Theories and Computational Models of Affordance and Mirror Systems: An Integrative Review

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Abstract

Neuroscientific and psychological data suggest a close link between affordance and mirror systems in the brain. However, we still lack a full understanding of both the individual systems and their interactions. Here, we propose that the architecture and functioning of the two systems is best understood in terms of two challenges faced by complex organisms, namely (a) the need to select among multiple affordances and possible actions dependent on context and high-level goals, and (b) the exploitation of the advantages deriving from a hierarchical organisation of behaviour based on actions and action-goals. We first review and analyse the psychological and neuroscientific literature on the mechanisms and processes organisms use to deal with these challenges. We analyse existing computational models thereof. Finally we present the design of a computational framework that integrates the reviewed knowledge. The framework can be used both as a theoretical guidance to interpret empirical data and design new experiments, and to design computational models addressing specific problems debated in the literature.

1 Introduction: affordances, canonical neurons, and mirror neurons

Studies on macaque monkeys have shown that brain area F5 (putatively homologous to human posterior Inferior Frontal Cortex, IFC, Rizzolatti & Arbib, 1998)[1] contains two varieties of visuo-motor neurons: *canonical neurons* and *mirror neurons* (Di Pellegrino et al., 1992; Gallese et al., 1996; Murata et al, 1997; Raos et al., 1996; Rizzolatti et al., 1996; Sakata et al., 1995; for a more recent review see Rizzolatti & Craighero, 2004). Both canonical and mirror neurons discharge when macaques execute specific actions, for example when they grasp an object with a precision grip or a power grip.

Canonical neurons also fire when the monkey simply observes an object. This points to a mechanism for detecting object affordances and activating actions on this basis. The concept of *affordance* was first introduced by Gibson (1966), who observed that the dynamical pattern of the optic flow can be used to guide navigation *reactively* through the environment. He used the term affordance to refer to the fact that visual perception of the environment is not just passive perception of objects as such, but direct perception of the potential actions that the perceiver can carry out with them without the need for high-level processes such as reasoning about object properties. In the realm of manipulation, for example, a person seeing an object would not necessarily only perceive colours, shapes and so on, but first and foremost also directly perceive the object's "graspability", "liftability" and so on. The affordances of any given object depend not on the object alone, but also on the embodiment (in particular the actuators) of the perceiving agent. A bottle, for example, affords grasping for humans but not for dogs (for which it might afford a biting action) or ants. A key aspect of the concept of affordance is the reactive nature of the resulting sensorimotor processing that tends to trigger or prime action in an automatic fashion (although we will later see that this tendency can be strongly modulated by the context and goals of the agent).

In some of the recent literature, the concept of affordances concept has been extended beyond the Gibsonian interpretation to consider the *brain representations of affordances*, (the possible sensorimotor interactions offered by objects, see for instance Fagg & Arbib, 1998 or Oztop & Arbib, 2002). These representations encode both the features of the objects needed to act on them (e.g., the size and location of the object) and the relation between the objects and the agent's body (e.g., that an object is within reach or in contact with a hand).

In cognitive psychology, the concept of affordances has been further developed with the definition of *micro-affordances* (Ellis & Tucker, 2000; Vainio et al., 2007), also referring to *brain representations* of possible sensorimotor interactions with objects. Micro-affordances do not concern the whole action but rather specific *action components*: for example, observing an object with a given size and orientation might activate two different components of the grasping action, such as the grip type (e.g., power vs. precision) and the wrist orientation (e.g., with the hand palm pronated or supinated).

In addition to the Gibsonian view, these extensions to the concept of affordance are very important for this review. To avoid confusion, we will use the term "(micro-)affordance representations" to refer to the brain representations of affordances unless the context clearly disambiguates between the Gibsonian or brain-related meaning of the simpler term "affordance".

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[1] All brain regions acronyms used in the article are summarised in Table 1 in the Appendix

Mirror neurons (also found in the parietal cortex (PC); Fogassi et al., 2005) fire when the monkey observes another monkey or a human being perform a *goal-directed* action such as, for example, grasping an object (Rizzolatti & Craighero, 2004). This points to a mechanism for *action* or *intention understanding* (Rizzolatti & Graighero, 2004; Iacoboni et al., 2005). A crucial difference with canonical neurons is that mirror neurons do not discharge to the simple presentation of an object. This evidence has led many authors to link mirror neurons to the representation of *goals of actions* (Rizzolatti and Craighero, 2004; Iacoboni et al., 2005; Craighero et al., 2007). For example, Johnson-Frey et al. (2003) have shown through an fMRI study that the frontal mirror regions of humans are preferentially activated by the sight of images showing a hand grasping an object compared to a hand touching it. This indicates that mirror neurons tend to encode action goals such as the *terminal state* resulting from an action grasp (for example a certain relation between the hand and the object). Fogassi et al. (2005) further found that some, but not all, mirror neurons in PC of monkeys are selective to ultimate (high-level) goals that a given action contributes to (e.g., "grasp to eat" vs. "grasp to place"). This indicates that the mirror system is sensitive to goals at different levels of abstraction (which can be represented in the same areas by different populations of neurons).

Finally, some compelling evidence that F5 mirror neurons encode action goals rather than action movements comes from Umiltà et al. (2008) and Rochat et al. (2010). In these studies, monkey motor neurons that activate during grasping (with the hand) for food were shown to also activate when grasping with pliers (as well as the observation of the performance of such actions). This remained true when the monkeys used "reverse" pliers that required a different movement to grasp an object (opening instead of closing the hand) and even for the observation of an experimenter spearing food with a stick. F5 mirror neurons thus appear to encode the goal of motor commands (e.g. a grasp) rather than the specific motor activation (e.g., close vs. open a hand to grasp) needed to achieve such goal.

In contrast to the wealth of data obtained from monkeys, there is still a relative lack of direct evidence on mirror neurons in humans. An exception to this is a recent study by Mukamel et al. (2010) who recorded single cells in human patients with intractable epilepsy. They found a subset of mirror neurons in the frontal (supplementary motor area, SMA, and pre-SMA) and temporal (hippocampal region) lobes that were activated both during the visual observation and the execution of grasping actions. Furthermore, other recent studies, mainly based on brain imaging techniques such as fMRI, also indicate the existence of both canonical and mirror systems in humans (Chao and Martin, 2000, Buccino et al., 2001; Grèzes et al., 2003; Johnson-Frey et al., 2003; Fadiga et al., 2006; Kilner et al., 2009; Gazzola & Keysers, 2009; for a review see Rizzolatti & Craighero, 2004). For example, Chao and Martin (2000) have shown with fMRI that tool naming activates the left ventral premotor cortex.

This review aims to contribute to the study of the affordance and mirror systems in three ways. A *first main contribution* is the integration of behavioural and neuroscientific evidence on both the affordance and the mirror systems. Although both systems have been extensively studied with behavioural and neuroscientific experiments as well as with the implementation of computational models, these different avenues of research remain largely separated. For example, the cognitive psychology literature on affordances is rarely related to the underlying brain processes and the same is true for some of the behavioural experiments relevant for the understanding of mirror neurons. There is thus a certain lack of an overall, integrative, picture of the different levels of analysis.

Two key insights (or principles) will guide our contribution to link the psychological, neuroscientific and computational analyses of the affordance and mirror systems. First, organisms face an important

cognitive challenge when interacting with their material and social environment: the environment continuously offers them a *great number of opportunities for action.* Organisms therefore need to continuously select appropriate affordances and actions based on the overall context and their high-level goals. Understanding the way the brain addresses this challenge helps to understand and explain many issues related to the neural mechanisms underlying the affordance system and canonical neurons as well as behavioural phenomena related to affordances investigated in psychology. This insight will be used in section 2.1 to present a unifying account of the psychological and neuroscientific evidence on the affordance system. In particular, we will show how the brain is organised along two major neural pathways, one encoding affordances and actions (the dorsal neural pathway) and one, including the prefrontal cortex, involving a number of mechanisms that allow the selection of affordances and actions on the basis of high-level goals (the ventral neural pathway).

The second insight is that *behaviour and the underlying brain mechanisms are organised in function of their goals*, represented at multiple levels of abstraction. This allows organisms to greatly enhance the flexibility of their behaviour, for example to learn behaviour in terms of simple motor acts (e.g. reaches or grasps), to monitor behavioural success, to compose actions to build more complex behaviours, to recognise actions when executed by others and so on. We will show that this organisation can explain many aspects of individual and social purposeful behaviour, including several aspects related to their underlying neural mechanisms. To this effect, we present an integrated view of the major psychological and neuroscientific experiments involving mirror neurons and the representation of goals at multiple levels of abstraction in section 2.2. That section analyses in particular the important role that goals play in behaviour organisation (especially in primates) as well as the putative brain structures involved in their encoding (e.g., the prefrontal and parietal cortex) and exploitation (e.g., the premotor and motor cortex).

The *second main contribution* of the paper is the presentation of an integrated view of the affordance and mirror systems with a focus on their function and the mechanisms that led to their development. Current research in this area remains fragmented, focussing mainly on either affordance processing and canonical neurons or action understanding and mirror neurons but not typically on both.

Here, we adopt a *system-level* approach in the analysis of empirical evidence on the affordance and mirror systems presented in section 2. In particular, we follow the idea that canonical and mirror neurons are neural populations whose function and development can only be understood in the context of wider neural systems with which they exchange afferent and efferent connections and with which they play key adaptive functions for the organism as a whole. We therefore identify the larger integrated systems and contribute to the understanding of their relations by discussing the interplay between their components. In this sense, although the paper presents research on affordance and mirror systems sequentially, the material presented is aimed at understanding their relationship.

The *third main contribution* of the paper is a *computational framework* that integrates the knowledge reviewed in section 2. This includes in particular:
- The principle of multiple affordance selection involving the affordance system;
- The principle of the goal-based organisation of behaviour involving the mirror system;
- The functional and neuroscientific relations between the affordance and the mirror systems.

To develop the framework, we first review existing computational models of affordance and/or mirror

systems (section 3). In doing so, we show that some system-level models capture the two insights guiding the reviews presented here (usually only one of the two) while others capture specific computational mechanisms that can be used as building blocks to investigate specific aspects of those systems. We then present a unified computational framework that draws from the models reviewed in section 3 to build an integrated view of the affordance and mirror systems (section 4). Given the complexity of the resulting framework, it is not meant to be understood as an actual model since the outcome of a complete implementation would be overly complex and not focussed on specific problems and predictions. Rather, the value of the framework lies in (a) the theoretical integration of research on affordance and mirror systems as well as the formation of a set of concepts useful for interpreting them in a coherent fashion and (b) the provision of guidance for the design of specific models capable of tackling specific problems and producing testable predictions. To illustrate the utility of the framework, we summarise some of the most important open problems of the field and give preliminary indications on how the framework could be used to investigate them in depth by facilitating the construction of specific models (section 5).

Given the breadth of topics addressed and the number of interdisciplinary perspectives it contains, the present review is rather substantial. However, if desired, the various sections of the paper can be read in a modular fashion based on the interests of the reader. Section 2.1 covers psychological and neuroscientific research on affordance systems with a particular focus on the problem of selecting appropriate affordances amongst all the available ones while section 2.2 presents the psychological and neuroscientific research on the mirror system, in particular regarding the encoding of behaviour in terms of goals. For this reason, sections 2.1 and 2.2 can be read individually if the reader is interested in only one of the two systems. Focussing only on the psychological aspects (sections 2.1.1 and 2.2.1) or the neuroscientific aspects (sections 2.1.2 and 2.2.2) is also possible. However, reading both sections 2.1 and 2.2 facilitates the understanding of the relations between the two systems.

Readers predominantly interested in existing computational models of either system can proceed directly to section 3 and refer to section 2 when needed. Readers mainly interested in the integrated framework and a computational view on the relationships between the affordance and the mirror systems can proceed to section 4, referring to section 3 only when needed (e.g., to envisage how the different computational components of the framework might be implemented in detail). Section 5 discusses open issues of the field and how the framework from section 4 might help address these, in particular by designing and implementing specific computational models. Finally, Section 6 draws conclusions of general interest.

2 Goal representation and selection among multiple affordances: psychological and neurophysiological evidence

Throughout the paper, we distinguish the following key aspects of actions (see Hamilton and Grafton, 2007, and Kilner et al., 2007 for similar definitions):
  (a) *High-level goals*: these refer to desired outcomes (e.g. "drinking from a bottle") that have a high rank in the hierarchical organisation of action. They are more abstract and closely related to the ultimate/adaptive/homeostatic needs of the agent. These goals usually involve long time scales and a sophisticated course of action to be accomplished (we prefer this more neutral term to the ones used in Hamilton and Grafton (2007) or Kilner et al. (2007), which were "outcome" and "intention" respectively);
  (b) *Goals:* these refer to desired outcomes (e.g. "reaching for the bottle" or "grasping the bottle")

that have a lower rank in the behavioural hierarchy. They are more concrete, involve specific actuators and are not closely linked to specific adaptive functions. This type of goals usually involves short time scales and "simple" motor acts such as those often referred to with language verbs (e.g., "reach", "grasp", "touch", "push", etc.);

(c) *Sensorimotor mappings* (or *skills*): these are formed by the neural processes that transform the signals from sensors into those to be issued to muscles and thus implement the on-line guidance of action execution.

(d) The *muscle activity* and *kinematic level:* the activity of muscles needed to produce the movements implementing the action and the resulting configuration changes in space and time of the actuators.

The distinction between the different levels of actions is important for the analyses presented in the paper. For example, *high-level goals* are a useful concept to explain some aspects of the functioning of the prefrontal and parietal cortex. *Goals* are relevant for interpreting the functioning of the mirror-neuron system components (e.g. some areas of premotor cortex and inferior frontal cortex). *Sensorimotor mappings* are relevant for interpreting the formation of affordance representations and the preparation/execution of actions in premotor/motor cortex.

Although useful, these distinctions should nonetheless be treated with care as: (a) what a brain area represents can only be inferred on the basis of the referents (parts of the world, sensors, actuators, internal body states, etc.) with which its activation correlates; (b) different brain areas often contain different populations of neurons that represent different things; (c) representations in the brain are often distributed over multiple areas; (d) representations in one brain area might cause similar activations in neurons of areas to which it is connected; (e) there is rarely a consensus in the literature on what different parts of brain represent (moreover, different terminologies are sometimes used).

2.1 Affordances and affordance control based on prefrontal cortex
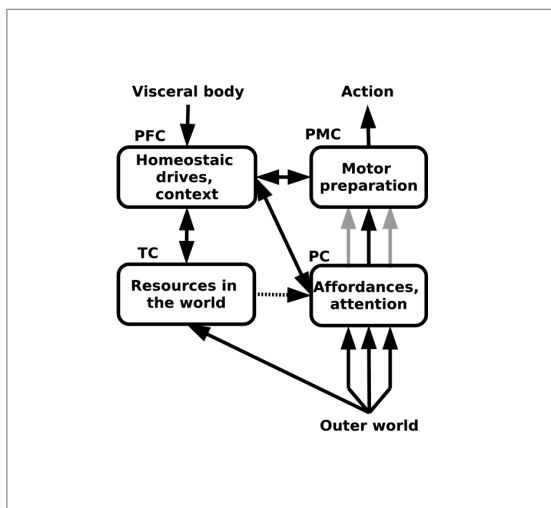
Figure 1: The brain areas and the functions played by them in the implementation of the *first principle of motor brain organisation* informing this review. PC: parietal cortex; PMC: premotor cortex; PFC: prefrontal cortex; TC: temporal cortex.

This section deals with the first principle guiding this review, namely the brain's solution to the

challenge of selecting appropriate affordances from those elicited by the environment. We first review relevant key psychological experiments and theories. This is then followed by relevant neuroscientific evidence on the underlying brain mechanisms and areas. These psychological processes and brain mechanisms are sketched in Figure 1. Within the dorsal neural pathway, the parietal cortex (PC) and the premotor cortex (PMC) implement the sensorimotor mappings that extract affordances from the world objects and lead to the selection, preparation, and execution of actions. Within the ventral neural pathway, the temporal cortex (TC) detects the identity of objects and other resources in the world. Based on this as well as external context and internal homeostatic drives, the prefrontal cortex (PFC) forms goals. With these goals, the PFC guides top-down overt and covert attention together with TC and PC. As we will see, it also biases the selection of affordances and actions by exploiting a number of mechanisms acting within the different stages of the dorsal pathway (these biasing processes will be also referred to as "affordance and action control" throughout the paper).

The analysis of affordances presented in this paper complements the work of Cisek and Kalaska (2010), which shares the insight that the sensorimotor system is organised into two major pathways (one implementing sensorimotor mappings for online control of actions and one biasing the selection among the available affordances and actions). The focus of Cisek and Kalaska (2010) is on a thorough analysis of the two pathways based on neuroscientific and neurophysiological evidence, showing in particular how the brain simultaneously specifies actions and selects among them in continuous dynamic interaction with the environment (rather than implementing behaviour based on sequentially organised perceptual, cognitive, and motor processes). The review presented here, on the other hand, focuses on the important role that the PFC plays in biasing the selection of affordances and actions (based on object identification and the internal states of the agent). It also provides an extensive review of behavioural evidence putatively related to the functioning and interaction of the two pathways and presents a critical review of the specific computational mechanisms used in past models that can be used to implement the processes related to the two pathways in future work.

2.1.1 Psychological evidence and theories on affordances and affordance control

In first three subsections of the following, we present research on the presence of multiple affordances elicited by the environment and the interference problems they may cause. This motivates the remaining subsections, which address the mechanisms through which we select appropriate affordances amongst the many available.

The environment elicits many affordances
Objects typically elicit multiple affordance representations and the context in which these are perceived can modulate their activation (with "context" we refer to the situation as a whole rather than merely the specific tasks performed). Tools, for instance, are manipulable objects that elicit multiple affordances. They activate not only affordances related to grasping (a form of manipulation) but also those related to their function (Creem-Regehr & Lee, 2005). Bub et al. (2008) addressed this characteristic by distinguishing between two kinds of grasping actions: those used to pick up an object and those associated with using an object for its intended purpose[2]. The authors showed that either affordance type can be activated to different degrees in function of the context.

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[2] Bub et al. (2008) refer to the first type of grasp as "volumetric" and to the second type as "functional", see also Pellicano et al., 2010).

Borghi et al. (2012) recently presented participants with pairs of objects that could be functionally related, spatially related or not related at all (e.g. fork and strawberry; fork and glass; fork and tennis ball). The objects were presented either by themselves, in presence of a hand close to one of the objects or in presence of a hand grasping the an object (e.g. the fork) with either a manipulative or functional posture (thus targeting the distinction between affordances elicited by shape and function of an object respectively). Participants were required to respond whether or not the two objects were typically seen or used together by pressing corresponding keys on the keyboard. Response times were found to be modulated by context and hand posture. Manipulative postures were the slowest in the functional context and functional postures were inhibited in the spatial context. These results are likely due to a mismatch between the inferred goal and the context. This interaction was present only when participants were required to provide hand rather foot hand responses, likely due to the activation of an effector-specific motor simulation.

Further evidence on the existence of multiple affordances comes from the literature on "conflict objects" and "non-conflict objects" (Jax & Buxbaum, 2010). "Conflict objects" are objects that elicit contrasting affordances for manipulations associated with the object structure and for manipulations for the specific use (function) of the objects. For example, a calculator affords a manipulative clench grasping response and a functional poke response. Evidence shows two forms of interference involving conflict objects: a short-term grasp-on-use interference (the structure-related affordance interferes with the use manipulation), and a long-term use-on-grasp interference (the use affordance interferes with the structure-related manipulation after the use of the object in previous experimental blocks). Buxbaum and Kalenine (2010) have recently proposed that two different circuits underlying different affordances might be activated: one based on object structure (dorso-dorsal stream), and another related to object function (ventro-dorsal stream; see Rizzolatti & Matelli, 2003, for the distinction of the two routes). Context-dependent multiple affordances are also generated at a more abstract level as demonstrated for instance by studies that focus on affordances and language comprehension. A number of behavioural studies have for instance shown that different affordances can be activated depending on linguistic context (see e.g., Borghi, 2004; Glenberg & Robertson, 2000; Zwaan, 2004).

Stable and variable affordances
An important distinction relevant for affordance representation and selection is the one between *stable and variable affordances* (Borghi & Riggio, 2009, which can be understood as *micro-affordances[3]* (Ellis & Tucker, 2000; Vainio et al., 2007, see introduction). In particular, these concepts take the view that each affordance is composed of a number of specific aspects. Stable affordances thus relate to features of objects that tend to be constant across different experiences and contexts (e.g., the size and shape of "apples" tend to be constant) while variable affordances relate to features of objects that can vary between different experiences (such as the location of apples).

The distinction between stable and variable affordances is related to the distinction between the ventral and dorsal neural pathways (Ungerleider & Mishkin, 1982); including the distinction between the dorso-dorsal and ventro-dorsal routes forming the dorsal neural pathway (Rizzolatti & Matelli, 2003). In this regard, the representation of some variable affordances (such as those dependent on location) might mainly involve the dorso-dorsal route (together with the neural route controlling the eyes, as they carry information relevant to guide reaching and gaze control movements). Conversely, stable

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[3] Note that Borghi & Riggio (2009) still refer to stable and variable affordances simply as affordances rather than micro-affordances

affordances (such as those given by size and shape) might mainly involve the ventro-dorsal route and the ventral pathway as they carry information relevant for guiding grasping and for recognising the nature of objects relevant to the formation of high-level goals within PFC. A meta-analysis of brain imaging studies relevant for stable and variable affordances supports this hypothesis as it shows the presence of partially segregated activation clusters for stable and variable affordances within the ventro-dorsal (inferior parietal, BA40) and dorso-dorsal (superior parietal, BA7) pathway, respectively (Sakreida et al., in preparation). It should be kept in mind, however, that the representations of the two types of micro-affordances may partially overlap as indicated by studies demonstrating that object position affects grasping and object size affects reaching (Gentilucci et al., 1991; Corradiniet al., 1992; Chieffi & Gentilucci, 1993; Milner & Goodale, 1995). Further empirical investigations are needed to clarify this point.

As recently argued by Binkofski and Buxbaum (in press), the distinction between stable and variable affordances is related to that between functional and manipulative affordances, and between the "use" and "grasp" system. In our view, the relation relies upon the fact that both functional and stable affordances are processed in the ventro-dorsal stream since they are the product of longer and more consolidated experience. Indeed, the object's function likely depends on the frequency of the types of action that can be performed with it. Similarly, stable affordances pertain to long-term perception-action patterns stored in memory rather than online responses to the current environment. In contrast, manipulative and variable affordances are more sensitive to the current context and are more closely related to the execution of online-controlled actions and hence are mainly processed in the dorso-dorsal stream.

The problem of interference

The existence of multiple affordances and affordance components, raises the problem of how they can be selected and used to produce coherent non-interfering actions. Behavioural experiments based on the "compatibility effect" paradigm turn out to be highly relevant for this issue. These experiments were originally proposed to show that even highly cognitive tasks (such as categorisation) and the underlying brain representations are strongly influenced by embodied aspects of behaviour (e.g. the affordances directly elicited by the objects). However, they also shed light on the mechanisms related to the selection among multiple affordances because they are based on experimental set-ups that concurrently elicit two or three affordances and study how they interact. In a typical experiment, participants might be instructed to perform a task in relation to an object by using an action that is either similar to or different from (i.e. is compatible or incompatible with) the action the object affords directly and most strongly. For example, Tucker and Ellis (2001) had participants perform a precision or power grip on a customised joystick in order to classify a target object as either "natural" or "artefact" (see Grèzes et al., 2003b, for a brain imaging study of the cortical regions mainly involved in performing the tasks in this experiment). The objects presented were either small or large, hence tended to afford a precision grip or a power grip respectively. The results show that even though the size of a given object is not relevant to accomplishing the categorisation task, the compatible/incompatible affordance it elicits facilitates/interferes with the selection of the task action. This illustrates that the many affordances elicited by the seen object and the touched joystick compete for triggering the related actions, requiring suitable selection mechanisms based on context and the high-level goals of the participants. In this case, these are represented by the experimental context and the task to be accomplished (as required by the experimenter).

Affordance selection and action modulation relies upon high-level goals

A growing body of recent studies suggests a strong involvement of high-level goals (formed on the basis of context and current motivational and emotional states) in the selection of affordances. These studies show that the kinematics of reach and grasp actions are modulated by the presence of other persons in the experimental setting (for an overview see Becchio et al. 2010). For example, Becchio et al. (2008) found that the kinematics of reaching, grasping and placing actions differed between moving an object from one location to another and passing an object to a partner (social intention condition).

Similarly, Ferri et al. (2011; 2010) investigated the kinematics of action execution in feeding behaviours. Ferri et al. (2011) found that a "social affordance" is activated when reaching, grasping, and placing a piece of food into the mouth of another person, leading to increased movement accuracy. This modulation of movement kinematics occurs even when the final aim of the task is not to feed but the other person simply opens the mouth, thus activating a social request. No modulation is observed when a non-human mouth-like aperture is presented. Ferri et al. (2010) showed that the kinematics of interacting with a piece of food in a way that simulates feeding a person are modulated by the facial expression of the recipient: the movement accuracy in particular is higher when participants simulated feeding a happy face compared to a disgusted, neutral, or sad face. Overall, these experiments show the level of sophistication of the processes leading to the formation of high-level goals and how these have an important impact on affordance selection and action execution.

Selection of affordances based on attentional processes
Another possible way in which high-level goals can influence affordance elicitation and action execution is through spatial (often overt) attention. Relevant to this is the "Simon Effect" (Simon, 1990; Kornblum et al., 1999; Hommel, 2010), namely the finding that reaction times tend to be faster when the stimulus is located in a location (e.g., left vs. right) congruent with the response requested by the experiment (e.g., pressing a left vs. a right button). This implies that reacting towards the location of the stimulation (Simon, 1969) is facilitated, likely because the allocation of attention to that location tends to activate a corresponding value for the spatial components of the affordance. Note that the converse also appears to be true as some studies have shown that object affordances attract attention. For example Handy et al. (2003) demonstrated with ERP and fMRI that graspable objects (tools) automatically direct visual attention towards their location, (albeit only in the right hemifield).

Tucker and Ellis (1998) provide important evidence on the role that attention plays in the definition of the spatial components of affordances. They devised a compatibility effect experiment in which the participants had to classify objects as appearing upright or reversed by pressing different keys on the keyboard (left, right). Response times were faster in case of congruency between the handle location (left, right) and the key to press. This might suggest that the affordance related to the handle was elicited (even though the handle was irrelevant to the task) and its spatial parameters (the spatial location of the handle) influenced the execution of the task action (pressing of the button). Elaborating on this study, Symes et al. (2005) investigated the role played by the affordance effect and the Simon effect, manipulating both the orientation of objects (e.g., the handle could be on the left or. on the right side of the object) and their location (e.g., they could be located either in the left or in the right visual field). With limited attentional involvement, (i.e. when participants were simply asked to categorize object's colour) only the Simon effect was present. However, when the attentional scan was deep and required representing the object, (i.e. when participants had to determine whether the objects were kitchen or garage objects) both an affordance effect and the Simon effect were found (both with manual and foot responses).

Riggio et al. (2008) ran an experiment to further clarify the relation between attention and affordance activation. They used a modified version of Tucker and Ellis (1998) paradigm in which the target stimulus could correspond or not correspond to a dynamic event capturing attention. As in Tucker and Ellis (1998), participants responded by pressing a different key in function of whether the object they saw was upright or reversed. The authors decoupled attentional effects from affordance effects: the location of the target was coincident or not with the location to which attention was automatically directed through the sudden disappearance of the object. Results showed that the affordance effect always occurred relative to the target object irrespective of the event, whereas the Simon effect occurred relative to the event capturing attention (i.e. the object disappearance). These findings suggest that automatic and controlled processes of visual attention may play a differential role in the occurrence of the two effects. In particular, the Simon effect related to the location parameters of actions depended more heavily on the automatic capture of attention. Affordance effects related to manipulation appeared to rely more on controlled attentional processes.

Further behavioural experiments have shed light on the mechanisms underlying the relationship between affordance and action elicitation on one side and the depth of the attentional scan on the other. Tipper et al. (2006) performed experiments to show that affordances are not automatically elicited but are strongly modulated by the task and the related attentional processes (see also Pellicano et al., 2010). They show that compatibility effects between the object's handle orientation and the key to be pressed to respond are present when participants engage in a shape discrimination task but not in a colour discrimination task. In addition, they investigate the effect of the "functional state" of the object stimuli. The authors show that in the shape discrimination task (but not in the colour discrimination task), objects in an active state (when it is used in line with its function, such as a depressed door handle), and in a "passive state" otherwise (e.g. a horizontal door handle)) produce larger compatibility effects compared to objects in a passive state. The experiments show that the interference of non-relevant affordances is present (or stronger) if the task to be accomplished requires a deep attentive investigation of object features (e.g., shape) that are more strongly related to those affordances, possibly based on the underlying mechanisms of neural activation enhancement (see next section). These results imply that the various aspects of affordance representations are activated only if the attentional processing of the object features related to them is sufficiently deep.

Some experimental studies have focused on the interplay between the affordance and mirror systems, possibly mediated by attention (e.g., Borghi et al, 2005; 2007; Fischer et al., 2008; Vainio et al., 2008; Yoon & Humpreys, 2005). Borghi et al. (2005; 2007) and Vainio et al. (2008) used a priming paradigm in which hands with a power or a precision grip posture preceded the presentation of large or small objects. They found a compatibility effect between the hand posture and the object size even if the task simply required a categorisation of objects into natural objects and artifacts. Two different mechanisms may have been operating in the experiment: a mirror mechanism triggered by the presented hand and a canonical neuron mechanism triggered by the affordance of the presented object. Similarly, Fischer et al. (2008) demonstrated that static images of different hand grip postures (precision vs. power) induced an attention shift toward the grasp congruent object within 350ms. Ellis et al. (2011) instructed participants to classify objects (using left/right key press responses) without taking into account the reaching actions toward the objects shown in a video clip. Participants' performance was nonetheless influenced by the observed reaching action: during the observation of a reach, it was easier to perform a response with the hand opposed to it. This reflects the interplay of canonical and mirror mechanisms and suggests that a mirror mechanism triggered not only by similar actions but also by complementary actions might be active (Newman-Norlun et al., 2007).

Selection of affordances based on inhibitory mechanisms
Inhibitory mechanisms also play an important role in the selection of affordances and actions. To investigate this issue, researchers have probed the mechanisms that allow the suppression of affordances elicited by distractors while participants are engaged in accomplishing a certain motor task. In the seminal work of Tipper et al. (1992), participants had to reach a target in the presence of distractors located in various positions relative to the target. Results showed that distractors eliciting responses located within the path of the target response caused substantial competition with the task action while the others did not. More importantly, when the hand passed over (or past) a distractor on its way to the target, the responses evoked by the distractor were actively inhibited.

In another study, Ellis et al. (2007) investigated the effects of distractor affordances using a compatibility paradigm that extended the basic experiment of Tucker and Ellis (2001) reviewed earlier by adding a distractor was added next to the target. This distractor suggested a type of grasp that was either compatible or incompatible with the requested task response. The presence of the distractor caused a reversed compatibility effect: reaction times were faster in the case of distractor affordances incompatible with the task responses, and slower with compatible ones. The authors suggest that the explanation of this result is likely the presence of inhibitory mechanisms that suppress the affordance elicited by the distractors. In doing so, these mechanisms interfere with the execution of the task actions if these share common features (e.g., type of requested grasp) with the suppressed affordances (see also section 3.1 for a review of a model (Caligiore et al., 2012) implementing this process).

The importance of inhibitory mechanisms for affordance selection is also highlighted by the experiments of Eimer and Schlaghecken (1998; see Eimer and Schlaghecken, 2002, for a review). In these experiments, participants had to press a button indicated by an arrow cue. The cue was preceded by a masked prime formed by another arrow compatible or incompatible with the main cue. The results indicated that the prime is automatically inhibited, resulting in a negative compatibility effect (faster reaction times in the case of incompatible vs. compatible primes). This effect is explained in terms of an active inhibition of the response automatically elicited by the prime as this interferes with the execution of actions sharing spatial features with the prime. Aron et al. (2003) show in an fMRI study that the inhibitory mechanism involved in these experiments encompasses the inhibitory action of basal ganglia (BG), namely of the striato-pallido-thalamic pathway involving them (see section 2.1.2).

Selection of affordances and actions depending on social context
There is also evidence that high-level goals related to the social context might influence the selection of affordances and actions. For example, a variety of studies on language processing paradigms have recently shown that social context influences the execution of actions associated to the detected affordances. Gianelli et al. (2011) have shown that the simple presence of another influences kinematics of reaching-to-grasp an object; particularly so when the other is interacting with the participant. Similarly, Gianelli et al. (2011b) have shown that the social relationship with the other person (friend or not) modulates the kinematics of reaching and grasping an object. Participants tend to move fast in the presence of unknown persons, as if to compete for grasping objects. When friends are present, movements are faster only when they sit close to the object (so that they could easily reach for it) or when they speak, particularly so when they use the first person pronoun ("I grasp") even if no action on their side follows. These studies suggest that the performance of actions afforded by a given object is affected by the intentions of the participant.

2.1.2 Biological perspective and evidence on the affordance and the affordance control systems

This section reviews neuroscientific work on the brain mechanisms underlying the behaviours reviewed in the previous section. These mechanisms (Figure 1), allow the brain to processes multiple affordances in parallel and to exploit the top-down biasing effect of PFC (informed on context and agent goals) to select them along the sensorimotor pathways that map sensations to muscle commands.

The dorsal neural pathway implements sensorimotor mappings
Affordance representations are partially based on the processing of object features. Various areas of PC have neurons activated by the shape of objects, their position, and the object-hand spatial relations (Murata et al., 2000; Rizzolatti et al., 1998). These representations can trigger and guide (via a parieto-frontal neural-pathway) action preparation and execution (e.g. for reaching and grasping) taking place within frontal areas and involving mirror and canonical neurons (Matelli et al., 1994). The parieto-frontal connections originate from the primary visual cortical areas (VC) and form the *visual dorsal neural pathway* of the brain. This pathway is widely believed to extract "where" information from scenes (i.e., the location of objects, Ungerleider & Mishkin, 1982), or – more generally – "how" information: all information about objects needed to guide the on-line execution of actions (Milner & Goodale, 1995, 2008).

It has been shown that the dorsal neural pathway is organised in partially segregated parallel routes (Gentilucci, 2003; Rizzolatti & Matelli, 2003). The most important of these are the *dorso-dorsal* and *dorso-ventral* routes (see the review of Caligiore et al., 2010, for more details) previously discussed in the context of stable and variable affordances. The first route controls the proximal arm and is mainly involved in executing reaching movements. In monkeys, this route involves, among others, the medial intra-parietal cortex (MIP; parietal reach region, PRR, in humans) and the dorsolateral premotor cortex (F2/F4; PMCdl in humans). The dorso-ventral route controls the distal arm (wrist, hand) and is mainly involved in executing grasping movements. In monkeys, this route involves the anterior intra-parietal cortex (AIP; named the same in humans) and the inferior premotor cortex (F5 in monkeys; IFC in humans). Additionally, one can consider a third important route, this one playing a key role in eye movements and involving the lateral intra-parietal cortex (LIP; parietal eye field, PEF, in humans) as well as the frontal eye fields (FEF, considered part of the PFC rather than of the PMC; Fuster, 2008).

The ventral neural pathway processes information for top-down control of affordances
The *ventral neural pathway* is another important neural pathway involving, as intermediate stages, the associative visual areas of the occipital and temporal cortex (in particular inferotemporal cortex) and terminating in PFC. This pathway encodes "what" information (i.e., information about the classes of objects, Ungerleider and Mishkin, 1982; Milner and Goodale, 1995, 2008). As previously mentioned, encoding multiple affordances (in the dorsal neural pathways) supports flexible behaviour but also increases the possibility of executing undesired actions and may lead to potentially dangerous interference problems. The brain deals with these problems through sophisticated mechanisms pivoting on PFC at the top level of the ventral neural pathway (Fuster, 2001, 2008; Miller & Cohen, 2001; Wallis et al., 2001; Cisek, 2007; Cisek & Kalaska, 2010; Caligiore et al., 2010). As detailed further below, PFC coordinates sensorimotor processes based on internal motivations and external context (known from a number of suitable input afferences). PFC also possesses the capacity to process information in ways relevant for its supervisory/executive role and a complex efferent connectivity suitable to modulate affordance and action selection within various stages of the dorsal neural

pathways.

The ventral neural pathway can also influence the dorsal pathway through direct connections from stages upstream of PFC. The information on objects encoded in the inferior temporal cortex (ITC) in particular might influence the formation of affordances in AIP. Jeannerod et al. (1994) for instance reported of a patient with parietal damage (dorsal pathway) who exhibited an exaggerated finger opening when grasping uncommon objects while remaining more accurate when grasping usual objects of the same size. The patient also had an intact capacity of mimicking the size of known objects with the hands. This suggests that the ventral pathway, encoding semantic knowledge on objects, could communicate some information on objects, such as size, to the dorsal pathway. See Goodale (2008) for a review on the interaction between the two pathways.

PFC as the main locus of high-level goal elaboration
On the input side, PFC is a top associative/integrative cortex that receives input from various sensory brain areas, typically associative themselves, such as the visual associative cortex (PC and ITC) and the auditory associative cortex (superior temporal cortex – STC). These inputs mainly reach the dorsolateral portions of PFC (PFCdl; Fuster, 2008). Based on them, PFC is able to integrate information from various sensory modalities and form a representation of the whole "context" related to the outer world. Moreover, PFC is also informed on the internal visceral body states and homeostatic drives as it receives both direct and indirect afferent connections from limbic areas such as amygdala (Amg), hippocampus (Hip), and hypothalamus (Hyp). These connections mainly reach the orbital portions of PFC (PFCo). PFC is able to attribute values and desirability to different objects and contexts using these connections carrying information on internal body states, drives, and the ultimate needs of the organism (Fuster, 2008). PFC can form high-level goals to guide behaviour by merging the two types of information, as explained in the following.

PFC has a number of properties allowing it to perform its supervisory/executive functions. First, PFC is able to form combinatorial representations of the inputs it receives (as discussed in the context and motivations above as well as from its position at the apex of multiple sensory modalities). It can then form complex "rules" (i.e. representations of complex multimodal and temporal compounds) to guide behaviour (for example "to perform a grasp action when a green object is at the right position and to perform a push action when it is at the left position"; Wallis, et al., 2001; see Deco and Rolls, 2003, for a computational model).

Second, PFC has a high degree of plasticity thanks to its connections to Hip and its rapid learning processes (Rolls & Treves, 1998). These allow storing memories, spanning minutes to hours, which are needed to formulate plans and to monitor their execution.

Third, its re-entrant features allow it to implement working memory functions based on dynamical reverberant circuits (Deco & Rolls, 2003; see O'Reilly & Frank, 2006, for a model). This allows PFC to encode not only the current context but also recent events, supporting decisions based on present and recent past perceptions.

Fourth, PFC is prospective, that is, it is capable of anticipating future events (Fuster, 2008). Specifically, PFC, working in synergy with the cerebellum for fast temporal scales (Middleton & Strick, 2000; Ito, 2008), might possess the capacity to anticipate future events based on "forward models" (Wolpert et al., 1995; Haruno et al., 2001; Miall, 2003). Since goals are desired anticipated

states, the capacity of PFC to project into the future is an important prerequisite for their formation. All these processes and pieces of information allow PFC to know "what is needed" (based on internal context and homoeostatic drives) and "what might be possible" (e.g., there is a particular resource and context in the environment that could potentially satisfy a particular need) in terms of action. With this basis, PFC can select among the multiple available affordances, as these indicate to the organisms which actions can be accomplished with success. PFC performs the actual selection of affordances via its connections to various stages of the dorsal neural pathway (see Figure 1) and based on neural mechanisms briefly reviewed in the following. All these mechanisms are closely linked to the behavioural phenomena that we have reviewed in the previous section.

Mechanisms through which PFC exerts its top-down bias on the selection of affordances and actions
A first important efferent connection of PFC is formed by the output of the FEF towards the sub-cortical motor centres controlling eye movements (Fuster, 2008). FEF, as mentioned above, can be considered part of the dorsal stream contributing to control of eye movements together with sub-cortical pathways involving BG and the superior colliculus (SC). FEF plays a key role in the control of *overt attention*, in particular top-down/voluntary attention based on the overall goals of the organism (Hikosaka et al., 1998). Sub-cortical pathways play a more important role in bottom-up attention. Overt attention allows the focus on different objects and parts of the environment to only elicit affordances related to relevant objects.

A second important efferent connection of PFC is directed towards PC (Fogassi et al., 2005; Murata et al., 2000; Rizzolatti & Craighero, 2004). This affects both covert attention and representations of affordances in PC. Regarding the first, PFC connections to PC play a key role in *covert spatial attention* (Colby & Goldberg, 1999; Knudsen, 2007). For example, they contribute to augmenting the neural sensitivity related the specific features of objects (Carrasco et al., 2000). These processes also influence overt attention as they modulate PC representations of the dorsal parieto-frontal neural stream, which controls eye moments (mentioned above).

Regarding the modulation of affordance representations, top-down control can, for example, contribute to updating the representations of objects and contexts suitable for controlling movements so as to best pursue the agent's high-level goals (Fogassi et al., 2005; Hamilton and Grafton, 2007; see also Section 2.2 on this). Note that PFC might also bias the processes in high-level visual stages of the ventral pathway carrying information to PFC itself, for example via reciprocal connections (Fuster, 2008) at the level of ITC (Chelazzi et al., 1993),).

A final important efferent connection of PFC is at the level of the later stages of the dorsal neural pathways – in particular PMC – mainly reached indirectly via the supplementary motor cortex (SMC – Rizzolatti et al., 1998; Lu et al., 1994). These connections have been shown to strongly affect motor preparation and control within SMC/PMC (Scangos & Stuphorn, 2010; Cisek & Kalaska, 2002), in particular in tasks where sequences of movements are involved (Hikosaka et al., 1998). SMC has also been shown to be active when humans passively observe graspable objects without interacting with them (Grèzes & Decety, 2002). This activation might reflect the fact that, in this case, the affordances elicited by the objects have to actively be suppressed to prevent undesired actions from being triggered (Nachev, Kennard & Husain, 2008; Sumner & Husain, 2008). This inhibition might rely upon the inhibitory circuits of BG with which SMC forms important cortico-striato-thalamo-cortical loops. Top-down bias from PFC also contributes to controlling the selection and timing of the performed actions and has been shown to be sensitive to rewards (Padoa-Schioppa et al., 2004).

The literature is starting to converge on a consensus on the specific mechanisms through which PFC exploits such inhibitory connections to bias the selection of the contents of the target areas. In this respect, Munakata et al. (2011) propose that PFC "inhibitory" control is implemented through two major mechanisms, one mainly involving cortical target areas and the second sub-cortical/hippocampal target areas. The first mechanism relies upon the fact that a large part (>99%) of long-range cortico-cortical connections are mediated by excitatory pyramidal cell efferents (Tamamaki & Tomioka, 2010) and most cortical inhibitory interneurons have rather diffused efferents (Markram et al., 2004). Since these neurons seem to play an overall regulating function, the implication is that PFC cannot exert direct inhibition on target regions nor can it target specific inhibitory interneurons to inhibit specific content. Instead, PFC can exert selected excitation of specific content represented in target areas using its contextual, integrative, multi-modality, goal-directed representations. These target areas can then inhibit all other content via local inhibitory connections, thus ensuring their own selection.

The second mechanism relies upon (excitatory) PFC connections targeting local inhibitory neurons in sub-cortical/hippocampal areas. This inhibitory action usually has a global nature and lowers the activity of whole areas specialised in the production of certain types of behaviours (e.g., fear responses) or functions (e.g., the formation of episodic memories). This is for example the case of the ventro-medial PFC targeting local inhibitory neurons of fear-related dorsal raphe nucleus (DRN). Here, the activation of the ventro-medial PFC in the presence of controllable stress conditions causes the inhibition of DRN activity, thus avoiding the manifestation of fear responses and favouring the implementation of an active coping/goal-directed strategy (Maier & Watkins, 2010). Another example is the possible inhibition of hippocampal regions by the middle frontal gyrus of PFC resulting in the formation of weaker memories (Anderson et al., 2004).

We close this section by noting that although the review focussed on cortical neural pathways, the various regions of the PC, PMC, M1 and PFC do not work independently of sub-cortical structures of brain. In fact each of them forms loops with specific portions of BG (Alexander et al., 1986; Houk, et al. 1995; Middleton & Strick, 2000; Yin & Knowlton, 2006). In this respect, those cortical areas and corresponding portions of BG form whole integrated systems (we return to this point in section 4). These portions of BG are also interconnected, mainly via striato-nigro-striatal dopaminergic connections and thalamic connections (Haber et al., 2000; McFarland & Haber, 2002), and thus form a hierarchy that starts in high-level regions (ventral striatum, connected to PFC regions) and moves to associative (globus pallidum, e.g. connected to PC and ITC) and sensorimotor regions (putamen, e.g. connected to PMC and M1). This aspect of the sensorimotor hierarchy is not further considered here but constitutes a fundamental means for high-level goals to influence behaviour (see also Yin and Knowlton, 2006, on this hierarchy).

2.2 Mirror neurons and the representation of goals

In this section we will extend the concept of goal as follows. An *external goal* of an action is the state of the sensorimotor body and/or environment that is produced by the execution of this action and that leads to learning the action itself (or to its evolution if the action is innate). Such a state can be either static (e.g., "hand in touch with the object") or dynamic (e.g., "walking"). The brain can have a representation of the external goal of an action, here called *goal representation* or simply *goal:* this is a neural pattern that correlates with the fact that the external goal state actually takes place in the body/world and is used by the brain to produce adaptive behaviour.
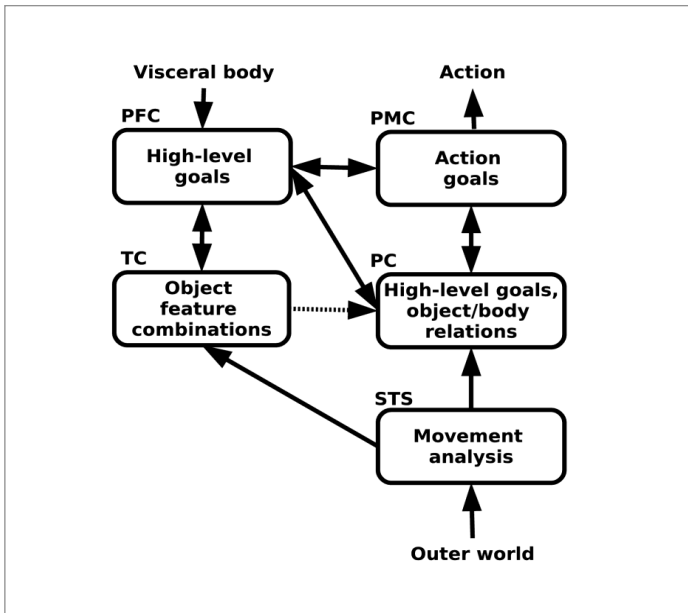
Figure 2: The brain areas and their functions in the implementation of the *second principle of motor brain organisation* guiding this review. PC: parietal cortex; PFC: prefrontal cortex; PMC: premotor cortex; STS: superior temporal sulcus; TC: temporal cortex.

Note that some authors propose a stronger definition of goal in cybernetic terms (Miller et al., 1960; Pezzulo et al., 2006). In this definition, a goal is the internally represented reference value of a controlled external variable that can guide action to reduce the mismatch between the reference and actual values. We will however use the "weaker" definition of goal given above. This allows us to consider important issues related to the acquisition/origin of actions and the adaptive value of goal representations. Specifically, the weaker definition includes the use of goal representations for purposes other than the triggering of action execution (as in the cybernetic definition). For example, they could be used to guide the learning of the sensorimotor mapping that accomplishes the external goal state (e.g., a learning signal is produced when this state is achieved), to monitor whether actions (e.g., produced on the basis of an S-R reactive behaviour) have achieved their external goal, to evaluate whether or not to further pursue a goal, or to recognise and process goals pursued by other agents. All these aspects are relevant for the analysis proposed here as they represent ways in which cognitive systems may be more sophisticated than simple reactive systems.

The second principle guiding this review refers to the idea that the hierarchically organised representation of actions in the brain relies upon the representation of their goals. We have seen that goals play a key role in the selection of affordances and actions at various levels of abstraction. The importance given to goals here builds on the idea (Rizzolatti and Craighero, 2004; Iacoboni et al., 2005; Craighero et al., 2007) that mirror neurons represent the immediate goals of action (for example "bring the hand in touch with the object" in a reach action). Figure 2 sketches key functional aspects of the principle and the main brain areas involved in its implementation. Within the dorsal neural pathway, PC and PMC/IFC implement the mirror system that recognises the effects of observed actions (in particular within the superior temporal sulcus, STS). On that basis, the mirror system encodes action goals (in particular within PMC/IFC) and integrates them with high-level goals (in particular within

PC). Within the ventral neural pathway, TC detects the features of objects; PFC – informed on objects and internal homeostatic drives – forms high-level goals and communicates them to the various stages of the dorsal neural pathway. Note that this system overlaps with the affordance system sketched in Figure 1.

2.2.1 Psychological evidence and theories on the goal and the mirror systems

Evidence and theories from cognitive psychology: ideomotor principle, event coding theory, internal models theories

Cognitive psychology has produced various theories and empirical evidence to support the idea that behaviour has an anticipatory nature and that motor actions are encoded in terms of goals. One of the first relevant theories is the *Ideomotor Principle* (IP; Greewald, 1970; see Pezzulo et al., 2006, and Pezzulo, 2009, for reviews). According to this principle, action selection and execution tend to follow the activation of internal causes – such as representations of goals or goal-related cognitive processes – rather than the perception of (only) external stimuli. In this respect, the key idea of the principle is the "goal-trigger hypothesis" according to which goal representations (anticipations of action effects) play a crucial role in action control (Hommel et al., 2001).

The *Theory of Event Coding* (TEC; Hommel et al., 2001) is a development of the ideomotor principle integrated with the *common coding theory* (Prinz, 1990; Prinz 1997) according to which perception and action have a common representation. TEC aims at providing a conceptual framework to better understand the relationship between perception and action planning. The theory does not refer to early aspects of perception or late aspects of motor processes, but to the representations and intermediate processes linking them. In this respect, it portrays late perception and early action planning as intimately related (or even indistinguishable) and pivoting on *event codes*. Event codes are distributed representations of feature codes linked by binding mechanisms such as neural synchronisation mechanisms and other mechanisms such as those considered to underlie attentional binding (Kahneman and Treisman, 1984) or action chunking. Event codes encode distal perceived/produced events rather than features related to proximal sensor or motor activations, which has various advantages. First, it supports abstraction from sensory and motor details. Second, it allows the integration of information from multiple sensory modalities, allowing the encoding of aspects like the affordances of objects. Third, it allows planning actions affecting several motor actuators with substantial flexibility. Fourth, it leads to several possible interactions between seemingly separate aspects of cognition, such as those studied in experiments on spatial or affordance compatibility effects (see Hommel et al., 2001, for other advantages). Note that in this proposal, event codes might be organised hierarchically even if the theory does not specify mechanisms or processes for doing this. Interestingly, the neuroscientific evidence closest to TEC has been found in premotor and parietal cortex mirror neurons (Hommel et al., 2001).

Kiesel and Hoffmann (2004) trained participants to execute sequences of actions and showed that the presentation of different tones associated to actions could speed up the execution. This was seen as indicating that the encoding of action effects plays an important role in action execution. In another experiment, Elsner and Hommel (2001) devised an experiment in which participants could acquire bidirectional associations between motor patterns (e.g., different key presses) and some events (e.g., differently-pitched tones) that followed them. In a subsequent test – in which tones preceded the actions – the learned associations had an effect on reaction times and response frequencies. This was interpreted as evidence that the learned action-outcome associations causes automatic response priming and that the anticipated activation of the goal representation has an important role in action control.

Growing evidence based on the same matching principle indicates that we tend to be particularly sensitive to actions that share features with self-produced actions (for a review, see Schutz-Bosbach & Prinz, 2007). For example, various studies have shown that children respond faster to hand primes representing children's hands than to adult hands (Liuzza et al., 2012) while people also respond faster when a hand prime is presented in an egocentric rather than in an allocentric perspective (Bruzzo et al., 2008). Further, different results are obtained in a line bisection task depending on whether participants observe human or robotic hands (Ranzini et al., 2011). All these results can be interpreted in terms of the facilitating effect of primes on the triggering of actions via the activation of the outcomes' representation ("goals" during action recall) of the same actions. Indeed, the ideomotor principle implies that a prime more similar to an action outcome than another cue activates the internal representation of the outcome faster and thus facilitates the triggering of the corresponding action.

Wolpert et al. (2003; see also Wolpert et al., 1995 and Haruno et al., 2001) have also made important theoretical contributions to the understanding of the anticipatory nature of behaviour, its relation to goals and intentions, and the role these play in social interactions. These authors use concepts from control theory to explain natural behaviour, claiming that the central nervous system (CNS) exploits a number of forward and inverse models to best control motor action. The anticipatory forward models in particular allow the CNS to identify hidden aspects of the world dynamics through the integration of evidence over time. The forward models with the lowest prediction error during interaction with the environment are those best attuned to the current context (hidden variables). Moreover, the inverse models associated with those forward models are the best candidates for action in the given context. Forward and inverse models can play a number of functions, such as enabling the CNS to deal with neural noise, sensory delays and the non-linear dynamics of the skeletomuscular system. The authors believe that the CNS can exploit this computational machinery to also solve a number of problems posed by social interactions, such as action recognition, intention understanding, and imitation. This is possible as the forward models can be applied in the same way as illustrated above to infer hidden variables related to the observed behaviour of others, for example the actions they perform and the intentions they have.

Evidence and theories related to social interactions
Mechanisms matching our own action goals to those of others are not only at the basis of action comprehension, but are also crucial in social interaction as they support shared actions and coordination with others. Shared action representations may allow individuals to predict others' actions and integrate those into their own action planning, for instance to collaborate on a given task. In this context, an interesting novel line of research uses the so-called Social Simon task (see also Section 2.1). Here, the classical paradigm used to investigate the Simon effect is modified to investigate whether or not shared representation are formed during task sharing (e.g., Hommel et al. 2009, Sebanz et al. 2006; Tsai and Brass, 2007). The successful accomplishment of such tasks might require not only the sharing of high-level goals (i.e., the overall purpose of the task) but also of the goals of the specific actions involved in them. In this respect, recent evidence on mirror neurons suggests that a matching process is present not only when we observe actions similar to ours, but also when another person performs complementary actions which are part of the our motor repertoire (Newman-Norlund et al., 2007). It has also been demonstrated that action production systems support the emergence of others' action understanding early in development (Cannon et al., 2011).

Evidence that actions are encoded in terms of goals can also be found in the literature on imitation. For

example, Bekkering et al. (2000) showed that when children imitate others grasping the ear on the same or opposite side of the acting hand, they tend to imitate the action goal (i.e., the ear to grasp) rather than the kinematic aspects of actions (e.g., the hand used to perform the grasping). Rao et al. (2004) review the progressive development of imitative capabilities from simple to more sophisticated ones and show that these start with the imitation of facial and body movements, then develop into the imitation of actions performed on objects and finally into the imitation of behaviour based on the inference of the intentions underlying observed, or even attempted, behaviour.

There is also a rich literature in comparative psychology addressing the fact that humans (both adults and children) and to some extent apes can understand the goals of others' actions to, for example, better pursue their own goals or to better collaborate with others (see Tomasello et al., 2005 for a review). This literature shows not only that both humans and apes possess important forms of goal understanding but also that humans have a unique motivation to share emotions and psychological states as well as to collaborate, thus increasing their ability to successfully engage in social interactions.

Behavioural evidence and theories on goal-directed behaviour
Further important evidence that behaviour is not only reactive but also goal-directed comes from the animal literature (Balleine & Dickinson, 1998; Yin & Knowlton, 2006; see Daw et al, 2005, for a review and computational account). The key experimental paradigm used to study the phenomenon (and to define the concept of "goal directed behaviour") in this literature is that of *devaluation* (Balleine & Dickinson, 1998; see Mannella et al., 2010, for a model). In this paradigm, rats are first instrumentally trained to associate a lever A to a food A and, in a separate session, a lever B to a food B. In a third session, the rat is satiated for one of the two foods; it may for example, be given free access to food A. The rat is put in front of both levers for the first time immediately following the third session and the frequencies with which it presses the two levers are measured in extinction (i.e., without food delivery). The results show that the rat presses the lever corresponding to the non-devalued food (for example lever B) with a higher frequency. This indicates that the current value assigned to the two possible goals ("getting food A" and "getting food B") is immediately translated into the selection of one of the two lever-pressing habits. Interestingly, subsequent research has shown that lesions of Amg or PFC (in particular the rat prelimbic cortex, PL, homologous to the human dlPFC) impair the devaluation effect. This indicates that the behaviour is controlled by the value that the organism assigns to goals (Balleine et al., 2003; Blundell et al, 2003; Hatfield, 1996).

Bayesian approaches
Another useful theory in this context is the predictive coding framework (Friston, 2003, 2005), which has been applied directly to the interpretation of mirror neurons (Kilner et al., 2007) and hence bridges functional/psychological and neuroscientific theories. Here, the mirror neuron system is organised in a hierarchy of cortical areas. This hierarchy includes in particular SMS at the lower level (visual recognition of movement), PC at the intermediate level, and IFC at the higher level (motor plans and intentions, i.e. high-level goals in our terms). Information encoded at each level of the hierarchy is the basis for forming an expectation of information that should be observed at the level directly below. For example, observing the higher-level goal "she is giving a farewell from far away" would imply an expectation that "arm waiving" should activate the lower level. Higher levels thus represent the causes (e.g., the intentions) and the lower levels the effects (e.g., the observed movements). At each level, expectations are compared with actual experience to form a mismatch error. The error is passed to the higher level, both to train the expectations and to form the activation at that level.

The theory produces various interesting predictions, namely that one should find (a) anatomical bidirectional connectivity between the involved brain areas, confirmed by the anatomy of the real mirror neuron system; (b) anticipatory activation of mirror neurons, confirmed for instance by Umiltà et al. (2001); (c) sensitivity of PC mirror neurons to context/intentions, observed in the experiments of Fogassi et al. (2005). The theory's advantage over to the psychological theories presented above lies in its Bayesian formulation. Using a probabilistic quantitative framework renders it operational and readily usable to produce detailed computational models.

2.2.2 Biological perspective and evidence on the goal and mirror systems

Mirror neurons and goal representation
Canonical neurons contribute to the preparation of actions by activating not only during action execution but also as a consequence of the perception of affordances (note, however, that they may be sensitive to the effects of top-down selection from the high-level goals and rewards reviewed in Section 2.1 even though they may not represent action goals,). Empirical evidence on mirror neurons, on the other hand, fits well with the idea that they represent the goals of actions (Figure 2). Evidence on the "social aspects" of mirror neurons in particular shows that they represent goals decoupled from the representation of action preparation/execution as they activate not only during action execution but also when a monkey observes the final hand/object state to which an action leads (for example a grasp executed by another monkey). Accordingly, they are often referred to as representing "goal-directed actions" or "a successfully terminated action pattern" (Gallese et al., 1996; Rizzolatti et al., 1996; Gallese & Metzinger, 2003; Rizzolatti & Craighero, 2004; Iacoboni et al., 2005).

Additional support that mirror neurons represent goals of actions comes from the anatomy of the mirror neuron system itself. The caudal portion of STS is known to respond to biological movements (Grossman et al., 2000; Hoffman and Haxby, 2000; Puce and Perrett, 2003), for instance of hands and arms. The information elaborated by this area is sent to parietal areas 7b and 7a. Specifically, area 7b receives connections from AIP and STS that transmit information about affordances and hand states while area 7a receives connections from STS and MIP/VIP and encodes information about the spatial relations between the hand and the object based on those (Rizzolatti et al., 1997; Rizzolatti & Singaglia, 2010). This information is then sent to IFC regions where mirror neurons are found and can thus support their activation with the final states (i.e., goals) of grasping actions involving particular relations between the target objects and the hand. Visual information reaching mirror neurons may thus be relevant in forming a representation of the body/environment relations representing the goals of actions.

Other evidence shows that mirror neurons can be anticipatory (which suggests a functional role), as they tend to activate before the action's final state is observed, or even when this is not seen at all. For instance, a slow readiness potential is observed in humans before the actual performance of a movement and the same anticipatory potential is recorded during action observation (Kilner et al., 2004). Moreover, Umiltà et al. (2001) showed that mirror neurons could activate not only when a monkey observes a hand grasping an object but also when the first part of the action is shown and the final part (previously seen by the monkeys) covered with a screen. This suggests that in some circumstances, the mirror neuron representation of action goals might activate before action execution or observation.

Experiments by Rizzolatti (1988) offer further indirect evidence that mirror neurons encode action

goals is. Here, a population of neurons in F5 was found that contained neither canonical nor mirror neurons and discharged both when the monkey grasped an object with the hand and with the mouth. The potential implications for the evolution of verbal communication from gestural communication aside (see section 5), this indicates that neurons in F5 tend to encode actions in an abstract form, which can be expected to hold for mirror neurons. Indeed, Umiltà et al. (2008) and Rochat et al. (2010) found compelling evidence that F5 mirror neurons encode action goals. Monkeys were trained to grasp pieces of food with both normal pliers and "reverse pliers" that required opening rather than closing the hand to perform a successful grasp. The results showed that some motor neurons that activated when grasping for food with the hand also did so when grasping with both pliers, when observing such actions by the experimenter and when observing an experimenter spearing food with a stick. This evidence strongly supports the idea that mirror neurons actually encode the goals of actions rather than the movements needed to perform them.

Mirror neurons and high-level goals
There is empirical evidence to suggest that the mirror system is sensitive to high-level goals of agents, putatively encoded in PFC. Iacoboni et al. (2005) devised an fMRI experiment focusing on human IFC in which participants were shown a video clip of an action performance ("grasping a cup") performed either in a context providing a clue to the long-term goal of the action ("having a cup of tea", "cleaning the table") or in a neutral one. Results showed that the observation of a grasping action performed within a context produces greater activity in the IFC mirror neuron area than the observation of grasping actions performed in the neutral condition or the observation of only the context. Based on these results, the authors suggest that the human mirror neuron system is not simply a mechanism for recognising actions, but also for encoding high-level goals.

Using fMRI, Cheng et al. (2007) showed that human participants who observe grasping actions directed at food exhibited a higher activation of IFC and PC mirror areas when they were hungry than when they were satiated, indicating that the mirror system is sensitive to the needs and drives of the participants. Moreover, the same scans showed a higher activation of orbital frontal cortex (OFC) as well as Amg and Hyp (known to interface the brain with the visceral body), indicating that OFC might be the origin of the observed modulation of mirror neurons activity.

Fogassi et al. (2005) illustrate the key role played by PC in merging information about goals encoded at different levels of complexity in their work on parietal mirror neurons. Here, the activation of a substantial number of those mirror neurons (but not all) was found to correlate not only with action goals (e.g., reach, grasp) but also with the high-level goal of these actions (e.g., place, eat). In the experiment a monkey had to perform either a "reach → grasp → transport" or a "reach → grasp → bring-to-mouth" sequence. Interestingly, the different phases of the sequence, for example the grasping action, are encoded by different neurons depending on the high-level goal (i.e., eating vs. placing). This indicates not only that mirror neurons encode action-goals, but also that the parietal region is a fundamental brain area where information of high-level goals encoded in PFC and information related to affordances and action goals are integrated.

Hamilton and Grafton (2007) provide further relevant insights on the representation of goals at different levels of abstraction within IFC and PC. In these experiments, human subjects were shown clips of a hand acting on an object (for example a box with a sliding lid) in order to obtain one of two different outcomes ("high-level goals" in our terminology); for example opening or closing the box. Crucially, the outcomes could be achieved with different actions involving different kinematics. For

example, the lid could be pushed with the index finger or with a precision grasp. This dissociation allowed the authors to identify IFC and inferior parietal cortex (IPC) – in particular their right portions (in right handed participants) – as the areas that most correlated with the outcome of the action rather than with its kinematics. The authors thus argue that PC (in particular IPC where parietal mirror neurons have been found; see Fogassi et al., 2005) has a notable importance in encoding high-level goals alongside PFC. PMC regions, on the other hand, might be more involved in encoding actions in terms of their kinematic aspects. These results indicate that the ultimate needs and high-level goals represented in PFC might actually be translated into specific actions via a strong bias exerted on the representations encoded by mirror neurons, in particular within PC, and that the latter plays an important role in representing high-level aspects of behaviour ("intentions", overall needs, etc.).

Further, research on the neural causes of autism spectrum disorders (ASD) can help to clarify the relation between mirror neurons and high-level goals. Some theories associate this syndrome with deficits in mental functions supporting the comprehension of others' intentions (Theory of Mind; ToM) whereas others associate it with deficits of the mirror system. The ToM account of autism derives from a symbolic, abstract view of cognition (Leslie, 1987) and originates in findings that children with ASD have specific difficulties with pretend play (Wing et al., 1977) and false belief tasks (Baron-Cohen et al., 1985). These difficulties are linked with the inability to represent others' mental states (Frith et al, 1991) or to decouple mental states from reality (Leslie, 1987). Note that the very nature of "mental states" is still debated as they often refer to different constructs such as desires, goals, emotions, beliefs, or perceptions (Frith et al, 1991; Saxe et al., 2004).

In contrast, the "broken mirror-system theory" is associated with an embodied approach highlighting the key role of mental simulation in understanding others (Gallese, 2003). These theories stress the importance of low-level mechanisms of social behaviours such as the recognition of actions and action-goals. Autistic patients have no difficulties in recognizing basic motor acts (e.g., grasping or reaching; Hamilton et al., 2007; Fabbri-Destro et al., 2008), indicating that their basic mirror system remains intact. However, they may show limitations in processing action chains forming whole behaviours (Fabbri-Destro et al., 2008), especially when the underlying actions involve a deep understanding of object function (Zalla et al., 2010). This in turn leads to a failure to understand other's intentions behind the observed motor acts (Iacoboni & Dapretto, 2006). It also causes deficits in imitation tasks (Williams et al., 2004; Iacoboni & Dapretto, 2006). Hamilton (2009) proposed that the complementary strengths of these ToM and mirror-neuron accounts should be exploited to close the gaps in the understanding of ASD and that computational models might play an important role in doing this.

A recent proposal (Kilner, 2011) strengthens the idea that the ventral pathway in general and the anterior inferior frontal gyrus (IFC) of PFC in particular encode high-level goals and thus bias areas in which mirror neurons are found. Kilner (2011) claims that "intentions and goals" (where the intention or goal of an action is understood as an *abstract representation* of the action for which there is a one-to-many mapping of the action onto possible implementations) are represented in PFC areas of the ventral pathway. The theory also proposes that they are organised hierarchically, from the more anterior IFC (Broadman area BA47) to the medial (BA45 and BA44) and the more posterior IFC (BA44 and B6 – the latter part of PMC). This is in agreement with the view that PFC plays a prominent role in the representation of high-level goals and extends it with the notion that "intentions and goals" are represented in PFC at multiple levels of abstraction.

We close this section by referring to an issue related to the high-level control of the mirror system and

the role that inhibitory mechanisms might have in the implementation of such control. In a physiological study involving monkeys engaged in a gaze control task, Shepherd et al. (2009) found two sub-populations of mirror neurons within LIP. Neurons of one population responded both to the direction of the observed gaze and when the monkey moved the eyes in that same direction whereas neurons in the second population were *suppressed* during the observation of the social gaze. The authors suggest that the population of neurons inhibited in the social conditions might possibly serve to maintain fixation on the observed face when this is useful. Similarly, Mukamel et al., 2010 (see introduction), found that a sub-population of neurons with mirror properties in human SMA and hippocampal areas exhibit inhibition during action observation. These authors interpret this inhibition as a possible means to distinguish between the perceptual and motor aspects of actions performed by the self and those performed by others. These experiments have two implications relevant for the issue of high-level control of mirror neurons. The first is that they illustrate a particular modality with which high-level goals (e.g., "to continue to fixate the face" or "to follow the observed gaze") might modulate the activity of mirror neurons. The second is that the specific mechanisms of this modulation likely involve inhibitory processes. We will expand on this when reviewing models of affordances and mirror neurons in the following section.

2.3 Interim summary

This section has presented a review of the psychological and neuroscientific literature supporting two general principles of organisation of brain and behaviour. The first is that the brain continuously accesses a multitude of affordances via multiple dorsal pathways. It therefore has to have a way to select only those that produce actions relevant for the agent's goals as well as to avoid interferences. This selection is accomplished on the basis of processes taking place mainly within the ventral neural pathways, in particular within PFC, which is informed on the external context and the internal needs of the agent. PFC exerts this selection on the basis of a number of top-down mechanisms and processes acting on various stages of the dorsal neural pathways. The second principle is that a fundamental component of the representation of actions is related to their goals and that mirror neurons play a key role in this. In the review, we highlighted the fundamental advantages in term of behavioural flexibility conferred by these goal representations.

Overall, the behavioural and neuroscientific reviews of the previous sections have not only highlighted a number of ways in which relations between affordance and mirror systems can be found, but they have also made it clear that we still lack a full understanding of these relations. The next sections aim to develop a framework that allows studying the two systems in an integrated fashion (or in isolation if desired). We believe this is an important methodological step required to further our understanding of the relations between these systems using computational models. We therefore first review existing models of affordance and mirror systems in the next section. We focus in particular on identifying the computational mechanisms that the brain might have evolved to implement the two principles mentioned above. Section 4 will then build upon this knowledge to propose the integrated framework.

3 Overview of existing models of affordance and mirror systems

This section presents a review of major computational models of affordance selection and mirror neuron systems with the aim of showing how the two principles illustrated in section 2 can be implemented in detailed computational terms. We first review scientific models of affordance processing and PFC affordance control, briefly discussing how they relate to each other. We then

review technological models of affordances that could be exploited in the future to model the processes that lead to the acquisition of affordance representations in a more detailed way even though they are more abstract with respect to biology. Finally, the section reviews data-driven models of the mirror neuron system discusses how they relate to affordance models.

3.1 Models of affordance processing and control

We classify affordance models as either *scientific* or *technological*. Scientific models aim to understand natural phenomena and to produce predictions that are testable in new psychological or neuroscientific experiments. For this reason these models are strongly inspired and/or constrained by psychological and/or neuroscientific empirical evidence collected in specific empirical experiments. Technological affordance models, on the other hand, usually aim to allow more efficient intelligent machines and robots. They may be inspired by experimental evidence but are usually not strongly constrained by it. The two approaches have complementary strengths and future models might benefit from the integration of the computational mechanisms they propose. In the following we first review some of the main scientific models of affordances and affordance control, focussing on those that are most relevant to the issues reviewed in the previous sections (see Caligiore et al., 2010, for a wider but less focussed review of models that touch these and other aspects related to affordances).
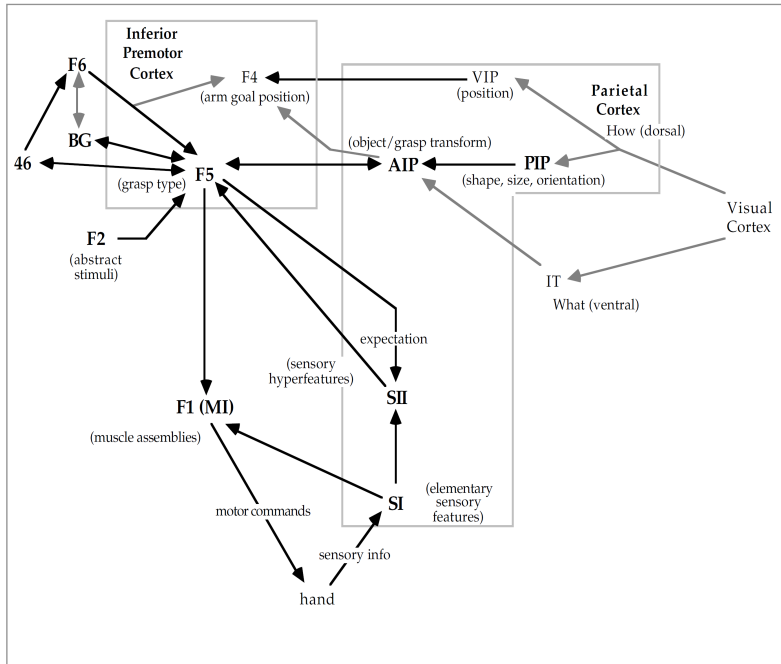
The FARS model

FARS (Fagg & Arbib, 1998, see Figure 3) is a seminal model of affordances that has inspired many subsequent models. It was developed to study the control of grasping in non-human primates and was constrained by multiple neuroanatomical and neurophysiological findings (Sakata et al., 1995; Jeannerod et al., 1995; Rizzolatti et al., 1997). The model was also tested within an embodied set-up using a 15-DOFs kinematic hand (the model also controlled an arm but this was abstracted).

In FARS, the parietal and somatosensory areas extract the state of the object and the body and pass this information to AIP to let it compute the object-body relation and hence the grasp affordances elicited by the object (e.g., the affordances related to a precision and a power grip). The affordances are then communicated to F5, which has the role of selecting one of them with a bias from F2 (encoding the task) and to transform it into a sequence of movements (e.g., wait → grasp → hold → release) aided by timing signals from area 46 and F6. At the same time, the VIP-F4 neural route guides the reaching movements of the arm. The movements are then executed via M1.

FARS also captures some of the mirror neuron properties reviewed in section 2. SII features bidirectional connectivity with F5, allowing the system to not only guide action based on proprioception, but also to form expectations about the possible outcomes of actions to eventually trigger a reprogramming of the grasp in the case its execution leads to outcomes different from the expected ones. FARS also has a VC-ITC-AIP neural pathway (dropped in the MNS models reviewed below), whose function it is to allow the ventral pathway to provide an approximate "default" affordance based on coarse aspects of objects, such as size (see the discussion on the results of Castiello and Jeannerod, 1991, in section 2).

Regarding the internal computational functioning of the model components, the initial extraction of the hand and object properties is carried out using non-neural computations based on 3D geometrical calculations. Each resulting affordance is represented in a neural unit in AIP. This activates the initial unit of a chain of neural units within F5, each representing a movement of the action sequence. These

cells have forward excitatory connections and backward inhibitory connections that assure a sequenced execution of the action movements with the support of timing signals from F6/BG. Units representing distinct affordances or actions within AIP and F5 are connected by mutual inhibitory connections implement (in particular within F5) a neural competition assuring that only one affordance/action is selected and executed. Within F5, this selection is facilitated by a top-down bias from F2. All connection weights within FARS are hardwired.

Figure 3: High-level overview of the FARS model (Reproduced from Fagg & Arbib (1998) with permission from Elsevier). FARS focuses on the AIP-F5 system within the dorsal neural pathway, but also considers other areas: (a) parietal areas (cIPS – here called PIP, posterior intraparietal area): for the extraction of object features such as shape, size and orientation, and VIP, for the detection of the target location; (b) prefrontal areas (area 46 of PFC): for implementing working memory, e.g. for remembering recently executed movements; (c) dorso lateral premotor cortex (F2 in monkeys): for the "instruction stimuli" that allow selecting a particular affordance/action among the available ones; (d) basal ganglia (BG) and the supplementary motor cortex (F6): both used for action sequencing; (e) premotor areas (F4): for the control of reaching; (f) primary motor areas (M1): for actually controlling the multiple joints of the system; (g) somatosensory areas (primary, SI, and secondary, SII, somatosensory areas): for encoding arm/hand proprioception and touch.

A dynamic neural field approach
Cisek (2007) introduced the *affordance competition hypothesis* (see also Cisek & Kalaska, 2010). The model was proposed to account for experiments involving monkey areas PMC and M1. These experiments show that neurons recorded within those areas tend to simultaneously implement a double function (Cisek & Kalaska, 2002): the selection of action parameters (e.g., the direction of reaching movements) and the selection of a certain action based on current affordances and PFC top-down control (e.g., the actual triggering of a reaching movement).

The model is based on a dynamic neural field network (Erlhagen & Schöner, 2002) that integrates affordance and PFC top-down information, similarly to what has later been done in TRoPICALS. The potential affordances compete against each other under biasing signals supplied by PFC until a single response is triggered. The PFC processes are not explicitly implemented in the model, and its

connection weights are hand-coded. The model, although simple, corroborates the idea that the top-down PFC bias can contribute to the selection among possible affordances based on a neural competition mechanism.

The TRoPICALS model
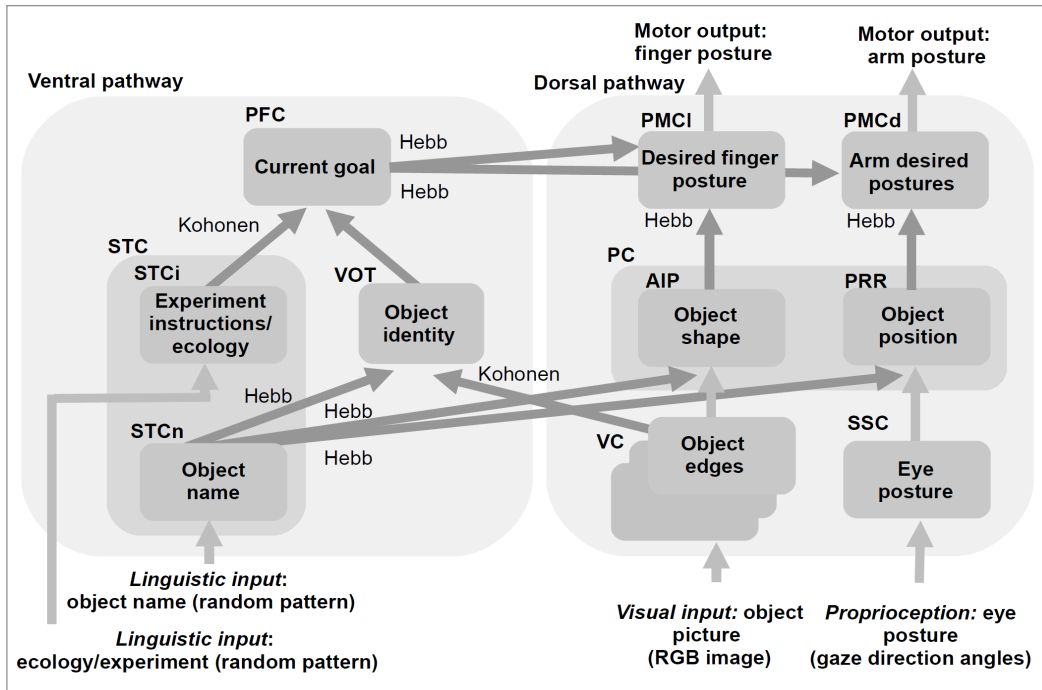
Figure 4: Architecture of TRoPICALS (Reproduced from Caligiore et al., 2010). Boxes indicate components of the model. The acronyms at the top-left corner of each box indicate the brain anatomical areas whose functional aspects are reproduced by the model (see Caligiore et al., 2010 for more details). The label inside each box indicates the type of information encoded by each component. The model architecture contains a ventral pathway (VC-VOT-PFC-PMC) and two dorsal pathways (VC-AIP-PMCl route for guiding grasping, and the VC-PRR-PMCd route for guiding reaching). In the ventral pathway, VOT is relevant for object recognition while the PFC-PMC connections abstract the PFC-SMC-PMC and PFC-PC-PMC connections. PFC also receives information from the superior temporal cortex (STC) representing the task to be accomplished in the experiment.

TRoPICALS (Caligiore et al., 2010) is a computational model of affordance control designed to account for compatibility effects studied experimentally in cognitive psychology. It does this based on an architecture that considers PFC as a key source of the top-down control of the areas that participate to the selection of affordances and execution of actions (the first principle of section 2). Compared to FARS, TRoPICALS is focussed more on functional aspects and less on neural details. However, it is a system-level model with a macro-architecture constrained by known brain anatomy and has been tested within a weakly embodied model (a camera and a simulated robotic hand controlled in open-loop).

With respect to function and learning, VC performs image edge extraction, AIP extracts the shape of objects, and VOT categorises objects using a self-organising map (SOM; Kohonen, 2003). The AIP-PMCl and PRR-PMCd routes (i.e., the two dorsal neural routes transforming affordances into grasping and reaching actions) are trained on the basis of a stylised Hebbian-based reinforcement learning process that allows the system to learn to associate suitable actions (PMCl, PMCd) to available

affordances (AIP, PRR). PFC uses a second SOM to form representations that combine the seen objects (VOT) and the task to be accomplished (STC) to shape the current high-level goals used to bias action selected within PMC. PMC integrates affordance information from PC and goal-based information from PFC using a dynamic neural field (Erlhagen & Schöner, 2002; Cisek, 2007) that selects actions through neural competition (actions are encoded using population codes as desired postures hand/arm). A crucial assumption is that the time needed by this network to achieve an "action-triggering threshold" corresponds to reaction times measured in psychological experiments on compatibility effects.

The account of compatibility effects given by TRoPICALS is based on four general brain organisation principles incorporated in its architecture: (a) the two-route organisation of the sensorimotor brain into the ventral and a dorsal neural pathways; (b) the guidance of action selection based on PFC "instructions"; (c) the selection of actions within PMC based on the competition between different affordances with bias from PFC; (d) the capability of language to trigger internal simulations of the referents of words (Barsalou et al., 2008; the latter principle, less relevant here, was introduced to account for compatibility effects involving language. The acronym "TRoPICALS" summarises these principles: Two Route, Prefrontal Instruction, Competition of Affordances, Language Simulation). The model reproduces compatibility effects as an agreement or disagreement (compatibility/incompatibility) of top-down PFC bias with the available affordances of objects produces slow or fast reaction times.

TRoPICALS was recently extended to augment the selection capabilities of the modelled PFC with inhibitory mechanisms (Caligiore et al., 2012). This was done to account for the experiment of Ellis et al. (2007) involving positive and negative compatibility effects produced by respectively target objects and distractors (recall from section 2.1.1 that the negative effects of the target experiment indicate the presence of an active inhibition of the affordances elicited by the distractors). The inhibitory effect was implemented by creating an inhibitory neural pathway from PFC to PMC: this pathway abstracts the inhibitory effects that PFC can exert on motor cortex preparing actions (e.g., PMC) via BG and SMC.

TRoPICALS provides a broad framework to account for several types of affordance related compatibility effects involving grasping, reaching and language, and is capable of generating novel testable predictions (see Caligiore et al., 2010), including some predictions on the possible outcomes of compatibility experiments with Parkinson patients (see Caligiore et al., 2011; 2012; the latter predictions are relevant as Parkinson patients have damaged excitatory and inhibitory neural circuits linking PFC to PMC via SMC).

Relations between scientific affordances models
Both FARS and TRoPICALS investigate the cooperation between the dorsal and ventral pathways to select the most suitable affordance in a given context but differ in an important way. FARS focuses on the role of parietal areas in forming affordances, in particular on the role of the AIP-F5 system in selecting an affordance among the available ones and in correctly executing the corresponding action-movement sequence. The influence of PFC on this process – and of the ventral neural pathway in general (e.g., via the ITC-AIP connections) – plays a marginal role in the model.

TRoPICALS, on the other hand, focuses on the role that the top-down PFC bias exerts on the selection among different affordances on the basis of the current context and the system high-level goals. This allows TRoPICALS to investigate the automatic activation of affordances and their eventual contrast or

agreement with the actions that are requested by the task (compatibility effects). In this respect, FARS and TRoPICALS focus on complementary aspects of affordances.

Another difference regards the models' development: while FARS is not trained at all, important connection weights of TRoPICALS are trained on the basis of biologically-inspired learning rules. FARS and TRoPICALS are also similar in the mechanisms used to select affordances, both based on a neural competition. TRoPICALS in particular uses a dynamic neural field to simulate affordance competition mechanisms within PMC: this has been shown to be a plausible model of the neural processes supporting affordance and action selection actually taking place within the premotor/motor cortex (Cisek, 2007).

3.2 Technological models of affordances

Technological affordance models are numerous and often focus on machine learning/engineering issues (rather than studying brain or behaviour), rendering a detailed review neither viable nor necessary within the scope of the present paper. However, the fact that these models are typically implemented in (simulated or real) robots implies that they may contain useful computational techniques that authors of scientific models may find useful. We therefore focus on these aspects here.

Several studies in the field of robotics have investigated the problem of *learning affordances* and their subsequent use in tackling different tasks. For instance, the biologically inspired behaviour selection mechanism proposed by Cos-Aguilera et al. (2004) uses clustering and self-organizing feature maps to relate object invariants to the success or failure of an action. In the work of Fitzpatrick et al. (2003), a robot learned the direction of motion of different objects when poked and used this information at a later stage to recognize actions performed by others. Both approaches learn specific types of affordances using relevant information directly extracted from sensory inputs. Fritz et al. (2006) propose a more sophisticated solution in which the learning procedure also selects the appropriate features from a set of so-called visual Scale Invariant Feature Transform (SIFT) descriptors. Stoytchev (2005) puts a stronger emphasis on action and focuses on the importance of sequences of actions and invariant perceptions to discover affordances in a behavioural framework.

More recently, Dogar et al. (2007) presented a goal-oriented affordance-based control for mobile robots based on the formalism suggested by Sahin et al. (2007). Here, previously learned behaviours (such as "traverse" or "approach") are combined to achieve goal-oriented navigation. The model proposed by Akgun et al. (2009) uses self-organising maps and support vector machines to learn a mapping between relevant features and effect categories in an affordances learning task. Böhme and Heinke (2009) propose a model in which the attention focus depends on the affordances and contact points suitable for grasping of the objects. Finally, Montesano et al. (2008) have proposed a model which uses a Bayesian network within an imitation learning framework, to efficiently deal with uncertainty, redundancy, and irrelevant information in training a humanoid robot to interact with objects according to suggested affordances.

The above models are all excellent examples of how to design a robotic platform capable of extracting relevant information from sensory inputs in order to learn object affordances. Furthermore, some of these models are inspired by the behaviour of real organisms. However, they do not typically take into account detailed neurophysiological or psychological evidence regarding the mechanisms underlying affordance processing. It is therefore of interest to discuss an approach which is guided by such

evidence more closely.

Sahin and Erdogan (2009) start from the affordance formalisation proposed by Sahin et al. (2007) and develop an affordance model that incorporates mirror and canonical neurons from a functional perspective. In their model, affordance relations can be seen as relations that connect three neural fields encoding (a) the object (along different features such as size and shape), (b) the behaviour as a motor chain that connects to motor areas, and (c) the effect. A goal signal can prime the effect desired in a certain context. The motor chain representation needs both exteroceptive feedback (such as visual observation of hand-object relation) and proprioceptive (e.g. motor) feedback to execute the behaviour in a closed loop manner. Crucially, *a second parallel field of motor chains* can be trained to imitate the first motor chain layer. After training, the second motor chain layer can provide predictive sensory feedback to the first motor chain layer which would allow it to execute faster. The parallel motor chains can also be used to activate the effect layer to indicate the intention of the agent being observed.

The model of Sahin and Erdogan (2009) has two main shortcomings. First, it has not yet addressed some recent experimental findings such as the possible interaction of mirror and affordance processes during action observation (see Bach et al., 2011). Second, the work has only proposed an outline still lacking in detail of how the model can be computationally implemented. However, the model idea is developed with a robotic implementation in mind and therefore presents suggestions on how to deal with some of the issues encountered in designing a model of mirror neurons and affordances processing embedded in a robotic body.

3.3 Relations between the technological and scientific models

It is clear, as stated above, that scientific and technological models of affordance processing have fundamentally different aims. While the former try to further elucidate the mechanisms underlying affordance processing in the human brain, the latter are concerned with providing artificial agents with improved functionality. Although this creates difficulties in establishing a "dialogue" between the two types of models and the scientific communities that develop them, there is potential for mutual improvement between the two approaches.

Scientific models, for example, tend to exist at best in simulation or as computational or mathematical implementations, or tend to perform strong abstractions and simplifications at the sensory and motor level. While powerful from a theoretical point of view, such implementations cannot capture the complexities faced by real organisms in the real world. These complexities however might require a certain brain structure that would be difficult to capture after the aforementioned simplifications.

Technological affordance models, on the other hand, tend to focus on typical engineering tasks that may miss some of the more interesting challenges encountered by real organisms, for example the problem of selecting affordances and actions based on multiple high level "needs" and goals, or the problem of understanding the intentions of the users or other robots. In this context, TRoPICALS for instance illustrates how scientific models might complement technological ones by providing a comprehensive mechanism to deal with issues arising from competing affordances.

3.4 Models of the mirror (neuron) system

The Oztop Taxonomy

Oztop et al. (2006) presented a comprehensive, computationally informed review of mirror system models. Rather than duplicating this review, we highlight some of its major conclusions and focus on data-driven models of mirror-neuron systems, more relevant for this work. One of the main contributions of Oztop et al. (2006) is a taxonomy of mirror neuron models based on their underlying methodologies (Figure 5), classifying models into four categories, of which the "data driven" category is the most important one for the present paper[4].
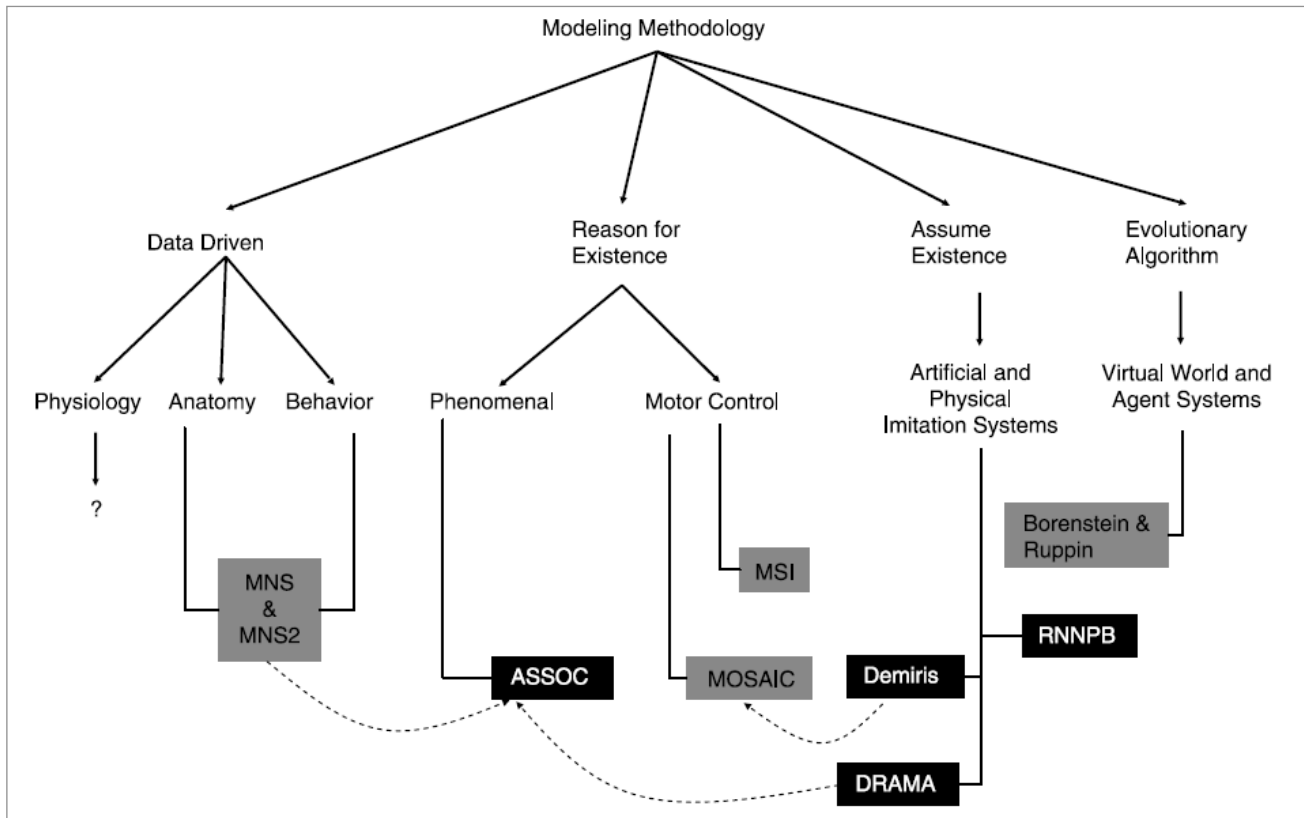
Figure 5: The Oztop taxonomy of mirror neuron models. Reproduced from Oztop et al. (2006) with permission from Elsevier.

Data-driven models are relevant for researchers interested in understanding brain and behaviour as they attempt to generate new accounts of the mirror neuron system and new empirical predictions, for instance on their possible functions. The main model in this category at the time of the Oztop et al. (2006) review was the Mirror Neuron System model (MNS model, Oztop and Arbib, 2002). Since then, however, the MNS2 I and II models (Bonaiuto et al., 2007; Bonaiuto & Arbib, 2010), a "chain model"

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[4] The other categories are: "reason for existence", "assume existence" and "evolutionary algorithm". Models in the "reason for existence" category determine a functional role of the mirror system from other assumptions incorporated in the models (e.g. Tani et al., 2004; Haruno et al., 2001). Models of the "assume existence" category simply assume the existence of the mirror neuron system and use it to implement higher level functions (e.g. the ability to imitate, see for instance Demiris and Johnson, 2003). Models from both categories are based on robotic or simulated models and generate or assume capabilities related to mirror neurons similar to those observed in real organisms. The "evolutionary algorithm" category includes models that are evolved to produce mechanisms and behaviours that can be related to mirror neurons (e.g. Borenstein and Ruppin, 2005). The general reasoning behind these models is that the emergence of a mirror neuron system supports the idea that the functions implemented by such system strongly enhance the biological fitness of organisms.

on action sequences (e.g. Chersi et al., 2006, 2011) and a model focussing on the formation of mirror neuron-based goal representations in PC (Thill and Ziemke, 2010; Thill et al., 2011) have been proposed. We now focus on these data-driven models as they are most relevant for this work, in particular in relation to the second principle (mirror neurons representing action goals) and to build the integrated model proposed in section 4.

The MNS model

The MNS model (Oztop & Arbib, 2002) is a seminal model that extends FARS through the addition of brain areas supporting mirror neurons within F5 (Figure 6). The whole system architecture is formed by three sub-systems (called "grand schemas" in the original paper). The first is based on a non-neural abstraction of FARS functionalities for grasping (pivoting on the AIP-F5_canonical interplay) and extended with the functionalities for controlling reaching (ascribed to the dorsal neural route (MIP/LIP/VIP)-F4-M1). The second sub-system computes the *hand-state* based on a visual analysis. This is a key concept of the model and includes both pure hand configuration parameters (e.g., hand aperture and hand velocity) and parameters relating the hand to the object to be grasped (e.g., hand-object distance, angle between hand and object axes). This visual processing involves the associative visual area STS, responsible for biological motion recognition as well as parietal areas 7a, (encoding the hand state) and 7b (important for integrating the information on the hand state received from 7a). The visual processing also involves information on object affordances (received from AIP). The third and most important sub-system is formed by the F5_mirror neurons and the connections they receive from area 7b. Interestingly, the ventral stream (including the ITC-AIP connection present in FARS) is completely left out of the model.
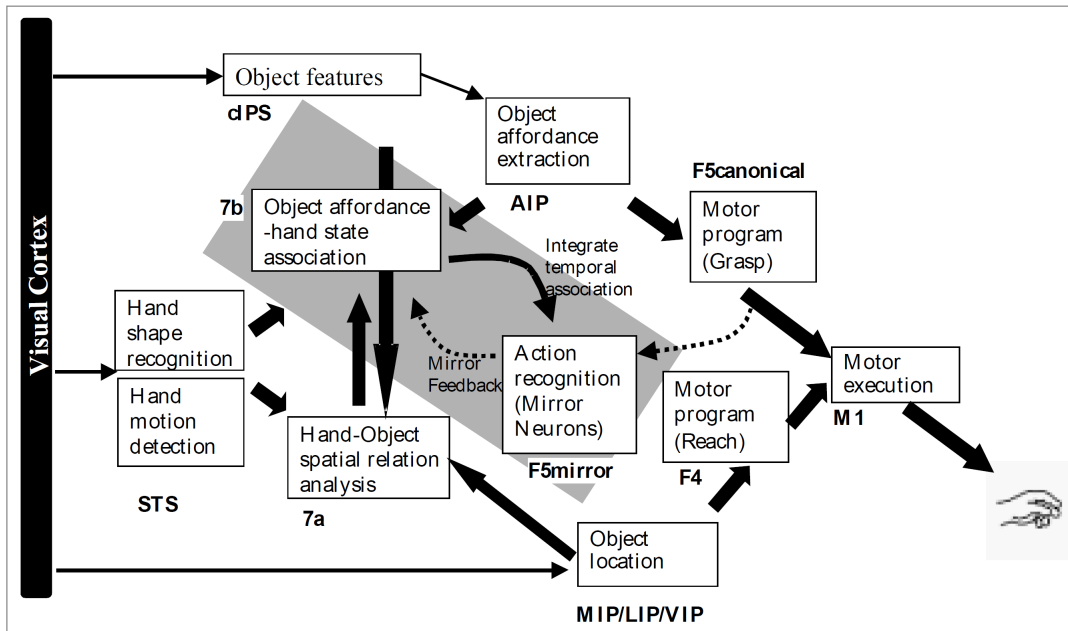
Figure 6: Architecture of the MNS model. Reproduced from Oztop and Arbib (2002) with permission from Springer.

The sub-system subserving grasping (equivalent to FARS reaching functions) and reaching functions (abstracted in FARS) is implemented in MNS using a non-neural "grasp simulator" that generates and executes the trajectory of the arm-hand system based on the positions of the object, arm and hand to perform a suitable reach-grasp. This simulator solves the inverse kinematics problem (generating motor

commands based on a desired grasp) based on a noisy gradient-descent mechanism. The subsystem computing the hand state is based on image processing techniques for colour segmentation and feature extraction that allow inferring the positions of hand-finger segments and finding the best matching posture-model for them. The mirror sub-system is implemented with a standard error-back propagation neural network trained to map the "hand state-object affordance" input (encoded in area 7b) onto the performed action output (encoded in area F5_mirror) based on the teaching signal (received from F5_canonical). The MNS model can operate in two modes: "prehension mode" and "action recognition mode". In prehension mode, the system performs actions (and trains the mirror system) based on the AIP-F5 and MIP/LIP/VIP-F4 circuits. In action recognition mode, the system observes a hand moving towards an object. The cIPS-F5 circuit still extracts and processes the affordances of perceived objects and sends them to area 7b; simultaneously, STS processes the motion and shape of the observed moving hand and again sends it to areas 7a and 7b. The 7b-F5_mirror system recognises the observed action based on information received from AIP and STS.

The crucial feature of the MNS model (apart from the introduction of the hand-state computation performed by the mirror system discussed above) is the postulated relation between the canonical and the mirror systems. Specifically, the activation of canonical neurons is used to train the mirror neurons (a) to recognise the visual appearance of the performed own actions and (b) to categorise this visual appearance in terms of the representation of the related motor commands. In this way, the model allows the reproduction of various empirical findings and the generation of a number of neurophysiological predictions (see Oztop & Arbib, 2002). One example of such a prediction is that mirror neurons often activate in anticipation of the achievement of the outcome of the observed actions.

The MNS2-I model
The MNS2-I model (Bonaiuto et al., 2007, Figure 7) is an enhanced version of the MNS model. It reproduces two additional key findings related to mirror neurons: (a) mirror neurons may fire not just when an action is observed but also when a sound associated with that action is heard (Kohler et al., 2002), and (b) mirror neurons fire during the execution of the last part of the observed action even if in this phase the observed hand or the object are hidden from view of the monkey (Umiltà et al., 2001). To account for these two additional functionalities, the system has been augmented with (a) components to perform audio-processing (simulating the processes taking place in auditory cortex), connected to the mirror neurons, and (b) components related to PFC and area 46, connected to areas 7a and 7b to implement working memory (which encodes information needed to drive the mirror-neuron system when the hand/object are hidden).

Computationally, the first extension (to process auditory information) is based on a recurrent neural network trained with back propagation through time (BPTT; Werbos, 1990) to associate some features extracted from the sound wave to sound categories related to the various possible actions (e.g., power and precision grasps). The output units of this network are then associated through Hebbian learning with the mirror neurons during action execution. The second extension (simulating working memory) is based on a second recurrent neural network, again trained with BPTT. The use of BPTT is a significant improvement the original MNS, which used a heavily pre-processed input to take into consideration the recent past of the observed movement sequence. MNS2-I can directly take the current hand state and object affordance as input that can be integrated over time. This allows the system to reproduce the target data related to mirror responses when the observed hand and object are hidden.
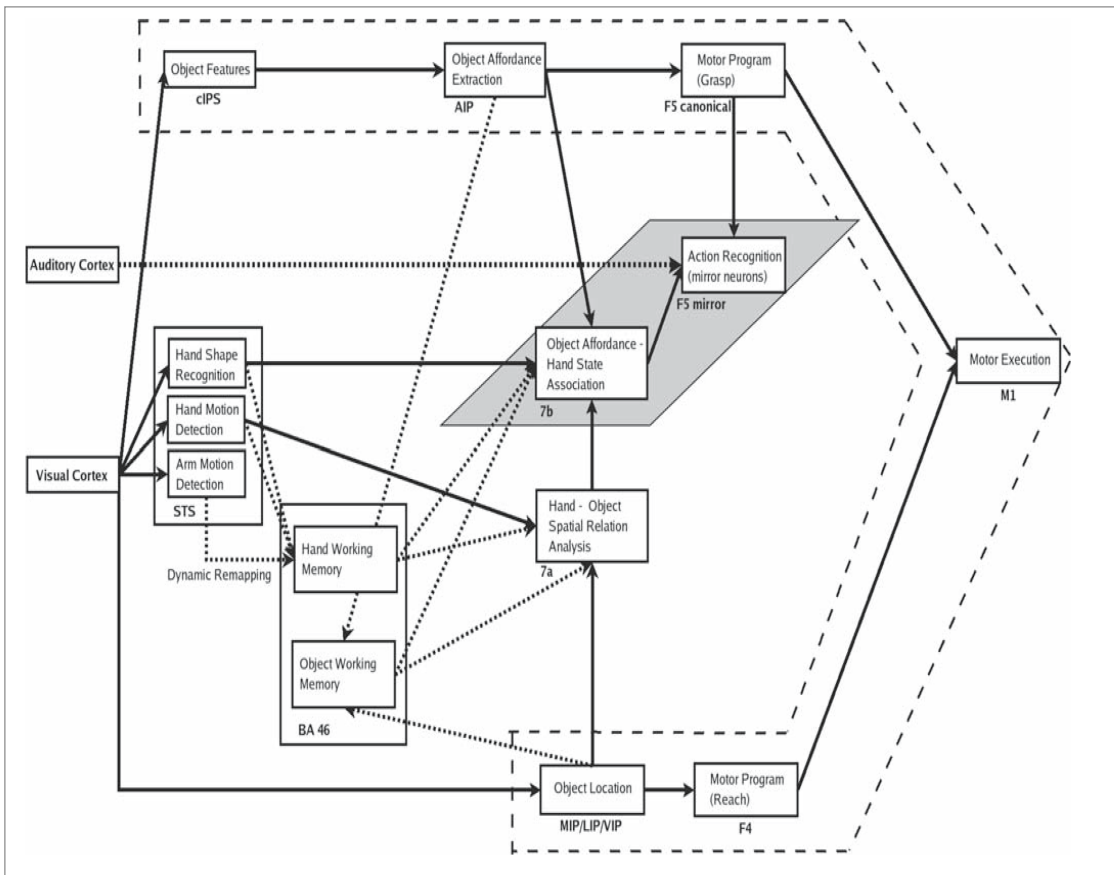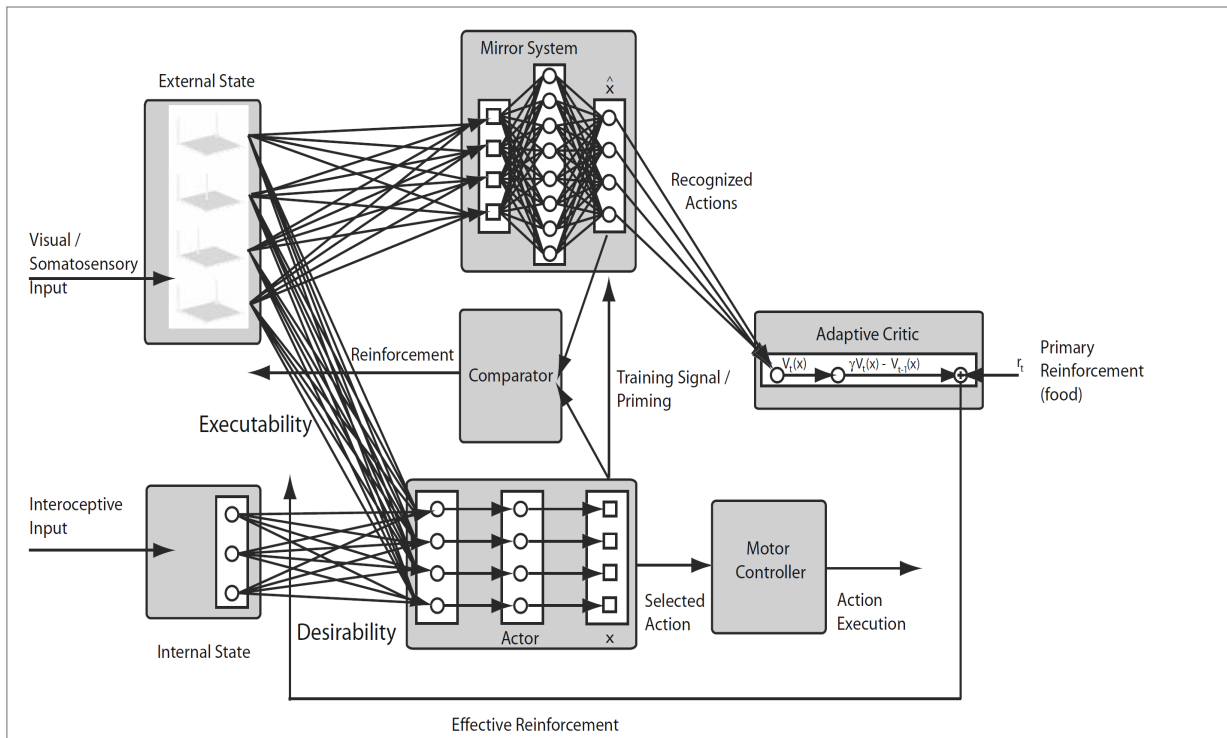
Figure 7: Architecture of the MNS2-I model. Reproduced from Bonaiuto et al. (2007) with permission from Springer.

The MNS2-II model

Recently, Bonaiuto and Arbib (2010) presented MNS2-II to study other aspects of mirror neurons (Figure 8). Computationally, this model represents a departure from its MNS and MNS2-I predecessors. First, the model does not consider the social aspects of mirror neurons but focuses on its function in monitoring the outcomes of own action execution. This is used to investigate how such a mechanism could be used to discover how known actions can be applied in novel ways if the environmental conditions change. Second, the system is tested in an abstract non-embodied setup (2D environment with x-y target object and actuator states), so actions (e.g., reach, grasp, eat) are encoded with localist units and the sensory input (object state, actuator state, objects-actuator spatial relations, etc.) with neural population codes. Third, the FARS functions are now (neutrally) implemented using an actor-critic reinforcement learning model (actor-critic RL; Sutton & Barto, 1998) which learns to select actions by trial-and-error based on a "food" reward. This is crucial as it introduces trial-and-error learning as an important learning process compared to the supervised learning algorithms used in previous models.

The mirror system is implemented, as in MNS, using a feedforward neural network trained with back propagation but its output is used as input to the "critic" of the model (motivated by the assumption that actions recognised by the mirror neurons indicate a successful achievement of an action outcome that

brings the system closer to the final high-level goal, thus serving as a viable basis to evaluate the current situation). The connections entering the actor (i.e., the connections between the hand state-object affordance and the actor neurons representing the actions) represent the *executability* of actions in the current sensed state. These connections are increased when there is a match (a pseudo-reinforcement) between the action selected by the actor and the mirror unit recognising the intended effect (i.e., the goal) of the same action and decreased otherwise. The system is thus capable of evaluating if an action can be executed with success in a given context based on mirror neurons encoding the expected outcomes following the execution of a certain action.

Figure 8: Architecture of the MNS2-II model. Reproduced from Bonaiuto and Arbib (2010) with permission from Springer.

The model also incorporates a second important concept: the *desirability* of actions. The system possesses internal motivational state units (only one in this implementation: "hunger") that project to the action units of the actor. The weights of these connections encode the desirability of actions given a particular internal state of the system. The desirability of one action is updated if the corresponding mirror neuron activates, even when it was not the intended action. This event signals that the achieved final state stood in an appropriate relation to the initial state fed to the mirror system. The desirability of an action is updated by increasing or decreasing it in proportion to the (signed) TD error of the RL algorithm[5]. The key idea here is that if the system has a certain internal homoeostatic need (e.g., "being hungry") and executes an action successfully retained by the mirror system (successful in that it achieves its goal), this action becomes desirable if it also leads the system closer to the satisfaction of the homoeostatic need. In this respect, desirability allows the model to capture the fact that high-level goals are related to the adaptive value of the overall course of action and not only to the

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[5] The discounted properties of TD learning assure that the desirability of actions in a given internal states are higher for actions closer to the final high-level goal (Sutton & Barto, 1998)

"perceptual/cognitive" aspects of the outcomes of actions.

In MNS2-II, mirror neurons accelerate the discovery of novel potential uses of actions in novel contexts if their outcome, while caused by other actions, is recognised as useful in the new context. This is one of the first models where (a) mirror neurons are used to monitor action outcomes, (b) high-level goals related to homoeostatic regulations are introduced and related to action-goals and (c) a realistic trial-and-error procedure for associating actions to affordances is exploited.

The model of Metta et al. (2006)
Metta et al. (2006) present a model in which mirror-like representations as observed in brain area F5 develop simply from the interaction of an agent with its environment. The overall functioning of the model is very similar to that of the MNS models, so we only review it briefly. The model was tested within a robotic implementation to explore the automatic acquisition of affordances: this was done based on the approach of Fitzpatrick et al. (2003) previously discussed. The core idea explored in the model is that mirror neurons can emerge based on learning processes taking place while the agent is autonomously interacting with the environment. In particular, the system can observe the effects of its own actions in the world while it acts (as can the MNS models). This information reaches the mirror neurons, which can (if activated by canonical neurons) develop the capacity to respond to the observation of actions even when other agents execute these.

Models of mirror neurons as goal representations
A number of models are concerned with neurophysiological results such as those reported by Fogassi et al. (2005). These models address how mirror neurons represent (low-level) action goals and high-level goals. As previously discussed, Fogassi et al. (2005) found that some mirror neurons in the inferior parietal lobe (IPL) tend to encode both specific *motor primitives* (e.g. "reach", "grasp", "bring to mouth") and the overall (high-level) goal of the action sequence to which the primitive belongs (e.g. "eat"). The models typically at least assume that PC receives strong afferent connections from PFC and play an important role in the representation of high-level goals.

Some models (e.g. Chersi et al., 2006, 2011) postulate that the "motor primitives" are encoded by separate pools of neurons that can "chain" together into an overall action with a certain overall goal. For example, eating a strawberry could involve a chain like "reach → grasp → bring-to-mouth" while putting an object into a box could be a chain like "reach → grasp → place". Even though these two chains share two primitives ("reach" and "grasp"), the neural pools encoding those remain entirely distinct in the model. However, Fogassi et al. (2005) found that about one third of IPL neurons encoding a given motor primitive fire independently of the goal of the action and are therefore not likely to be sensitive to specific high-level goals. More recent models take this additional evidence into account (e.g. Chersi et al., 2010; Thill et al., 2011). In these models, the neural pools encoding the same motor primitive within different chains are no longer completely distinct but overlap partially. Chersi et al. (2010) were able to show that these updated chain models can explain apparently contradictory findings related to motor grounding of language processing[6].

Thill et al. (2011) present a model aimed at understanding the conditions that influence the percentage of neurons that develop to encode (or not) the overall high-level goals of action chains. This model,

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[6] Specifically, some studies in this domain found facilitating effects of irrelevant affordances on task execution while others found inhibitory effects (see Chersi et al., 2010 for details)

which builds on initial work presented by Thill and Ziemke (2010), is based on a SOM (Kohonen, 2003) whose input is an encoding of observed or executed motor primitives and of the context in which the motor primitive is executed. The model is then used to investigate how different key parameters, putatively related to self-organising processes in the cortex, might lead to the organisation observed in IPL mirror neurons. The model succeeds in reproducing the target findings to a remarkable degree: nodes in the map encoding the same motion primitive are shown to group together and form pools (see also Thill and Ziemke, 2010); moreover some nodes only react if the motion primitive is shown in a specific context while others activate irrespective of it. It is also shown that the percentage of goal-encoding nodes that emerges during learning is simply regulated by geometric relationships existing between the different inputs. The model thus also clarifies how a single brain area can develop to represent different aspects relevant for behaviour, from perception to high-level goals.

The model of Thill et al. (2011) can also predict the percentage of goal specific neurons that will emerge in function of the relationship between the units encoding motor primitive and those encoding context. In practical implementations, for instance a robot endowed with a mirror system, this can be used to fine-tune the relations between the sensory inputs to reproduce, for instance, the proportions found by Fogassi et al. (2005). At present, however, the exact mechanisms that would provide the contextual input remain to be identified since the model merely suggests that affordances may play an important role in this. Mechanisms from FARS and TRoPICALS might however be able to serve this purpose. It is also an open question how this model might learn complete motor primitive chains (but see Thill et al. 2012 for initial work on an approach that combines this model with the sequence learning algorithm of Sandamirskaya et al., 2010).

Relations between the MNS models and the goal-related models
In terms of the Oztop taxonomy, the MNS models and the goal-related models are firmly data-driven as they take into account a considerable amount of anatomical and/or physiological empirical evidence. Furthermore, most of these models provide a developmental account of mirror neuron formation during the lifetime of the model. However, while MNS models mainly focus on premotor mirror neurons, goal-related models focus mainly on parietal mirror neurons and their capacity to simultaneously represent high-level goals and perception. Various studies (e.g. Fogassi et al., 2005; Hamilton & Grafton, 2007; Bonini et al., 2010) have shown that premotor and parietal mirror neurons are related but have different properties. The two types of models are thus complementary and unifying them in an integrated model may help future investigations of this relationship.

The models also differ in the scope of the modelled systems and in the biological plausibility of their detailed implementation. MNS models are systems-level models which include all the necessary brain components that feed into the mirror neuron system (and that process affordances), but often use feed-forward or recurrent neural networks trained with a biologically non plausible learning algorithm and other abstract engineering approaches (e.g., for visual processing). The goal-related models, on the other hand, are more focussed on specific areas and often do not explicitly include realistic sensory and motor modalities; however, they model some aspects of the mirror system more in detail and on this basis succeed in replicating fine physiological findings, in particular those reported by Fogassi et al. (2005).

4 Integrating models of affordance control and mirror neurons

This section presents the design of an overall framework integrating the different neuroscientific and psychological insights reviewed in section 2 as well as the computational principles reviewed in section 3. It is not the goal of this exercise to present a specific model that could be directly implemented as such since that would be overly ambitious given the current state of the art. Rather, we aim at a *theoretical framework* serving two distinct purposes. First, it will allow the theoretical integration of the so far largely disconnected knowledge reviewed in the previous sections. Second, it should prove useful in guiding the construction of future models that study specific issues related to affordance control and mirror neurons. The section first presents the framework architecture and then discusses possible alternatives for implementing some of its components based on specific computational mechanisms that depend on the specific research goals to be addressed. Finally, we discuss some examples of how one could address some of the important questions currently debated in the literature using the framework provided.
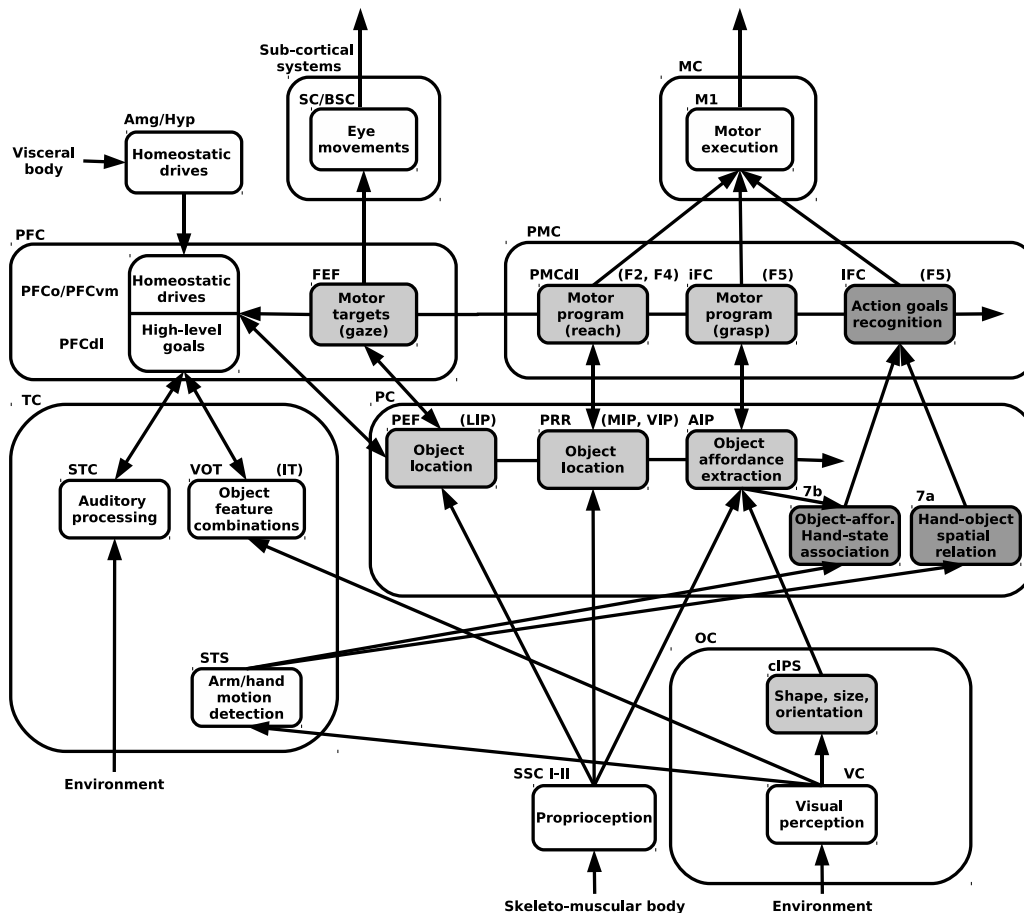
Framework architecture
Figure 9 presents the architecture of the framework. The framework integrates different aspects of the models reviewed in section 3 into one overall scheme. The previously reviewed models contribute to this endeavour as follows:
- Affordance and affordance control
  - FARS (Fagg & Arbib, 1998): the role of parietal areas in forming affordances.
  - TRoPICALS (Caligiore et al., 2010): the top-down bias from PFC and mechanisms for selecting affordances and actions; the role of affective/sub-cortical brain components.
- Mirror system
  - MNS models (Bonaiuto & Arbib, 2007, 2010): the main functionalities of the mirror system for action execution and understanding.
  - Chain models (Chersi et al., 2006; Thill et al., 2011): the encoding of goals by parietal mirror neurons; mechanisms for action chaining and hierarchy.

This list again illustrates that the different models are both distinct and complementary, which is also evident from the brain areas and connectivity considered by the models. We can illustrate this briefly using aspects of MNS2 and TRoPICALS as an example: both models include the visual cortex as well as PRR (MIP/LIP in MNS2), AIP and IFC/PMC (F5 in MNS2). PRR has the same functionality in both models; its main role is the detection of the position of objects. The function of AIP is object affordance extraction in MNS2 and extraction of shape information for guiding manipulation in TRoPICALS (which is a simplification that stands as a proxy for the various object properties encoded in the real AIP). TRoPICALS and MNS2 also differ in the level of detail in premotor areas modelling. Of the three areas considered (the ventral, lateral and dorsal premotor cortex or areas F4, F5 and F2 respectively), only PMCl (F5) is considered in both models. It is more detailed in MNS2, where a distinction between canonical and mirror neurons is made. The former are used to encode motor programs (for grasping; the motor programs for reaching are stored in area F4) whereas the latter are used in action recognition and form the main area of interest in MNS2. TRoPICALS, on the other hand, makes the distinction between the lateral and dorsal premotor cortex (corresponding to monkey areas F5 and F2 respectively), with the former encoding planned finger postures and the latter encoding planned arm postures.

In integrating insights from the different models, it is important to remember that they are based to

different degrees on monkey and/or human data. MNS2 and FARS, for instance, refer to both human and monkey brain regions while the goal-related models are predominately based on monkey data and TRoPICALS mainly addresses the human brain but assumes human-monkey homologies. Although it appears reasonable to assume the existence of such homologies (see Arbib, 2006), this complicates the integration, for example because it creates some confusion in the naming of areas and in the attribution of functions to them.

Figure 9: The architecture of the integrated framework, formed by the ventral neural pathway and the dorsal neural pathway, the latter including the mirror and canonical neural circuits (dark and light grey boxes respectively). The dorsal pathway is divided in three neural routes for controlling eye, arm, and hand movements (incorporating the affordance/canonical neuron system) and one additional neural route for the implementation of the mirror system. The ventral pathway includes PFC which controls affordance selection (within PMC and PC) based on the high-level goals of the individual that are in turn formed from external and internal context (e.g., the nature of the seen object from VOT, task instructions from STC and internal homeostatic regulations of the system from Amg/Hyp). The affordance routes involve cIPS within OC, PRR AIP and LIP within PC, PMCdl within PMC and FEF within the frontal lobe. The mirror system circuit involves areas 7a and 7b within PC (these get visual information, in particular that related to movement, from STS within OC and proprioceptive information from somatosensory areas not detaileded for simplicity) as well as mirror areas within PMC/IFC.

The components of the framework implement the same functions as in the models they originate from, so we only briefly mention them here and refer the reader to the previous sections for details. First and foremost, the framework contains both ventral and dorsal neural pathways. The ventral pathway involves visual, temporal, and prefrontal cortex areas. PFC forms high-level goals on the basis of two types of information: the outer-world context (based on information received from associative cortex

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such as the temporal cortex) and the inner-world context (based on information received from sub-cortical areas). The dorsal pathways contain three segregated neural routes for encoding sensorimotor mappings that "translate" affordances into actions: one for controlling reaching, one for controlling grasping, and one for controlling eye movements. Although the latter route is not present in any of the reviewed models, it reflects our belief that most cognitive phenomena cannot be fully understood without considering (at least overt) attention (see Caligiore et al., 2010).

Computational mechanisms to implement the framework components

While the selection of the framework components drawn from previous models was quite straightforward (given the goal of integrating the processes involving affordances control and the mirror system), the selection of specific *computational mechanisms* with which the different components could be implemented is more challenging for at least two reasons: (a) the models (whether scientific or technological) allow for a number of different possible implementations, and (b) the selection ultimately depends on the specific scientific (or indeed technological) target of the research. It is therefore more interesting to identify viable possibilities and discuss them with respect to different possible research goals than merely providing unitary directions. Here, we discuss possible implementations of framework components by dividing them into four groups:

    (a) the affordance-action system involving circuits controlling eye movements (SSC-PEF-FEF), reaching (SSC-PRR-PMC-M1), and grasping (VC-cIPS-AIP-PMC-M1)
    (b) the formation of high-level goals at the basis of top-down control (VC-VOT/STC-PFC (Amg/Hyp))
    (c) the mirror system (VC-STS-7ab-PMC/IFC) and its relation to the representation of action goals
    (d) the top-down control of the affordance and the mirror systems, specifically the selection of affordances and actions as well as the modulation of mirror neurons.

Implementing the affordance-action system
Looking back at affordance models (see section 3), it is apparent that there are (at least) three paths that one can follow. If the research focus is on the autonomous acquisition of affordances and the capacity to use them to interact with the environment, then the approach to follow is the one offered by the technological models based on embodied systems equipped with realistic sensors and actuators and efficient learning algorithms. Indeed, in this case the emergent phenomena related to a rich and realistic sensorimotor apparatus are required to study the target issue. Moreover, the use of autonomous learning mechanisms facilitates the discovery/representation of fine computational processes in the development of affordances. For example, one might use the approach of Cos-Aguilera (2004; use a SOM to relate object invariants to success or failure of actions) or that of Fitzpatrick et al. (2003; record effects produced by actions on objects to classify objects) to autonomously learn affordances of objects. Of course, this may eventually also use sophisticated image-processing techniques (e.g., SIFTS, Fritz et al., 2006). Alternatively, one might use other techniques to more strongly exploit affordances in the production of useful/novel motor behaviours, as done for instance by Stoytchev (2005; relation between affordances and *sequences* of actions) and Dogar et al. (2007; exploitation of affordance-based actions to build more complex goal-directed behaviours).

If the focus is not on autonomous affordance acquisition as such, but affordances are nonetheless needed to study the actual aspects of interest, one could simply hard-wire the affordance extraction process to function with a relevant degree of detail. For example, FARS (Fagg & Arbib, 1998), MNS (Oztop & Arbib, 2002), and MNS2-I (Bonaiuto et al., 2007) use 3D geometrical computations to

extract object affordances from objects to obtain sophisticated representations of objects or "hand-states" that in turn allow the study of how these affect selection and execution of affordances and actions within the AIP-F5 circuit.

Alternatively, if the focus is mainly on other processes working on/involving the affordance/action system, one may want to strongly abstract affordances, using for instance simple 2D population code representations. This path was followed in MNS2-II (Bonaiuto & Arbib, 2010) to study new putative functions of the mirror system in monitoring action execution and in determining executability/desirability of actions as well as in TRoPICALS (Caligiore et al., 2010) to study how the affordance/action system and the ventral neural pathway pivoting on PFC can produce the various types of compatibility effects studied by cognitive psychology experiments.

A related yet slightly different issue concerns how actions are actually found and associated to affordances. Robotic models have developed a variety of approaches and algorithms to deal with this issue (see section 3), but those are not necessarily inspired by biology. If biological plausibility is important, there are two main choices from the models reviewed above. One is Hebbian learning used together with some form of exploratory *motor-babbling* (used, for instance, in TRoPICALS) while the other is reinforcement learning (used for instance in MNS2-II). The former currently represents the best way to capture associative learning processes taking place in cortical pathways (Doya, 2000) while the latter represents the best way to mimic these processes not in isolation but as supported by trial-and-error learning taking place within BG and, in particular, the striatum (Houk, et al. 1995; Barto et al., 1995).

The last point also touches upon a fundamental issue which tends to be neglected given the usual focus on the cortex within the neuroscientific literature on affordances and mirror neurons but cannot be further expanded upon here. Associative and frontal cortical areas do not work in isolation from sub-cortical structures; rather, these areas all form partially segregated loops with corresponding areas of BG (Alexander et al., 1986) and cerebellum (Middleton & Strick, 2000). These loops play a critical role in the functioning and learning processes implemented by the related cortical areas as each loop works as a complete system. This should be kept in mind when designing implementations of the framework and is especially important for studies involving the autonomous acquisition of actions based on affordances.

Implementing the formation of high-level goals
The reviewed models offer less diversity when implementing the formation of high-level goals. This is mainly due to lesser attention (within the computational literature) on the selection of affordances and mirror neurons using top-down control exerted by the ventral pathway onto the dorsal pathway (one could argue that this is also, at least partially, due to a bias from a focus on cognitive issues that do not necessarily emphasise issues related to affect and motivations).

The simplest route one can follow is that of MNS2-II (Bonaiuto and Arbib, 2010): a simple representation of internal states based on localist units. A more sophisticated solution is that followed by TRoPICALS (Caligiore et al., 2010): an implementation of PFC that can "explode" all possible combinations of contexts and instructions/internal states (e.g., using a SOM) which might then assume the role of high-level goals once suitably linked (e.g., using Hebbian learning) to the affordance/action components of the framework.

One can also take into account more sophisticated mechanisms originally proposed outside the field of research on affordances or mirror neurons if these are better suited to one's research goals. While it goes beyond the scope of this paper to review those models in detail, we refer the interested reader to representative papers where relevant. These can for instance be of interest if there is a need to represent the "executive functions" of PFC in a biologically plausible way. For example, one might refer to the model of Deco and Rolls (2003; see also a review in Caligiore et al., 2010) to study how PFC biases affordances and actions selection using complex "rules" of behaviour. A detailed implementation of the "working memory" function of PFC could use mechanisms proposed by O'Reilly and Frank (2006). If there is a need to implement PFC role in goal-directed behaviour using the notions of reward and value, one might refer to Daw et al. (2005) for a functional model and to Mannella et al. (2010), for a bio-constrained architecture (see Mirolli et al., 2010, for a review on the key role of Amg in these processes). Finally, one can capture key functional properties of PFC by referring to more abstract yet computationally more powerful and "principled" models developed within the Bayesian framework (Friston, 2003, 2005; Botvinick & An, 2008).

Implementing the mirror system
The models reviewed in the previous sections offer different ways of implementing the mirror system in general and its development in particular. All MNS models compute a hand-state (an encoding of the state of the hand in relation to the target object) and use supervised learning algorithms to train mirror neurons to associate specific hand-states with specific types of grasps (encoded by canonical neurons). This is a useful approach if there is no need for online learning in the mirror system. Alternatively, one could consider using a Hebbian learning process to associate affordance representations with action representations (see for instance Metta et al., 2006, whose system can "autonomously" develop a mirror system structure through repeated interaction with objects).

An alternative approach for capturing the essential functional operation of the mirror system is to follow Friston (2003, 2005, see section 2.2) who suggested the use of the principled mechanisms of predictive coding and Bayesian inference. This can capture the "backward" generation of expectations on percepts (e.g., related to the observed action of another agent) based on their ultimate causes (related to the intentions of the agent) as well as the "forward" inference of the causes from percepts (e.g., the intention of others from the perception of their actions).

Implementing top-down control of affordances/actions and of the mirror system
To decide which computational mechanisms can be used to implement the effects of top-down control of affordances and action execution pivoting on PFC, one has to distinguish between the different ways in which such control can take place (see section 2): bias of action selection (e.g., within the PMC), bias of affordance selection (e.g., within PC), control of covert attention (e.g., within ITC, PC and, via these, the lower visual areas) and control of overt attention.

Regarding the biasing effects, FARS, TRoPICALS as well as the goal-representation models all use some types of competitive neural mechanisms to allow the selection of actions (FARS and TRoPICALS) or affordances (FARS and goal-related models; some of the latter used an abstraction of the competition represented by a winner-take-all or many-take-all competition). These mechanisms are based on the encoding of affordances or actions with different (eventually overlapping) neural pools that have within-pool excitatory connections and between-pool inhibitory connections. Given the biological plausibility of the general principle (cortical neurons have a typical locally-excitatory/globally-inhibitory connection pattern, see Cisek, 2007), this would be the recommended

approach.

Inhibitory mechanisms should also be considered when implementing affordance selection (Tipper et al., 1992; Ellis et al., 2007; Eimer & Schlaghecken, 2002). Indeed, adaptive and flexible behaviour involves not only the positive bias of useful affordances and actions but also the active inhibition of affordances and actions elicited by cues and objects irrelevant for pursuing the agent's goals. Inhibition can be implemented abstractly through the addition of an inhibitory neural pathway connecting PFC to areas where affordances and actions are elaborated (e.g., PC and PMC), as done in Caligiore et al. (2012). Alternatively, the implementation can be based on a more detailed representation of inhibitory mechanisms involving BG (Munakata et al., 2011; Aron et al., 2003), exploiting existing models (e.g., Houk, et al. 1995; Gurney, Prescott & Redgrave 2001; Joel et al., 2002; O'Reilly & Frank, 2006). Shepherd et al. (2009) and Mukamel et al. (2010) illustrate that inhibition may also be important for mirror neurons as these authors have shown that sub-populations of mirror neurons are *inhibited* by the observation of the performed action. These neurons, and their inhibition, could play an important role, both in the prevention undesired overt action execution when observing other agents performing an action and in the selection of suitable actions to execute when multiple actions are observed (for example in imitation tasks). Interestingly, the specific neural mechanisms for implementing these functions might be the same as those considered above for the modulation of affordances and executed actions.

With respect to covert attention, relevant models have been proposed outside the affordance/mirror neuron literature (e.g., Itti et al., 1998; Itti & Koch, 2000). Similarly, one can refer to a number of models within the literature of attention and active perception to implement overt attention mechanisms (e.g., Ballard, 1991; Ognibene et al., 2008). It is important to again underline the significant role that overt attention may play in phenomena related to affordances (see, Kornblum et al., 1999; Tipper et al., 2006). Indeed, once an object is perceived, the brain has a strong bias to elicit the internal representations encoding its affordances and this can affect all downstream processes ("out of sight, out of... action"). Attention may thus play a paramount role in controlling affordance-based behaviour, a role that cannot be ignored in explaining various empirical findings. It should be noted that we do not intend to downplay or underestimate the importance of the control of affordances and action execution at later stages of the dorsal pathways (e.g., via the PFC-SMA-PMC route, see Section 2) nor overemphasise the automatic nature of affordances. We simply would like to emphasise that attention remains a fundamental way by which PFC can perform such control.

5 Investigating specific problems and implementing specific models with the framework

This section discusses some open issues related to the affordance and mirror systems that might be investigated through the implementation of specific models based on parts of the framework presented in section 4. This discussion has two aims. First, it illustrates the framework's potential for contributing to the theoretical investigation of some of the most important open issues related to the affordance and mirror systems. Second, it provides indications on how to build specific models based on the framework to address such problems in detail. These specific models are expected to lead to the production of specific interpretations and predictions. The discussion here will also highlight the complementarity of the mechanisms underlying affordance learning and computation, affordance control and the representation of goals based on mirror neurons, thereby highlighting the utility of the framework in the integration of these concepts.

Canonical and mirror neurons
The first open issue regards the relation between canonical and mirror neurons. The functions of canonical and mirror neuron systems have each been intensely investigated separately using, for instance, the models reviewed in section 3. Few works consider the relations between the two, although it is clear that significant relations do exist. Some models investigate how mirror neurons emerge under the guidance of canonical neurons (e.g. Metta et al., 2006). Other models investigate how mirror neurons might be used for other functions, for example to monitor action outcomes to improve the course of action (MNS2-II, Bonaiuto & Arbib, 2010). However, we still do not understand the principles underlying the relations between the affordance and mirror systems. Consider, for example, the neural processes taking place in the brain when an action fails to achieve its intended desired outcome (Brown & Braver, 2005; Matsumoto et al., 2007), or the question of how goals can drive the learning of affordances and actions (the problem of "goal-based action learning"; see Redgrave & Gurney, 2006). A specific implementation of the components of the framework supporting affordance and action selection as well as those related to the mirror system would allow studying these issues. An example would be the effects that a *failure of action execution*, detected from a mismatch with its goal represented by mirror neurons, might have on the current course of action as well as future action selection (see Bonaiuto & Arbib, 2010). The issue of *goal-based action learning* could be studied by implementing (a) a reinforcement learning implementation for affordance learning; (b) the mirror system for the encoding of goals of actions; (c) a motivational system to allow the system to autonomously generate goals (e.g., based on intrinsic motivations, see Redgrave & Gurney, 2006, and Baldassarre, 2011). In general, we expect that such models will lead to the discovery of a division of labour between the mirror and canonical systems, with the former guiding learning and playing a prominent role in action monitoring while the latter plays an important role in storing information about the actual implementation of actions (see Bonaiuto & Arbib, 2010).

Goal representations at different levels of abstraction
Another issue concerns the relation between goal representations at different levels of abstraction. Investigating this issue requires in particular a study of the effects caused by the top-down control exerted by PFC on the mirror system at both the PMC/IFC and PC levels. The critical questions here are: how do high-level goals encoded in the PFC actually affect the mirror neuron activation observed in empirical experiments (Fogassi et al., 2005; Hamilton and Grafton, 2007)? What is the precise adaptive function of this activation and what are the underlying mechanisms (see Thill et al, 2011)? Note how these issues touch the fundamental open problem on the exact structure and functioning of the *hierarchical organisation of motor behaviour* stressed by many authors (e.g., Fuster, 2008; Botvinik et. al., 2008). An implementation encompassing the mirror neuron system and the top-down affordance/action control from the framework might help allow this investigation. It would, for example, allow the study of how high-level goals might be accomplished based on actions differing in their proximal goals (see the experiments of Hamilton and Grafton, 2007) or how high-level goals are formed from low-level ones. To the best of our knowledge, no model currently investigates these issues in a biologically constrained fashion. The framework suggests that such a model will show that the mirror and affordance systems tend be hierarchically related, with the former having a stronger link to high-level goals (e.g., encoded in PFC). The affordance system would be subordinated and more closely related to action implementation (see Fagg & Arbib, 1998; Caligiore et al., 2010).

Affect and motivation

The relevance of affect and motivation for high-level goals as well as action goals relying on the mirror system is another important issue that is not yet well understood but can be studied using the framework. As mentioned in Section 4, research on affordances and mirror neurons tends to overlook the importance of affective and sub-cortical areas. The framework presented here highlights the role of affect and motivations (processed within the sub-cortical areas at the interface between the brain and the visceral body, such as Amg and Hyp) as a fundamental source of information for the formation of high-level goals within PFC (Fuster, 2008). Given the strong interdependence between the high-level goals in PFC and the action-goals within the mirror system discussed previously an implementation would require PFC, the mirror areas and, at a minimum, the effects of affective information from the visceral body on high-level goals (e.g, Mannella et al., 2010) from the framework to investigate these issues. This would facilitate the understanding of how the homeostatic drives of an organism guide the formation and selection of high-level goals (Balleine & Dickinson, 1998), including the impacts thereof on affective and motivational aspects of action goals within the mirror system. Such a model would therefore clarify how the affordance and mirror systems are affected by motivational aspects of behaviour and sub-cortical areas of brain. This remains an important issue often neglected by the current literature (Cheng et al., 2007).

Functional roles of mirror neurons in higher-level cognition
An important, often debated issue in mirror neuron research concerns their potential functional contributions to (higher-level) cognitive phenomena. Although the literature is swamped with hypotheses regarding the possible roles of these neurons in high-level cognition – action understanding being the prime example (see Rizzolatti and Sinigaglia, 2010, for a review) – very few of these have actually been verified (see Hickok, 2008, for a discussion). Most mirror neuron models cannot contribute much to the debate because they do not model how mirror neurons actively contribute to action understanding in a way that would not otherwise be possible. In this respect, it has been shown that the organisation of mirror neurons itself, including goal-specific (parietal) neurons as found by Fogassi et al. (2005), can emerge in models that do not explicitly consider action understanding at all (Thill et al., 2011). Building system-level models within the framework proposed here is expected to give indications of why the specific functioning of mirror neurons is very well suited/economical within an overall system that has to accomplish multiple functions (Kilner et al., 2007).

Merging cortical and sub-cortical mechanisms
It is possible to study the processes of selecting and learning of affordances and actions within PC and PMC including the support given by sub-cortical structures using the framework presented here. It is becoming increasingly clear that these processes may play a crucial role in the explanation of various phenomena related to affordances and mirror neurons to date typically studied with a focus on the cortex in cognitive psychology or neuroscience (see for instance MNS2-II and TRoPICALS).

As mentioned in section 4, BG play a key role in these processes (Houk et al., 1995). Yet there are, to our knowledge, no biologically constrained models that explicitly simulate relevant functions of BG in the literature on affordances or on mirror neurons. Nonetheless, research and modelling related to BG, habits acquisition, and goal-directed behaviour pivoting on PFC has produced several models (e.g., Gurney, Prescott & Redgrave, 2001; Baldassarre, 2002; Joel, Niv & Ruppin, 2002; O'Reilly & Frank, 2006). The integrated framework proposed here provides an important starting point for merging the two types of models ("cortical" and "subcortical") since it emphasises sub-cortical mechanisms leading to the formation of high-level goals and provides a comprehensive representation of the cortical neural pathways. Building such a model would also help clarify the different properties of inhibitory

mechanisms through which PFC exerts its top-down control via cortical excitation and sub-cortical inhibition (Munakata et al., 2011).

Automatic activation of affordances
Work on the automatic activation of affordances would also greatly benefit from models considering the affordance-action system not just by itself but in function of the top-down control exerted on it by the ventral pathway. Whether affordances are elicited automatically or modulated by the agent's goals (Tucker & Ellis, 1998, 2001; Tipper et al., 2006) remains an active topic of research. Recent behavioural evidence (from tasks requiring a detailed processing of shapes compared to superficial judgements on colour) has for example shown that the activation of affordances is modulated by the degree of object processing (e.g., Pellicano et al., 2010; Tipper et al., 2006). Other studies indicate that the activation of affordances is modulated by spatial context; it is for example stronger when objects can easily be reached compared to when they are in extrapersonal space (Costantini et al., 2010; Ambrosini et al., 2012). Costantini et al. (2011) demonstrated that affordances are also activated when objects are located in the peripersonal space of another person (e.g., an avatar) but not when they are in the peripersonal space of an inanimate cylinder, which suggests that affordance activation, the mirror mechanisms, and the high-level goal system of the agent are all involved. Models such as TRoPICALS demonstrate that addressing these issues requires including not only the dorsal neural pathway (to implement affordances and actions), but also the ventral pathway (to form the agent's high-level goals and modulate the selection of affordances and actions). As seen in the reviews earlier, research on these topics produces a wealth of information that could greatly benefit from integrated modelling such as outlined by the framework here. The models thus produced are likely to lead to the identification of general mechanisms and principles possibly linking a number of phenomena that are currently often studied separately (such as selective attention, Simon effects, compatibility effects, and stable/variable affordances).

Stable and variable affordances
The framework also has the potential to facilitate further investigations within the theory on stable and variable affordances (Borghi & Riggio, 2009). Compared to variable affordances (e.g., object position), representations of stable affordances are likely to involve the more ventral neural routes of the dorsal pathway (e.g., to encode the common size of a certain class of objects), or even the ventral pathway (for instance where stable aspects related to object recognition in temporal areas or the object's common use and function are concerned, see Creem-Regehr & Lee, 2005). Such issues could be investigated with models encompassing some of the dorsal routes and the ventral route involving temporal and prefrontal cortex from the framework. The location of stable/variables affordances within the ventral/dorsal pathways (or within the different dorsal neural routes) remains a topic of debate (see section 2.1). Different hypotheses on this matter could result in different predictions from the integrated framework allowing their validation using empirical tests. The relations existing between stable/variable affordances and the brain systems underlying them, such as the different cortical streams within the dorsal neural pathway (Sakreida et al., in preparation), could be clarified in this way.

The emergence of communication
It would also be possible to address the possible emergence of human verbal communication from gestural communication. According to Ferrari et al. (2003), a sub-population of F5 discharges when observing and executing mouth gestures like biting, grasping or ingesting. Additional neurons discharge when executing/observing communicative facial gestures, such as lip-smacking. These results suggest that area F5 may also be involved in gestural communication (see also Gentilucci and

Corballis, 2006, and Gentilucci and Dalla Volta, 2008, for reviews). Models derived from the framework and including mirror neurons and the areas forming high-level goals can be used to investigate these theories further. These models could exploit the associative mechanisms used in Caligiore et al. (2010) to represent the meaning of words in terms of internal representations of objects and actions (e.g., to represent verbs and nouns), and link these representations first to gestural actions and then to the production of linguistic utterances (e.g., again with associative mechanisms, for example as those used in Mirolli and Parisi, 2005).

Implementing theories from cognitive psychology
The framework can also be used to create operational implementations of the core hypotheses proposed by important cognitive psychology theories such as the ideomotor principle (Elsner & Hommel, 2001; Kiesel & Hoffmann, 2004), the common coding theory (Prinz, 1990) and the event coding theory (Hommel et al., 2001). One core idea of these theories is that late-sensory/early-motor representations are intrinsically related to goals in addition to being strongly grounded in the sensorimotor brain. Since the framework presented here includes both action goals (within the mirror neurons) and high-level goals (encoded in PFC), it can help in the reproduction of results from psychological experiments on these theories and in relating them to specific brain mechanisms, similar to the approach of Caligiore et al. (2010). This aspect of research in cognitive psychology stands to greatly benefit from interdisciplinary approaches, such as advocated by the present framework, and thus link behavioural phenomena (e.g. the ideomotor principle) to the underlying brain mechanisms (e.g. mirror neurons) with the aid of computational models.

Mirror neurons and the predictive coding theory
Bayesian/predictive coding approaches (Friston, 2005; Kilner et al., 2007) tend to produce models with powerful computational capabilities that capture key principles working at the heart of cortical information processing, yet at the same time often remain only weakly constrained by biology in terms of the overall architecture of the system. The framework presented could contribute in this aspect by facilitating the design of a suitable, biologically constrained macro-architecture of models whose components would then be implemented in Bayesian terms. Such an approach is for example becoming increasingly important for Dynamic Causal Modelling, a type of modelling technique developed within the Bayesian framework and used to account for brain data, in particular from brain imaging (Stephan et al., 2007; Friston, 2009). In this approach, Bayesian statistics are used to compare the quality of competing models (i.e., the likelihood with which they produce the data) and to tune their parameters on the basis of brain data. The construction of these models has to be guided by functional considerations ("what role does this area play within the functioning of the system as a whole?") and brain-anatomy constraints expressed at the system-level. The framework presented here provides appropriate constraints than can be used to design models within this approach and used to study phenomena related to affordance and mirror systems. The translation of parts of the framework into specific Dynamic Causal Models should directly produce predictions testable against biological data, in particular from brain imaging studies (Rizzolatti & Craighero, 2004).

6 Conclusions

The first goal of this paper has been to provide a comprehensive and integrative review of the affordance and mirror neuron systems, including work from psychology, neuroscience, and computational modelling efforts. We proposed that a first unifying principle underlying the brain organisation of motor behaviour is the ability to select between multiple available affordances and

actions. We have shown that the ventral neural pathway of brain carries out this function, involving in particular PFC, its input and output connectivity and its specific information processing mechanisms. PFC can use information from the outer context and the homeostatic drives to form high-level goals. With this information, PFC can bias the selection of affordances and actions and guide attention. This biasing activity is based on various features of PFC, including its capacity to integrate multiple sources of information, to implement working memory, and to form complex behavioural "rules".

A second unifying principle underlying the brain organisation of motor behaviour is the ability to represent goals of actions at the mirror neuron level within both the parietal and the premotor cortex. Mirror neurons have a number of properties that suggest they may be encoding action goals: they can activate independently of action performance, they posses anticipatory features, they receive information from brain areas suited to process seen actions, and they respond not only to action goals but also to the overall (high-level) goals of actions. These properties allow mirror neurons to play important adaptive functions not only in social contexts (for which they have become widely known) but also in individual behaviour, for example for action monitoring.

The second goal of this paper has been to investigate possible relationships between the affordance and mirror systems. Our analysis of the psychological, neuroscientific, and computational studies on these systems has detailed how the two systems might be hierarchically related. We have related the mirror system more closely to the encoding of goals of behaviours represented at different levels of abstraction while the affordance system has been related more to the planning and execution of actions. Moreover, we have suggested that the mirror neuron system may lead the processes of learning suitable affordances and actions based on the representations of desired outcomes (goals) while the affordance system may play a key role in the acquisition of new specific sensorimotor mappings by which they can be implemented.

We then presented an extensive review of key computational models of affordance representation learning and action execution, of affordance control, and of the mirror neuron system. Here, our aim has been to leverage this knowledge with that gained from the reviews in the previous sections. This has allowed us to propose an integrated framework based developed with two main aspects in mind: (a) its macro-architecture, encompassing all brain areas relevant for the implementation of the affordance and mirror systems; (b) the specific computational approaches that might be used to implement specific models of these areas. Given its scope, the framework is rather ambitious and complex and a complete implementation thereof would be difficult. Its main utility rather lies in the theoretical framework that it can provide for building specific models aimed at investigating specific issues related to affordance and mirror systems. To support the viability of this idea, we have given various indications on how parts of the framework could be implemented to investigate specific open research questions.

Specific models that might derive from the integrated framework presented here could also be highly relevant to technological applications in addition to their potential for furthering scientific understanding. Indeed, much work in bio-inspired and cognitive robotics takes inspiration from biology to build machines endowed with life-like cognitive abilities. The affordance and the mirror system are surely key building blocks of the most sophisticated natural intelligent systems and hence might serve as a basis from which to develop architectures and algorithmic principles within artificial cognitive systems (see Oztop et al., 2006; Montesano et al., 2008).

Arbib (2010) has recently argued that models which focus only on a specific subsystem of the brain

cannot fully address the challenges of cognitive neuroscience and that progress in the simulation of adaptive behaviour requires "a balancing act between large scale models and focussed research" (p 9). We believe that specific implementations of parts of the integrated framework proposed here would be a suitable approach towards such a balancing act. Indeed, the framework offers a broad system-level perspective on affordance/prefrontal/mirror systems while simultaneously guiding the construction of specific models focussed on and tailored to specific problems.

Appendix

Table 1
Acronyms of the brain regions used in the article. Cortical areas of monkeys that are homologues to human cortical areas are indicated in parentheses.

AIP	Anterior Intraparietal Area
Amg	Amigdala
BG	Basal Ganglia
cIPS	caudal Portion of the Intraparietal Cortex
FEF	Frontal Eye Field
Hip	Hippocampus
Hyp	Hypothalamus
IFC (F5)	Inferior Frontal Cortex
IPC	Inferior Parietal Cortex
M1	Primary Motor Cortex
OFC	Orbital Frontal Cortex
PC	Parietal Cortex
PEF (LIP)	Parietal Eye Field (Lateral Intraparietal Area)
PFC	Prefrontal Cortex
PFCdl	Prefrontal Cortex, dorsolateral region
PFCo	Prefrontal Cortex, orbital region
PFCvm	Prefrontal Cortex, ventromedial region
PIP	Posterior Intraparietal Area
PMC	inferior Premotor Cortex
PMCdl (F2, F4)	Premotor Cortex, dorsolateral region
PRR (MIP)	Parietal Reach Region (Medial Intraparietal Cortex)
SC	Superior Colliculus
SI	Primary Somatosensory Area
SII	Secondary Somatosensory Area
SMA	Supplementary Motor Area
SMC (F6)	Supplementary Motor Cortex
STC	Superior Temporal Cortex
STS	Superior Temporal Sulcus
TC	Temporal Cortex
VC	Visual Cortex
VIP	Ventral Intraparietal Area
VOT (ITC)	Ventral Occipitotemporal Cortex (Inferior Temporal Cortex)

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