-grasping network. Abbreviations as in Fig. 1.

by the observation of motor acts having the same behavioural valence, independent of the observed effector. More specifically, there was a subdivision between the localization of self-directed (grasping and dragging) and outward-directed motor acts (dropping and pushing). Therefore, it appears that, while in the premotor cortex motor acts executed with the same effector tends to cluster together, in the parietal cortex the encoding is biased by the action valence.

A few studies also showed that in humans the mirror network is involved in intention understanding (Iacoboni et al., 2005; Ortigue, Sinigaglia, Rizzolatti & Grafton, 2010). In an fMRI experiment Iacoboni and co-workers (Iacoboni et al., 2005) tested volunteers in three conditions: a) “context”; b) “action”; c) “intention”. In the context condition individuals were presented with a scene showing either a “ready breakfast” or a “finished breakfast”; in the action condition, they saw pictures of a hand grasping a mug, without context; in the intention condition, the individuals saw the same hand grasping the mug within one of the two contexts. The context represented the clue that allowed the participants to understand the agent’s intention. The comparison between conditions showed that intention understanding determined the strongest increase in the activity of the mirror system, in particular of its frontal node.

## 7.2 Vitality Forms

Actions might take different forms, for example a hand shaking can be delicate or vigorous. Attention to the “forms” of the observed gestures provides information about the agent’s affective states, moods and attitudes. Stern coined the term “vitality affect” or “vitality form”, in order to highlight that they are routed in our more basic social interactions, thus deeply shaping our experience of ourselves or others (Stern, 1985, 2010).

Vitality form attracted very little attention from neurophysiologists. Recent human functional imaging studies (Di Cesare et al., 2015) have provided evidence that the middle dorsal insula is modulated by the affective aspects of the movements, during both execution and observation of actions. Based on this finding, it has been suggested that during the execution of an action, the dorso-central insula modulates how it is performed according to the affective state of the agent, whereas during action observation it allows the observer to recognize the affective state of the agent. An interesting question points to discovery of the anatomical substrate allowing the insula to modulate the parieto-frontal circuit for action execution and observation. Recent diffusion tensor imaging evidence demonstrated that the dorso-central insula is connected with all the parietal, premotor and prefrontal nodes of the action execution and observation network. The results of this study provided the anatomical pathways through which the insula influences the expression of the affective state of the agent and/or allows recognizing those of the others (Di Cesare et al., 2018).

## 8 Emotions in Humans and Monkeys

### 8.1 Disgust

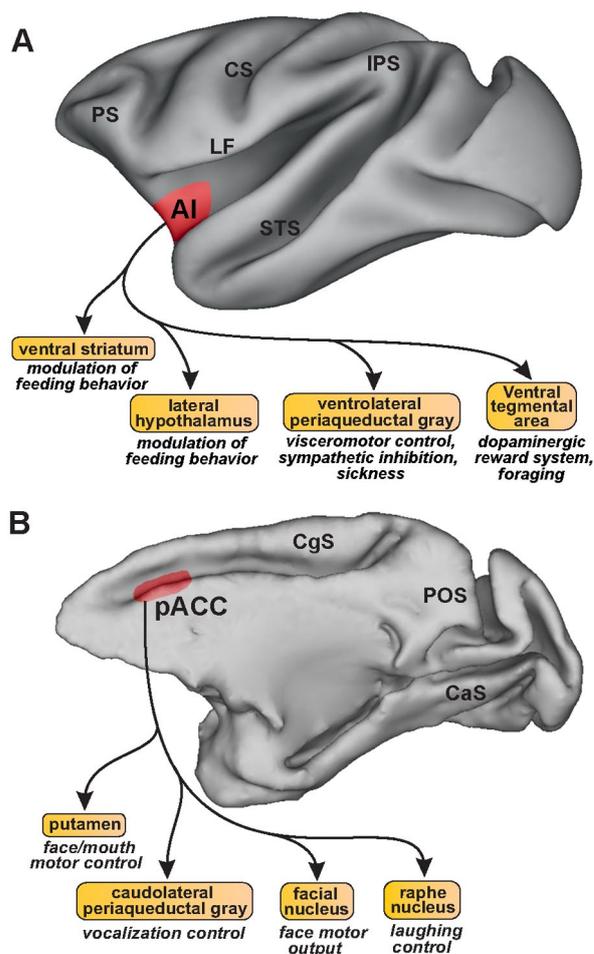
In contrast to the dorso-central part of the insula, its anterior part is involved with oro-alimentary behaviours in both humans and monkeys. In particular, an extensive mapping of the monkey insula using electrical stimulation showed that its anterior sector determines positive or negative ingestive behaviours (Jezzini et al., 2012). In particular, the stimulation of the dorsal part produces a series of mouth and tongue movements typical of food ingestive behaviours; in contrast the stimulation of the ventral sector determines typical disgust behaviours, such as grimaces, spitting out the food, etc. Similar results were found in experiments carried out in drug-resistant epileptic human patients (Krolak-Salmon et al., 2003).

The anterior insula became activated, not only following electrical stimulation, but also after the administration of natural disgusting stimuli, such as unpleasant odors (Wicker et al., 2003). Most interestingly, this fMRI study showed that the anterior insula mediates

both the experience of disgust determined by natural stimuli, and also the observation of someone else expressing disgust (Wicker et al., 2003). More specifically, in some runs of this study participants were exposed to disgusting or pleasant odorants, whereas in other runs they observed short movie clips of other individuals displaying a facial expression of disgust or pleasure. The main finding was that the observation of others' disgust activated the same neuronal substrate within the anterior insula that was activated by first-person exposure to the disgusting odorants. Further evidence supporting the role of the anterior insula in disgust observation and experience comes from lesion studies showing a selective impairment in recognizing disgust from others' faces following insula damage (Calder, Lawrence & Young, 2001). In addition, the deficit for others' disgust was mirrored by an equivalent deficit in the patient's first-person experience of the same emotion. Of particular interest is an observation by Calder and co-workers of a patient with a lesion involving the insula and adjacent putamen. Compared to controls, the patient was less disgusted, or even indifferent to a disgust provoking scenario (Calder, Keane, Manes, Antoun & Young, 2000). The studies described above suggest that the anterior insula is endowed with the mirror mechanism, and when activated determines a complex visceromotor response. The anatomical basis underpinning this behaviour consists of several subcortical centres (Fig. 7A) modulating autonomic reactions for controlling feeding behaviour and visceromotor responses. These centres include the lateral hypothalamus, the ventral tegmental area, the ventral striatum, and the ventrolateral sector of the periaqueductal gray (An, Bandler, Ongür & Price, 1998; Ongür, An & Price, 1998; Jezzini et al., 2015; Venkatraman, Edlow & Immordino-Yang, 2017).

## 8.2 Laughter

The cingulate cortex is another territory that has recently been thought to comprise of neurons endowed with the mirror mechanism. A study carried out by Caruana et al. (2018) on a large number of drug-resistant epileptic patients, showed that there is a specific part of the anterior cingulate cortex whose stimulation determines smiling and laughter, with or without mirth. This region is located in the pregenual sector of the ACC (pACC). Furthermore, since in most patients mirth and merriment accompanies the production of laughter triggered by pACC stimulation, Caruana and co-workers concluded that this region is involved not only in generating the motor aspects of laughter, but also its emotional content. Evidence showing that pACC is a fundamental node for both the production of mirthful laughter, and for encoding observation of this behaviour, is provided by the finding that the same pACC site from which laughter is evoked by electrical



**Figure 7:** Localization and subcortical projections of anterior insula and pregenual anterior cingulate cortex. **A:** Lateral view of the monkey brain showing the anterior insula field in which electrical stimulation induced disgust-related behaviour (red area), and its subcortical projections. **B:** Mesial view of the monkey brain showing the localization of the pregenual sector of the anterior cingulate cortex (red area), and its subcortical projections. Abbreviations as in Fig. 1. Modified from Gerbella, Caruana and Rizzolatti (2017).

stimulation, is also activated (gamma activity) by the presentation of movies showing laughing individuals. In contrast, movies depicting the same individuals expressing sadness, or showing a neutral face, do not elicit any response (Caruana et al., 2017). This evidence suggests that the pACC is endowed with the mirror mechanism, transforming sensory representation of other's laughter into the motor representation of the same behaviour. In line with this result, a meta-analysis of more than one hundred fMRI studies on emotional face processing showed that, when compared to neutral faces, happy faces selectively activate the ACC (Fusar-Poli et al., 2009).

Although there is not clear evidence in humans of the circuit leaving the pACC and reaching the subcortical centres controlling laughing, some inferences can be drawn from monkey anatomical studies. In the monkey the pACC projects to the caudal raphe nucleus, a brainstem structure whose damage may result in an uncontrolled motor pattern of laughing in humans, the so called “Fou rire prodromique” (Hornung, 2003). Additionally, the pACC involves the face/mouth field of the motor putamen, the vocalization centres of the caudolateral part of the periaqueductal gray, and the facial nerve nuclei (Müller-Preuss & Jürgens, 1976; Porriño & Goldman-Rakic, 1982; Devinsky, Morrell & Vogt, 1995; An et al., 1998). These latter projections bilaterally reach both the dorsal and intermediate subnuclei of the bulb, thus controlling upper face muscles, which are those characterizing the “true” emotional laughter (Fig. 7B). If these projections are preserved in evolution, one can depict the nervous network enabling human pACC to produce the complex pattern of visceromotor and motor activations which characterize laughing.

## 9 Conclusion

Traditionally, the motor system was not thought to be involved in cognitive functions, however, the discovery of the mirror mechanism radically changed this view. There is now rich evidence to support that numerous cognitive functions, such as space perception around the body as well as action and emotion recognition, not only require the activity of the motor system, but are also deeply embedded in it. In particular, we showed that both action and emotion understanding rely on potential motor acts that originally evolved for motor behaviour, and subsequently became the substrate for understanding others.

In this review, we discussed evidence indicating that the arm/hand action execution-observation network is not only constituted by classical parieto-frontal areas (F5 and PFG/AIP), but also by additional cortical sectors such as the F6/preSMA and prefrontal areas (12r and 46v). In addition, we described that the mirror mechanism is also present in centres whose primary function is to control emotional behaviour. In particular, we discussed one region controlling a negative emotion, the rostral insula, and one region that controls a positive one, the anterior cingulate cortex.

The data reviewed here could be useful for guiding future studies aimed at discovering other areas endowed with the mirror mechanism, in terms of emotional centres as well as areas involved in motor behaviour without emotional content.

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## References

- An, X., Bandler, R., Ongür, D. & Price, J. L. (1998). Prefrontal cortical projections to longitudinal columns in the midbrain periaqueductal gray in macaque monkeys. *J. Comp. Neurol.* *401*, 455–479.
- Belmalih, A., Borra, E., Contini, M., Gerbella, M., Rozzi, S. & Luppino, G. (2009). Multimodal architectonic subdivision of the rostral part (area F5) of the macaque ventral premotor cortex. *J. Comp. Neurol.* *512*, 183–217.
- Bonini, L., Rozzi, S., Serventi, F. U., Simone, L., Ferrari, P. F. & Fogassi, L. (2010). Ventral premotor and inferior parietal cortices make distinct contribution to action organization and intention understanding. *Cereb Cortex*, *20*, 1372–1385.
- Borra, E., Ferroni, C. G., Gerbella, M., Giorgetti, V., Mangiaracina, C., Rozzi, S. & Luppino, G. (2017). Rostro-caudal Connectional Heterogeneity of the Dorsal Part of the Macaque Prefrontal Area 46. *Cereb Cortex*.
- Borra, E., Gerbella, M., Rozzi, S. & Luppino, G. (2011). Anatomical Evidence for the Involvement of the Macaque Ventrolateral Prefrontal Area 12r in Controlling Goal-Directed Actions. *J. Neurosci.* *31*, 12351–12363.
- Borra, E., Gerbella, M., Rozzi, S. & Luppino, G. (2015). Projections from caudal ventrolateral prefrontal areas to brainstem preoculomotor structures and to basal ganglia and cerebellar oculomotor loops in the macaque. *Cereb Cortex*, *25*, 748–764.
- Borra, E., Gerbella, M., Rozzi, S. & Luppino, G. (2017). The macaque lateral grasping network: A neural substrate for generating purposeful hand actions. *Neurosci Biobehav Rev*, *75*, 65–90.
- Borra, E., Gerbella, M., Rozzi, S., Tonelli, S. & Luppino, G. (2014). Projections to the superior colliculus from inferior parietal, ventral premotor, and ventrolateral prefrontal areas involved in controlling goal-directed hand actions in the macaque. *Cereb Cortex*, *24*, 1054–1065.
- Bruni, S., Gerbella, M., Bonini, L., Borra, E., Coudé, G., Ferrari, P. F., ... Rozzi, S. (2018). Cortical and subcortical connections of parietal and premotor nodes of the monkey hand mirror neuron network. *Brain Struct. Funct.* *223*, 1713–1729.
- Buccino, G., Binkofski, F. & Fink, G. (2001). Action observation activates premotor and parietal areas in a somatotopic manner: an fMRI study. *Eur J Neurosci*, *13*, 400–404.
- Caggiano, V., Fogassi, L., Rizzolatti, G., Pomper, J. K., Thier, P., Giese, M. A. & Casile, A. (2011). View-based encoding of actions in mirror neurons of area

- F5 in macaque premotor cortex. *Curr. Biol.* *21*, 144–148.
- Caggiano, V., Fogassi, L., Rizzolatti, G. & Thier, P. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Sci. (80-. ).* *324*(5925), 403–406.
- Calder, A. J., Keane, J., Manes, F., Antoun, N. & Young, A. W. (2000). Impaired recognition and experience of disgust following brain injury. *Nat Neurosci*, *3*, 1077–1078.
- Calder, A. J., Lawrence, A. D. & Young, A. W. (2001). Neuropsychology of fear and loathing. *Nat Rev Neurosci*, *2*, 352–363.
- Carmichael, S. T. & Price, J. L. (1994). Architectonic subdivision of the orbital and medial prefrontal cortex in the macaque monkey. *J Comp Neurol*, *346*, 366–402.
- Caruana, F., Avanzini, P., Gozzo, F., Pelliccia, V., Casaceli, G. & Rizzolatti, G. (2017). A mirror mechanism for smiling in the anterior cingulate cortex. *Emotion*, *17*, 187–190.
- Caruana, F., Gerbella, M., Avanzini, P., Gozzo, F., Pelliccia, V., Mai, R., ... Rizzolatti, G. (2018). Motor and emotional behaviours elicited by electrical stimulation of the human cingulate cortex. *Brain*, *141*, 3035–3051.
- Caspers, S., Zilles, K., Laird, A. R. & Eickhoff, S. B. (2010). ALE meta-analysis of action observation and imitation in the human brain. *Neuroimage*, *50*, 1148–1167.
- Devinsky, O., Morrell, M. J. & Vogt, B. A. (1995). Contributions of anterior cingulate cortex to behaviour. *Brain*, *118* (Pt 1), 279–306.
- Di Cesare, G., Di Gio, C., Marchi, M. & Rizzolatti, G. (2015). Expressing our internal states and understanding those of others. *Proc Natl Acad Sci U S A*, *112*, 10331–10335.
- Di Cesare, G., Pinardi, C., Carapelli, C., Caruana, F., Marchi, M., Gerbella, M. & Rizzolatti, G. (2018). Insula Connections With the Parieto-Frontal Circuit for Generating Arm Actions in Humans and Macaque Monkeys. *Cereb Cortex*, 1–8.
- Di Dio, C., Di Cesare, G., Higuchi, S., Roberts, N., Vogt, S. & Rizzolatti, G. (2013). The neural correlates of velocity processing during the observation of a biological effector in the parietal and premotor cortex. *Neuroimage*, *64*, 425–436.
- di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V. & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Exp Brain Res*, *91*, 176–180.
- Dum, R. P. & Strick, P. L. (2002). Motor areas in the frontal lobe of the primate. *Physiol Behav*, *77*, 677–682.
- Ferrari, P. F., Gallese, V., Rizzolatti, G. & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *Eur J Neurosci*, *17*, 1703–1714.
- Ferrari, P. F., Gerbella, M., Coudé, G. & Rozzi, S. (2017). Two different mirror neuron networks: The sensorimotor (hand) and limbic (face) pathways. *Neuroscience*, *358*, 300–315.
- Filimon, F., Nelson, J. D., Hagler, D. J. & Sereno, M. I. (2007). Human cortical representations for reaching: mirror neurons for execution, observation, and imagery. *Neuroimage*, *37*, 1315–1328.
- Fogassi, L., Ferrari, P. F., Gesierich, B., Rozzi, S., Chersi, F. & Rizzolatti, G. (2005). Parietal lobe: from action organization to intention understanding. *Sci. (80-. ).* *308*, 662–667.
- Fusar-Poli, P., Placentino, A., Carletti, F., Landi, P., Allen, P., Surguladze, S., ... Politi, P. (2009). Functional atlas of emotional faces processing: a voxel-based meta-analysis of 105 functional magnetic resonance imaging studies. *J Psychiatry Neurosci*, *34*, 418–432.
- Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.
- Gallese, V., Fadiga, L., Fogassi, L. & Rizzolatti, G. (2002). Common mechanism in Perception and Action. In H. Prinz & B. Hommel (Eds.), *Attention and Performance XIX*. Oxford: Oxford University Press.
- Gamberini, M., Passarelli, L., Fattori, P., Zucchelli, M., Bakola, S., Luppino, G. & Galletti, C. (2009). Cortical connections of the visuomotor parietooccipital area V6Ad of the macaque monkey. *J Comp Neurol*, *513*, 622–642.
- Gazzola, V. & Keysers, C. (2009). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: Single-subject analyses of unsmoothed fMRI data. *Cereb Cortex*, *19*, 1239–1255.
- Gazzola, V., Rizzolatti, G., Wicker, B. & Keysers, C. (2007). The anthropomorphic brain: the mirror neuron system responds to human and robotic actions. *Neuroimage*, *35*, 1674–1684.
- Gerbella, M., Belmalih, A., Borra, E., Rozzi, S. & Luppino, G. (2007). Multimodal architectonic subdivision of the caudal ventrolateral prefrontal cortex of the macaque monkey. *Brain Struct Funct*, *212*, 269–301.
- Gerbella, M., Belmalih, A., Borra, E., Rozzi, S. & Luppino, G. (2010). Cortical Connections of the Macaque Caudal Ventrolateral Prefrontal Areas 45A and 45B. *Cereb Cortex*, *20*, 141–168.

- Gerbella, M., Belmalih, A., Borra, E., Rozzi, S. & Lupino, G. (2011). Cortical connections of the anterior (F5a) subdivision of the macaque ventral premotor area F5. *Brain Struct. Funct.* *216*, 43–65.
- Gerbella, M., Borra, E., Mangiaracina, C., Rozzi, S. & Luppino, G. (2016). Evidence for multiple hand-related input channels. *Cereb Cortex*, *26*, 1–20.
- Gerbella, M., Borra, E., Tonelli, S., Rozzi, S. & Lupino, G. (2013). Connectional heterogeneity of the ventral part of the macaque area 46. *Cereb Cortex*, *23*, 967–987.
- Gerbella, M., Caruana, F. & Rizzolatti, G. (2017). Pathways for smiling, disgust and fear recognition in blindsight patients. *Neuropsychologia*.
- Gerbella, M., Rozzi, S. & Rizzolatti, G. (2017). The extended object-grasping network. *Exp Brain Res*, *235*, 2903–2916.
- Grosbras, M. H., Beaton, S. & Eickhoff, S. B. (2012). Brain regions involved in human movement perception: A quantitative voxel-based meta-analysis. *Hum Brain Mapp*, *33*, 431–454.
- Haroush, K. & Williams, Z. M. (2015). Neuronal Prediction of Opponent's Behavior during Cooperative Social Interchange in Primates. *Cell*, *160*, 1233–1245.
- Hihara, S., Taoka, M., Tanaka, M. & Iriki, A. (2015). Visual Responsiveness of Neurons in the Secondary Somatosensory Area and its Surrounding Parietal Operculum Regions in Awake Macaque Monkeys. *Cereb Cortex*, *25*(11), 4535–4350.
- Hornung, J.-P. (2003). The human raphe nuclei and the serotonergic system. *J Chem Neuroanat*, *26*, 331–343.
- Iacoboni, M., Molnar-Szakacs, I., Gallese, V., Buccino, G., Mazziotta, J. C. & Rizzolatti, G. (2005). Grasping the intentions of others with one's own mirror neuron system. *PLoS Biol*, *3*, e79.
- Ishida, H., Fornia, L., Grandi, L. C., Umiltà, M. A. & Gallese, V. (2013). Somato-Motor Haptic Processing in Posterior Inner Perisylvian Region (SII/pIC) of the Macaque Monkey. *PLoS One*, *8*(7), e69931.
- Jastorff, J., Begliomini, C., Fabbri-Destro, M., Rizzolatti, G. & Orban, G. A. (2010). Coding observed motor acts: different organizational principles in the parietal and premotor cortex of humans. *J Neurophysiol*, *104*, 128–140.
- Jezzini, A., Caruana, F., Stoianov, I., Gallese, V. & Rizzolatti, G. (2012). Functional organization of the insula and inner perisylvian regions. *Proc Natl Acad Sci U S A*, *109*, 10077–10082.
- Jezzini, A., Rozzi, S., Borra, E., Gallese, V., Caruana, F. & Gerbella, M. (2015). A shared neural network for emotional expression and perception: an anatomical study in the macaque monkey. *Front Behav Neurosci*, *9*, 1–17.
- Keysers, C., Wicker, B., Gazzola, V., Anton, J.-L., Fogassi, L. & Gallese, V. (2004). A touching sight: SII/PV activation during the observation and experience of touch. *Neuron*, *42*, 335–346.
- Kohler, E., Keysers, C., Umiltà, M. A., Fogassi, L., Gallese, V. & Rizzolatti, G. (2002). Hearing sounds, understanding actions: action representation in mirror neurons. *Sci. (80-. )*. *297*, 846–848.
- Kraskov, A., Dancause, N., Quallo, M. M., Shepherd, S. & Lemon, R. N. (2009). A shared neural network for emotional expression and perception: an anatomical study in the macaque monkey. *Neuron*, *64*, 922–930.
- Krolak-Salmon, P., Hénaff, M.-A., Isnard, J., Tallon-Baudry, C., Guénot, M., Vighetto, A., ... Mauguière, F. (2003). An attention modulated response to disgust in human ventral anterior insula. *Ann Neurol*, *53*, 446–453.
- Lanzilotto, M., Ferroni, C. G., Livi, A., Gerbella, M., Maranesi, M., Borra, E., ... Orban, G. (submitted). Anterior Intraparietal Area: a Hub in the Observed Manipulative Action Network. *Cereb Cortex*.
- Livi, A., Lanzilotto, M., Maranesi, M., Fogassi, L., Rizzolatti, G. & Bonini, L. (submitted). From object to action: agent-based representations in monkey pre-supplementary motor cortex. In *Proceedings of the National Academy of Sciences*.
- Luppino, G., Matelli, M., Camarda, R. & Rizzolatti, G. (1993). Corticocortical connections of area F3 (SMA-proper) and area F6 (pre-SMA) in the macaque monkey. *J Comp Neurol*, *338*, 114–140.
- Maeda, K., Ishida, H., Nakajima, K., Inase, M. & Murata, A. (2015). Functional properties of parietal hand manipulation-related neurons and mirror neurons responding to vision of own hand action. *J Cogn Neurosci*, *27*, 560–572.
- Matelli, M., Camarda, R., Glickstein, M. & Rizzolatti, G. (1986). Afferent and efferent projections of the inferior area 6 in the macaque monkey. *J Comp Neurol*, *251*, 281–298.
- Matelli, M., Luppino, G. & Rizzolatti, G. (1991). Architecture of superior and mesial area 6 and the adjacent cingulate cortex in the macaque monkey. *J Comp Neurol*, *311*, 445–462.
- Molenberghs, P., Cunnington, R. & Mattingley, J. B. (2012). Brain regions with mirror properties: A meta-analysis of 125 human fMRI studies. *Neurosci Biobehav Rev*, *36*, 341–349.

- Morecraft, R. J., Stilwell-Morecraft, K. S., Cipolloni, P. B., Ge, J., McNeal, D. W. & Pandya, D. N. (2012). Cytoarchitecture and cortical connections of the anterior cingulate and adjacent somatomotor fields in the rhesus monkey. *Brain Res Bull*, *87*, 457–497.
- Müller-Preuss, P. & Jürgens, U. (1976). Projections from the “cingular” vocalization area in the squirrel monkey. *Brain Res*, *103*, 29–43.
- Nelissen, K., Borra, E., Gerbella, M., Rozzi, S., Lupino, G., Vanduffel, W., ... Orban, G. A. (2011). Action Observation Circuits in the Macaque Monkey Cortex. *J Neurosci*, *31*, 3743–3756.
- Nelissen, K., Luppino, G., Vanduffel, W., Rizzolatti, G. & Orban, G. A. (2005). Observing others: multiple action representation in the frontal lobe. *Science (80-. )*, *310*, 332–336.
- Ongür, D., An, X. & Price, J. L. (1998). Prefrontal cortical projections to the hypothalamus in macaque monkeys. *J Comp Neurol*, *401*, 480–505.
- Ortigue, S., Sinigaglia, C., Rizzolatti, G. & Grafton, S. T. (2010). Understanding actions of others: the electrodynamics of the left and right hemispheres. A high-density EEG neuroimaging study. *PLoS One*, *5*, e12160.
- Pandya, D. N. & Seltzer, B. (1982). Intrinsic connections and architectonics of posterior parietal cortex in the rhesus monkey. *J Comp Neurol*, *204*, 196–210.
- Pani, P., Theys, T., Romero, M. & Janssen, P. (2014). Grasping Execution and Grasping Observation Activity of Single Neurons in the Macaque Anterior Intraparietal Area. *J Cogn Neurosci*, *26*(10), 2342–2355.
- Peeters, R., Simone, L., Nelissen, K., Fabbri-Destro, M., Vanduffel, W., Rizzolatti, G. & Orban, G. A. (2009). The representation of tool use in humans and monkeys: common and uniquely human features. *J Neurosci*, *29*, 11523–11539.
- Porrino, L. J. & Goldman-Rakic, P. S. (1982). Brainstem innervation of prefrontal and anterior cingulate cortex in the rhesus monkey revealed by retrograde transport of HRP. *J Comp Neurol*, *205*, 63–76.
- Raos, V. & Savaki, H. E. (2016). The Role of the Prefrontal Cortex in Action Perception. *Cereb Cortex*, *27*, 4677–4690.
- Rizzolatti, G., Camarda, R., Fogassi, L., Gentilucci, M., Luppino, G. & Matelli, M. (1988). Functional organization of inferior area 6 in the macaque monkey. II. Area F5 and the control of distal movements. *Exp Brain Res*, *71*, 491–507.
- Rizzolatti, G. & Craighero, L. (2004). The mirror-neuron system. *Annu. Rev. Neurosci*, *27*, 169–192.
- Rizzolatti, G., Fadiga, L., Gallese, V. & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Brain Res Cogn Brain Res*, *3*, 131–141.
- Rozzi, S., Calzavara, R., Belmalih, A., Borra, E., Gregoriou, G. G., Matelli, M. & Luppino, G. (2006). Cortical connections of the inferior parietal cortical convexity of the macaque monkey. *Cereb Cortex*, *16*, 1389–1417.
- Rozzi, S., Ferrari, P. F., Bonini, L., G. R. & Fogassi, L. (2008). Functional organization of inferior parietal lobule convexity in the macaque monkey: Electrophysiological characterization of motor, sensory and mirror responses and their correlation with cytoarchitectonic areas. *Eur J Neurosci*, *28*, 1569–1588.
- Sakreida, K., Schubotz, R. I., Wolfensteller, U. & von Cramon, D. Y. (2005). Motion class dependency in observers’ motor areas revealed by functional magnetic resonance imaging. *J Neurosci*, *25*, 1335–1342.
- Saleem, K. S., Miller, B. & Price, J. L. (2014). Subdivisions and connectional networks of the lateral prefrontal cortex in the macaque monkey. *J Comp Neurol*, *522*, 1641–1690.
- Shmuelof, L. & Zohary, E. (2005). Dissociation between ventral and dorsal fMRI activation during object and action recognition. *Neuron*, *47*, 457–470.
- Simone, L., Bimbi, M., Rodà, F., Fogassi, L. & Rozzi, S. (2017). Action observation activates neurons of the monkey ventrolateral prefrontal cortex. *Sci Rep*, *7*, 44378.
- Simone, L., Rozzi, S., Bimbi, M. & Fogassi, L. (2015). Movement-related activity during goal-directed hand actions in the monkey ventrolateral prefrontal cortex. *Eur J Neurosci*, *42*, 2882–2894.
- Sliwa, J. & Freiwald, W. A. (2017). A dedicated network for social interaction processing in the primate brain. *Sci. (80-. )*, *356*, 745–749.
- Stern, D. N. (1985). *The Interpersonal World of the Infant*. New York: Basic Books.
- Stern, D. N. (2010). *Forms of vitality exploring dynamic experience in psychology, arts, psychotherapy, and development*. United Kingdom: Oxford University Press.
- Tsunada, J. & Sawaguchi, T. (2012). Neuronal Categorization and Discrimination of Social Behaviors in Primate Prefrontal Cortex. *PLoS One*, *7*, e52610.
- Ulloa, E. R. & Pineda, J. A. (2007). Recognition of point-light biological motion: mu rhythms and mirror neuron activity. *Behav. Brain Res*, *183*, 188–194.
- Umiltà, M. A., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., ... Rizzolatti, G. (2008). When pliers become fingers in the monkey motor system. *Proc Natl Acad Sci U S A*, *105*, 2209–2213.
- Umiltà, M. A., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C. & Rizzolatti, G. (2001). I know what you are doing. a neurophysiological study. *Neuron*, *31*, 155–165.

- Venkatraman, A., Edlow, B. L. & Immordino-Yang, M. H. (2017). The Brainstem in Emotion: A Review. *Front Neuroanat*, *11*, 15.
- Wheaton, K. J., Thompson, J. C., Syngieniotis, A., Abbott, D. F. & Puce, A. (2004). Viewing the motion of human body parts activates different regions of premotor, temporal, and parietal cortex. *Neuroimage*, *22*, 277–288.
- Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V. & Rizzolatti, G. (2003). Both of us disgusted in My insula: the common neural basis of seeing and feeling disgust. *Neuron*, *40*, 655–664.
- Wilson, S. M., Saygin, A. P., Sereno, M. I. & Iacoboni, M. (2004). Listening to speech activates motor areas involved in speech production. *Nat Neurosci*, *7*, 701–702.
- Yoshida, K., Saito, N., Iriki, A. & Isoda, M. (2011). Representation of others' action by neurons in monkey medial frontal cortex. *Curr. Biol.* *21*, 249–253.
- Yoshida, K., Saito, N., Iriki, A. & Isoda, M. (2012). Social error monitoring in macaque frontal cortex. *Nat Neurosci*, *15*, 1307–1312.