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Neurophysiological bases underlying the organization of intentional actions and the understanding of others' intention

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ABSTRACT

Philosophical and neuroscientific investigation on intentional actions focused on several different aspects, making difficult to define what should be meant with the concept of intention. Most of our everyday actions are constituted by complex and finely organized motor sequences, planned and executed in order to attain a desired final goal. In this paper, we will identify the final goal of the action as the motor intention of the acting individual. First, we will review the relative contribution of the vast neuroscientific literature on the role of different cortical areas in the organization of goal-directed movement. In particular, we will describe recent data on the cortical organization of natural action sequences, showing that this organization could be at the basis not only of our capacity of acting intentionally, but also of our ability to understand the motor intentions underlying others' behaviour which is crucial during social interactions.

1. Introduction

The concepts of "intention" and "intentionality" of human actions are, since centuries, the focus of philosophical reasoning and dispute, but in the last few decades even neuroscientists and biomedical engineers started focussing their efforts on decoding neuronal intentional signals from the human brain for building brain-machine interfaces (Andersen, Hwang, & Mulliken, 2010; Hochberg et al., 2006). However, in spite of the advances of modern neurophysiological and neuropsychological techniques and their crucial contribution to the clarification of the basic mechanisms underlying intentional actions, there are still some fundamental neuroscientific and theoretical issues that remain unresolved.

First, concepts such as "action" and "intention/motor intention" are still elusive and not well defined. Second, the relationships between an overt intentional behaviour and its correspondent covert representations must be clarified. This last issue is critical for any attempt to identify the neural mechanisms underlying our capacity to plan and perform intentional actions, as well as to predictively understand the motor intentions of others.

2. Movements, motor acts, actions and intentions: hierarchical organizations of goals in the motor system

According to Libet's seminal works, an act is regarded as intentional when (1) it arises endogenously, (2) there are no externally imposed restrictions or compulsions that directly or immediately control its initiation, and (3) subjects feel introspectively that they are performing the act on their own initiative, starting or not as they wish (Libet, 1985). In the time domain, "*intentionality is the premotor detail of the desired result of movement (…): the choice of what to do before the doing of it*"

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(Llinas, 2002). Most philosophical and neurophysiological studies in the literature dealt with the concepts of intention and intentionality in such a way, suggesting that the intention of doing a certain act is something that precedes its actual motor execution, and that it is usually associated with the conscious experience of 'agency'.

Wittgenstein (1953) already envisioned the complexity of this issue by posing the question: "*what is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?*" A plausible answer to this question could be "some sort of conscious experience to intentionally lift the arm", but the philosophical debate has considered the concept of "intention" as by far more complex. One of the most influential of these views (Searle, 1983) maintains that intentions can be considered at two distinct levels: prior intentions (e.g. to replace a burned out light bulb *later on*) and intention-in-action (i.e. the internal state that guides and monitors the arm lifting movement *while* reaching the light bulb). Several other theorists followed this dualistic approach, distinguishing between prospective and immediate intentions (Brand, 1984), future- and present-directed intentions (Bratman, 1987), distal and proximal intentions (Mele, 1992), while others proposed even more articulated models (Pacherie, 2008), identifying distal, proximal and motor intentions. What appears to be shared by all these views is some concept of motor goal that – although at different levels of complexity – constitutes the core of what intentions represent, that is, "*goals and means to those goals*" (Pacherie, 2008).

The concept of goal is also central to the neurophysiological literature dealing with the correlates of intentional actions. Let's consider a simple example. Opening a candy box can constitute the goal of an agent and, therefore, the content of his/her intention. However, to attain this goal, the agent must organize a reaching-grasping action formed by a sequence of motor acts (see Rizzolatti et al., 1988), each of which is aimed at an immediate motor goal (e.g. reaching, grasping, lifting the handle of the lid). Motor acts are formed by more elementary muscle synergies, often called simple movements, which could serve for the execution of several different acts and actions, regardless of their goal. Thus, what is the agent's intention in this example? One might say to grasp the lid, to remove the lid or even to eat a candy. This action clearly includes many goals and sub-goals, but it is unclear firstly at which level we should search for the agent's intention in this motor hierarchy and, secondly, if some unifying concept of intention does exist at all.

Usually, by definition, we consider an action as associated with only one goal. Bernstein (1996), for example, defined actions as "*whole sequences of movements that together solve a motor problem (...) and all the movements parts of such a chain are related to each other by meaning of the problem*". In this definition "motor problem" clearly refers to what we usually identify with the concept of motor goal. Nevertheless, even very simple discrete movements – such as arm reaches, saccades or extension/flexion of a finger – can be considered as goal-directed, provided that they are performed in order to reach a specific state and their execution is under voluntary control. This latter consideration is extremely useful in order to reconcile the many and diverse findings reported by neurophysiological studies on intentional actions, using behavioural paradigms extremely different one from the other in terms of motor complexity.

2.1. When, what and how of intentional actions

Many authors employed different behavioural paradigms to investigate intentional actions focussing on motor details that are specified in advance to the actual movement execution. Neurophysiological studies showed, for example, that mesial premotor regions (supplementary and pre-supplementary motor areas) and rostral cingulate motor cortex encode '*when*' a general intention to act rises (Fried, Mukamel, & Kreiman, 2011; Hoshi, Sawamura, & Tanji, 2005), particularly prior to self-generated actions (see Passingham, Bengtsson, & Lau, 2010). Others (Andersen & Buneo, 2002; Snyder, Batista, & Andersen, 1997) studied neuronal activity during the planning phase of simple reaching and saccadic movements directed to a target and showed that lateral intraparietal neurons specifically encodes '*what*' the monkey intends to do (a reaching act or a saccade) prior to movement onset. Other authors, although not explicitly focussing on the issue of motor intention, demonstrated that planning-related neuronal activity in different premotor and parietal areas can specify '*how*' an act has to be done, either in terms of specificity for the direction of the forthcoming reaching (Cisek & Kalaska, 2005) or for the grip selectivity of the planned grasping (Baumann, Fluet, & Scherberger, 2009), as soon as contextual information sufficient to make a decision becomes available (see Andersen & Cui, 2009). Taken together, these studies suggest that an intentional action stems from decisional processes carried out on potential concurrent motor plans simultaneously activated in a network of parietal and frontal areas and specifying the 'whether', 'when', 'what' and 'how' of the action to be performed (see Haggard, 2008).

Most of these processes can occur covertly, automatically and without any need of conscious access: when grasping a handful of popcorn while watching a movie, we will not be certainly attending to when starting to move or how shaping the hand for doing it. Nevertheless, we could, if we want, carefully look at a single popcorn, precisely grasping it between our thumb and index finger tips, and specifically attending to when we decide to start the movement, what action to perform or even how to do it (Lau, Rogers, Haggard, & Passingham, 2004): in both cases, i.e. attending or not to the action, our phenomenological experience of acting intentionally appears to us as a sort of unitary perception that is always inherent in our own voluntary behaviour. However, motor intention cannot be considered, as our phenomenological experience would suggest, a unitary phenomenon from a neurophysiological point of view, since different brain areas have been shown to play a role in processing different aspects of intentional actions. The pioneering studies by Penfield and Boldrey (1937) and more recent data by Desmurget et al. (2009) have shown that it is possible to dissociate the processes leading to motor execution of an action from those related to the awareness of the corresponding motor intention. For example, by means of electrical stimulation of the human right inferior parietal cortex, Desmurget and coworkers evoked the patients' subjective feeling of intending to move the hand, the arm or the foot without any overt muscle activation, while through the stimulation of the right premotor cortex they produced overt contralateral movements, but the patients firmly denied that they had moved (Desmurget et al., 2009). Furthermore, recent studies on patients with anosognosia for hemiplegia due to lesions in the territory of the right middle cerebral artery (with large involvement of subcortical structures) showed that motor intentions related to movement plans for the paralyzed hand can influence the performance of what the intact hand does (Garbarini et al., 2012). Taken together, these data indicate that conscious representations of motor intention - in terms of what to do and when doing it – can be anatomo-functionally dissociated from the motor representations underlying the actual motor behaviour, and both of them normally interact in the parieto-frontal circuits subserving the organization of intentional action.

2.2. Neural basis of the organization of intentional action sequences

The studies reviewed so far dealt with a specific aspect of the concept of motor intention, that is, ''*the premotor details of the desired result of movement*'' (Llinas, 2002). However, intention does not terminate with action onset. In fact, ''the desired result of movement'', that is, the final goal of the action, does not fade out with movement onset, but remains still present in the agent's phenomenological experience during action unfolding until its completion.

A number of behavioural studies on humans' reaching-grasping actions (Ansuini, Santello, Massaccesi, & Castiello, 2006; Ansuini, Giosa, Turella, Altoe, & Castiello, 2008; Armbruster & Spijkers, 2006; Gentilucci, Negrotti, & Gangitano, 1997; Marteniuk, MacKenzie, Jeannerod, Athenes, & Dugas, 1987; Rosenbaum, Chapman, Weigelt, Weiss, & van der Wel, 2012) indicated that the first motor acts (i.e. arm reaching and hand shaping when grasping an object) of a longer action sequence are influenced by the final action goal and, more specifically, by the forthcoming motor acts following grasping (e.g. lifting, placing). This peculiar organization of intentional actions seems to develop very early in life (Butterworth & Hopkins, 1988; Sparling & Wilhelm, 1993; Takeshita, Myowa-Yamakoshi, & Hirata, 2006). Indeed, kinematics studies (Zoia et al., 2007) carried out on foetuses in the womb by mean of ultrasonography revealed that while at the 14th week of gestation foetuses' movements are by no means uncoordinated, since the 22th week of gestation they begin to assume the recognizable form of intentional actions, with kinematic patterns depending on the goal of the action (hand movements to-the-mouth or to-the-eyes). This conclusion supports the idea that an action, since very early in ontogeny, is planned and organized as a whole chain of acts well before its actual onset, and the bio-mechanical and temporal structure of motor acts embedded in the action depend on its final goal (for example bringing the hand to the mouth), that is, the motor intention of the acting individual.

Recent neurophysiological studies shed new light on the possible neural mechanisms underlying the goal-related chained organization of motor acts into actions. Fogassi and co-workers (Bonini et al., 2010; Fogassi et al., 2005) recorded the activity of inferior parietal (area PFG) and ventral premotor (area F5) grasping neurons in monkeys while they performed simple grasping actions. In the basic experimental conditions the target was a piece of food or a metallic solid of the same size and shape of the food: the monkey was required to grasp the food and eat it (Condition 1) or grasp the object and place it into a container located near the target in order to receive a reward (Condition 2). Since the grasping motor act was the same in both conditions, one should expect that grasping neurons discharged similarly independently from the motor act following grasping. In contrast, most of the recorded neurons discharged stronger during grasping depending on the action (i.e. grasp-to-eat or grasp-to-place) in which the act was embedded. Control experiments were carried out to investigate which factors could determine grasp-to-eat or grasp-to-place neuronal selectivity. First, grasp-to-place neurons did not change their selectivity when the container in which the target had to be placed was located near the mouth rather than near the target: thus, neuronal selectivity was largely independent from target location and, therefore, from the motor sequence following grasping. Second, in a modification of Condition 2, monkeys were trained to grasp and place the same piece of food used for grasp-to-eat trials in order to receive a more palatable food reward. This condition was introduced in order to have the same target in both conditions. Neuronal selectivity remained unchanged even when a piece of food was used as target for placing actions. Third, motivational aspects are known to play a relevant role in driving the selection and execution of goal directed actions (Glimcher, 2003; Schultz, 2004), but the manipulation of the rewarding value of the food obtained by the monkey upon correct task accomplishment did not change the neuronal preference for eating or placing (Bonini et al., 2011). Taken together, these findings indicate that the discharge of PFG and F5 grasping neurons can reflect the goal of the action in which the coded act is embedded. Furthermore, they also support a model in which neurons coding distinct motor acts might be organized in chains in which each neuron is facilitated by the activation of the previous one in the sequence (Chersi, Ferrari, & Fogassi, 2011; Fogassi et al., 2005; Rizzolatti, Ferrari, Rozzi, & Fogassi, 2006).

The chain model of action organization has been further assessed in monkeys by directly comparing, using the same grasp-to-eat and grasp-to-place motor task, the relative impact of action goal on the discharge of parietal and premotor grasping neurons (Bonini et al., 2010). Results showed that parietal area PFG has a greater proportion of neurons discharging differently according to the action goal and with a higher degree of action goal selectivity compared to F5. Furthermore, neuronal selectivity for the action goal significantly increases over time during grasping unfolding in PFG. Interestingly, we also found that the later was the peak of a neuron's activity, the higher was its action goal preference, while this did not occur in F5.

Tracers injections in the recorded regions of parietal and premotor areas of the monkeys employed for the neurophysiological experiments demonstrated the existence of a direct anatomical link between these two sectors (Bonini et al., 2010).

Therefore, areas PFG and F5 form an anatomo-functional circuit playing a crucial role in the organization of intentional actions. In particular, area PFG appears to have a leading role in linking the motor acts one to the other based on the goal of the action in which they are embedded.

Models of neuronal chains underlying complex sequential behaviors have been also proposed, based on direct evidence derived from intracellular recording studies in songbirds. Strikingly, it has been found that the production of strings of syllables during singing reflect the propagation of activity through a chain network localized within a telencephalic premotor area (HVC) with high temporal precision (Long, Jin, & Fee, 2010). The structure of this network appears to be compatible with the hypothesized organization in neuronal chains proposed for primates parieto-premotor networks related to hand-arm movements, suggesting that an evolutionary ancient mechanism could underlie a wide range of functionally distinct sequential behaviours.

In all single neuron studies in monkeys reviewed so far neuronal activity was recorded only during the execution of a single type of grip (i.e. precision grip). However, intentional grasping actions often imply not only the organization of the appropriate chain of acts leading to the achievement of the action goal, but also the selection of the appropriate type of grip, depending on the object's physical properties. For instance, when grasping a fruit, a specific grip type has to be selected depending on the physical properties of the fruit (i.e. its size and shape). However, the agent could grasp the fruit in order to eat it or to place it in a basket, and the chosen action could imply the use of a different type of grip, so that the coding of action goal and of grip type must be strictly linked. A recent study (Bonini, Ugolotti Serventi, Bruni, et al., 2012) demonstrated that both parietal and premotor grasping neurons can integrate information concerning the type of grip and the action goal. In fact there are neurons in both cortical sectors that discharge stronger during a given type of grip (e.g. finger prehension) and at the same time show a modulation of their discharge due to the action goal. Furthermore, with a more detailed analysis of the temporal dynamics of grip and goal selectivity, it appears that grasping neurons activity, particularly in the parietal area PFG, reflects first "how" the object has to be grasped (grip), to guide and monitor the hand shaping phase, then "why" the action is performed (goal), very likely to facilitate the motor acts following grasping.

While during simple actions the target is usually visible and directly cues the final goal, during many of the actions we perform in our everyday life the target is concealed, and has to be internally generated or kept in mind to shape action unfolding. For example, to eat a candy, one needs to open the candy box, grasp the candy and eat it: the first part of this action sequence is memory-driven, because the agent has to know that the candy is inside the box, although not visible, and has to use this knowledge for action planning. A neurophysiological study in monkeys (Bonini et al., 2011) investigated PFG and F5 grasping neurons activity with a behavioral paradigm more complex than those previously used, including two sequential grasping acts in the same action: the monkey had to grasp and open a container (1st grasping) in order to grasp the target hidden inside it (2nd grasping) and eating it (in case of a piece of food) or placing it in a container located near the mouth (in case of a metallic solid). Before each trial, the set was prepared by the experimenter behind a transparent screen, which allowed the monkey to see which object was put into the container and, therefore, to select in advance the action to perform. Recordings revealed that a relevant percentage of neurons, almost only in area PFG, reflected the final goal already during the first grasping act of the sequence, when only memory-driven information was available. Crucially, when an opaque screen was used during set preparation to prevent the monkey from seeing the target of the forthcoming action, these neurons lost their early action goal selectivity. Interestingly, the discharge during the first grasping act was still present, but was the same for both actions, suggesting that the monkey brain very likely activated at the same time two motor chains, until contextual information (vision of the target) did not allow to disentangle the type of action to be selected. In fact, during the second grasping act the differential discharge reappeared. These findings indicate that parietal neurons can reflect action goals also at a rather abstract level, depending on the availability of contextual information necessary to define the agent's motor intention.

3. From action organization to others' intention understanding

3.1. Mirror neurons and the role of the motor system in understanding others' motor acts and motor intention

Recent models on the selection of object-directed motor acts (see Cisek & Kalaska, 2010), together with the recent data so far reviewed, can provide an integrated account on how natural actions are organized in a world full of objects and of potential action choices. However, the natural environment of humans as well as of other primate species is not only crowded with inanimate objects, but it is also populated by other conspecifics as well as by other animal species. As Gibson wrote, "*animate objects differ from inanimate objects in a variety of ways, but notably in the fact that they move spontaneously (...). Animals are thus by far the most complex objects of perception that the environment presents to an observer*" (Gibson 1979).

Since the beginning of the nineties, the general idea on the neuronal substrates for the representation of others' actions maintained that sectors of the infero-temporal cortex processed increasingly complex information about others' face and limb movements (see Puce & Perrett 2003), constituting the cortical mechanism for the recognition of biological motion. The discovery of mirror neurons (MNs) in the ventral premotor cortex of the macaque (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Gallese, Fadiga, Fogassi, & Rizzolatti, 1996) challenged this view, suggesting that the dichotomy between sensory, associative and motor brain regions was untenable.

Mirror neurons are a class of cells originally discovered in the ventral premotor area F5 of the macaque that discharge during execution of hand (Gallese et al., 1996) or mouth (Ferrari, Gallese, Rizzolatti, & Fogassi, 2003) motor acts, as well as during the observation of similar acts done by another agent. Assuming that the output of a neuron provides the same information every time action potentials are generated, then its output during grasping execution encodes unequivocally this act. Thus, also its activation during the observation of the same act done by another agent would correspond to the activation of an internal motor representation of the observed act. The others' motor behaviour, besides being described pictorially by the activation of visual brain areas, is mirrored by the activation of correspondent motor representations in the observer's brain. Since an individual masters and controls his own behaviour, as a consequence he/she knows the meaning of the motor representations underlying this behaviour. Thus, the activation of the same representations while observing others' actions enable the observer to immediately recognize and understand what others are doing. In other words, the motor behaviour of others is ''reflected'' in the observer's motor repertoire.

Similarly to monkeys, a human mirror system (MS) has been demonstrated by means of electrophysiological (Fadiga, Fogassi, Pavesi, & Rizzolatti, 1995; Gangitano, Mottaghy, & Pascual-Leone, 2004; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010) and neuroimaging (Buccino et al., 2001; Rizzolatti et al., 1996; see for a meta-analysis Molenberghs, Cunnington, & Mattingley, 2012) techniques, showing that the crucial nodes of this system are represented by the posterior parietal cortex, premotor cortex and inferior frontal gyrus. In both monkeys (Kohler et al., 2002; Rochat et al., 2010; Umilta et al., 2001) and humans (Buccino et al. 2004; Cattaneo, Caruana, Jezzini, & Rizzolatti, 2009; Gazzola et al., 2007), a considerable set of data supports the idea that the activation of cortical motor areas during the observation of hand, mouth or foot actions, enables the observer to decode the immediate goal (i.e. grasping, biting, etc.) underlying the observed movements. In particular, two studies on monkey MNs of area F5 can illustrate this concept. In one study (Umilta et al., 2001) it has been shown that MNs discharged both when the monkey fully observed a grasping act and when it saw only the initial part of it, because the hand-target interaction was hidden behind a screen. This suggests that, during action observation, the corresponding motor representations are retrieved, despite the absence of a full visual description of the motor event. In a second study (Kohler et al., 2002), the monkey could both observe a noisy motor act (e.g. breaking a peanut) and listen to its noise. The results showed that a sub-class of MNs, called ''audio-visual MNs'', discharged not only during execution and observation of the noisy act, but also when the monkey listened to its noise, suggesting that the meaning (goal) of an act can be accessed through different sensory modalities.

As in monkey studies, several human data support the concept that understanding other's observed acts require the retrieval of one's own motor representations of the corresponding acts. An example of one of these studies is that reported by Gazzola et al. (2007) on two aplasic individuals, born without arms or hands, who participated in an fMRI study in which they were visually presented with goal-related hand motor acts. Interestingly, compared with control subjects, during the observation of hand motor acts they activated the motor representations of the mouth and the foot. These are the effectors that aplasic subjects use to achieve the same motor goals that control subjects typically achieve with the hand.

As previously discussed concerning the motor organization of intentional action sequences, humans as well as other primates do not usually perform single hand or mouth acts (i.e. grasping, biting) in isolation, but as part of motor chains in which these acts (i.e. reaching, grasping, biting), besides their immediate goal, are linked together to enable the achievement of a *final* behavioural goal (i.e. eat a piece of food). Fogassi and coworkers studied parietal (Fogassi et al., 2005) and premotor (Bonini et al., 2010) grasping neurons not only during the execution of simple grasp-to-eat and grasp-to-place actions, but also during the observation of similar actions done by an experimenter. The target of the observed grasping act could be either a piece of food or a metallic solid, and an empty container was present *only* in the context of grasp-to-place actions, informing the observer about the most likely final goal of the observed agent. Surprisingly, although the recorded neurons were all activated during grasping observation, the intensity of their discharge varied strongly according to the final goal of the observed action (either eating or placing the target). Noteworthy, their visual selectivity for grasp-to-eat or grasp-to-place matched their motor selectivity for the same action. According to the chain model of action organization (Chersi et al., 2011; Fogassi et al., 2005; Rizzolatti et al., 2006), the observation of a motor act in a given context would activate a neuronal chain associated to a specific behavioural goal (i.e. eating or placing), which corresponds to the agent's motor intention. Thus, the activation of this chained representation of an action has a predictive value and allows the observer to generate an internal representation of the agent's motor intention.

3.2. Understanding others' intention: contextual information and movement kinematics

If we accept that the activation of a chained set of neurons could underlie both the motor organization of intentional actions and the understanding of the same actions when observed, a fundamental issue concerns how the correct motor chain is selected in the observer's brain. Overall, what the observer looks and the neurons code are simply motor acts. Converging data from neuroimaging and behavioural studies point to the idea that understanding others' actions and intentions rely not only on one's own motor competence, but also on previous experiences with actions in similar contexts. In fact, several elements in the contextual setting in which actions are performed and observed crucially contribute to our possibility to decode what others are doing and why they are doing it.

A functional MRI study (Iacoboni et al., 2005) directly assessed the impact of contextual information in the cortical representation of grasping actions. In this experiment, human subjects watched three kind of visual stimuli: a hand grasping a cup without a context, a scene containing objects related to a table set for breakfast, and a hand grasping a cup in two different contexts. In this latter condition, the context could suggest two different intentions underlying the grasping action: to drink or to clean. Results indicated that actions embedded in contexts yielded a significantly greater signal change, compared with the other conditions, in the posterior part of the right inferior frontal gyrus and ventral premotor cortex, where hand actions are represented. This result suggests that the motor system can not only encode the immediate goal of observed motor acts but, when sufficient contextual information is available, it can also contribute to the understanding of the intentions of others. Note that in this study the same activations have been obtained both when subjects were instructed to explicitly infer the intention of the observed grasping act and when the request was just to observe. This finding supports the idea that understanding intentions rely on the automatic, effortless and not inferential activation of the mirror system.

Other studies employed high density electroencephalography (EEG) to explore the time course of cortical activation while human subjects watched similar type of stimuli (Ortigue, Sinigaglia, Rizzolatti, & Grafton, 2010): objects and tools were grasped either in presence or absence of contextual information suggesting potential motor intentions underlying the observed action. Results revealed that, following an early bilateral posterior activation after the visual presentation of the stimulus (a grasping hand in a context), a strong activation occurred in the left posterior temporal and inferior parietal cortices: this activation was associated with a complete disappearance of the activity in the right hemisphere, suggesting that this early lateralized temporo-parietal network mediates the understanding of the immediate goal of object-directed motor acts. Subsequently, the increased activation of the right temporo-parietal and frontal regions with simultaneously co-active left hemispheric sources showed longer duration when actions were presented embedded into contexts that allowed the decoding of the underlying motor intention. These findings suggest that areas of the mirror system in the right hemisphere of the human brain play an important role in understanding the intention of others based on contextual information.

Although actions usually occur in contextual situations that provide a number of useful elements to understand the agent's intention, sometimes these elements could be absent or not sufficient for identifying the agent's final goal. In particular, several studies demonstrated that it is possible to understand biological motion from impoverished visual stimulation such as that provided by the movement of light-point displays (Blakemore & Decety, 2001; Elsner, Falck-Ytter, & Gredeback, 2012; Johansson, 1973). These studies indicate that we can recognize others' actions based on internal representation of movement kinematics. Is it possible to exploit kinematic information on others' action also to predict his/her intention? In fact, it might be argued that movement kinematics can be sufficient to decode *what* the agent is immediately doing (i.e. grasping), but not necessarily *why* he/she is doing it (i.e. for eating, drinking, cleaning up, etc.) (see Jacob & Jeannerod, 2005). Recent kinematic studies in humans have shown that different motor intentions translate into different kinematics patterns (Ansuini, Giosa, Turella, Altoe, & Castiello, 2008; Ansuini et al., 2006; Sartori, Straulino, & Castiello, 2011). Interestingly, early kinematics features can be exploited by an observer to decode the intention underlying an observed action sequence (Becchio, Manera, Sartori, Cavallo, & Castiello, 2012; Sartori, Becchio, & Castiello, 2011; Stapel, Hunnius, & Bekkering ,2012). For example, in the study of Stapel et al. (2012), participants observed movements of an actor in presence or absence of a context, and in presence or absence of an object. They were instructed to indicate how an observed action would continue. The results showed that participants' predictions were more accurate when the action was contextualized and object-directed. However, these predictions appeared to depend more on movement cues provided by the observed actor rather than from direct visual information on object and context.

Altogether, these studies suggest that both context and kinematics cues can be used for recognising the motor intention of another agent and can be exploited by the observer to anticipate others' behaviour during social interaction.

3.3. Understanding others' actions in social contexts

Movement kinematics do not vary solely in relation to object features or forthcoming motor acts in an action sequence, but also depending on the more general context in which actions occur. In particular, social contexts are by far the most complex situations humans, and animals in general, have to deal with.

Social interactions often consist of at least two interacting individuals who cooperate or compete to attain a certain goal. Studies on the movement kinematics pattern during a cooperative or competitive social interaction (reaching-to-grasp a wooden block) revealed that each of these contexts was associated to a specific kinematics pattern, which was different from that of the same action performed by the subject alone (Georgiou, Becchio, Glover, & Castiello, 2007). In a further study, participants were asked to collaborate or compete with a partner in the same task, but the partner was an actor instructed to show either a cooperative or competitive attitude. In congruent trials, in which both participants had a collaborative or competitive attitude, the kinematics pattern was that expected based on previous findings, and coherent with the task instructions. In incongruent trials, in which the actor displayed an attitude manifestly in contrast with the task instruction provided to the subject, the subject's kinematics pattern became more similar to that typical of the attitude shown by the actor (Becchio, Sartori, Bulgheroni, & Castiello, 2008). These findings suggest that participants can infer the partner's incongruent intention and use this information to plan and organize a more appropriate interaction. However, the fact that the actor displays an actually different kinematics pattern during cooperation and competition raises an alternative interpretation of the findings: possibly, a social affordance directly provided by the observed movement might automatically induce a variation in the subject's kinematics pattern to match that of the partner.

The concept of 'social affordance', first proposed by Loveland (1991), refers to all those (typically) human activities that occur during social interaction and indicate to other individuals a required or appropriate pattern of behaviour. An example is unfolding the hand showing the palm as if to ask for an object. Becchio, Sartori, Bulgheroni, and Castiello (2008) reported that when an agent performs an action sequence constituted by reaching and grasping an object and places it on the hand of a conspecific, there are significant variations in the kinematics of the reach-to-grasp action compared to the same sequence aimed at placing the object into a container. Interestingly, when the same hand-begging gesture is performed unexpectedly by an agent in front of a subject committed to perform a simple task consisting in grasping an object and placing it on a platform, the arm trajectory of the grasping action varies significantly, suggesting that this social affordance is powerful enough to override and alter the ongoing motor plan (Sartori, Becchio, Bulgheroni, & Castiello, 2009). Similar findings have been reported by studies focused on feeding behaviours. When an agent reaches and grasps a piece of food to directly put it into the mouth of a human receiver, the final phase of the reaching and the placing acts slow down compared to when the food has to be put into a mouth-like aperture placed on the 'face' of a fake human body shape (Ferri, Campione, Dalla Volta, Gianelli, & Gentilucci, 2010). Ferri, Campione, Dalla Volta, Gianelli, and Gentilucci (2011) also showed that the request gesture of mouth opening by a receiver during feeding behaviour was *necessary* to produce the kinematics variation in the agent's feeding action, but also *sufficient* to induce the same variation when the sequence was not finalized to feed but to put the food into a mouth-like aperture.

Summing up, the activation of a social affordance is extremely powerful and automatic, suggesting that in our everyday interactions the automatic and fast decoding of social cues influences our intentional behaviour, in order to maximize the efficiency of our responses.

4. Understanding intention through inferential processes

According to "simulation theories" (see Gallese & Goldman, 1998; Gallese, Keysers, & Rizzolatti, 2004), we usually rely on fast, automatic mirror mechanisms to understand others' actions and intentions. However, there could be ambiguous situations in which direct observation of others' behaviour does not allow to directly disentangle the different goals underlying it. A number of studies have been carried out in order to investigate the neural substrates of humans' inferential and "mentalizing" abilities (see Csibra & Gergely, 2007; de Lange, Spronk, Willems, Toni, & Bekkering, 2008; Dodell-Feder, Koster-Hale, Bedny, & Saxe 2011; Frith & Frith, 2006), suggesting that the temporo parietal junction (TPJ), the superior temporal sulcus (STS) and the medial prefrontal cortex form a so-called 'mentalizing network'. The proponents of this view, often claimed that simulation mechanisms cannot explain how we understand others' mind in many complex social situations. However, they further extend the limits of simulation theories arguing that they are not relevant to the explanation of any socio-cognitive process (Saxe, 2005).

More recent proposals stand in favour of the idea that understanding others' mind in real-life situation can be hardly achieved in an efficient manner relying on purely simulative or purely inferential mechanisms, and suggest that simulation and mentalizing networks are often concurrently activated (Keysers & Gazzola, 2007; Thioux, Gazzola, & Keysers, 2008), with a variable degree of prevalence of one or the other depending on the contextual situation. For example, recent fMRI studies showed that, when volunteers were required to judge the intentions behind different observed actions, areas of the MS *were* activated, regardless of the condition, but there was, in addition, a specific activation of areas that do not belong to the classical mirror circuit, being considered as part of the mentalizing network (de Lange et al., 2008). In another fMRI study (Brass, Schmitt, Spengler, & Gergely, 2007) the observation of unusual actions performed in plausible versus implausible contexts was compared. Results showed that the activation of the MS was the same in all conditions, but interpreting unusual actions in implausible contexts required, in addition, the activation of areas of the mentalizing network. Another recent fMRI study (Becchio et al., 2012) showed that both areas of the MS and of the mentalizing network activate more strongly when the kinematics features of the observed movements are typical of social actions. This finding led to the hypothesis that social intentions, through the activation of the MS, might automatically engage regions of the mentalizing network which are required for social reasoning in complex situations.

In conclusion, the observation of others' actions in everyday life always recruits the mirror system, enabling an immediate understanding of the observed acts and of the agent's intentions when sufficient contextual information is available. Instead, in presence of novel or ambiguous actions/contexts, inferential processes are *also* needed, requiring the activation of further brain areas (Van Overwalle & Baetens, 2009), strongly indicating that intention understanding is a complex process which cannot be attributed to a single neuronal mechanism.

5. Conclusions

The present review proposes a specific neurophysiological account of intention coding that can explain both how we can organize our intentional actions and how we decode the motor intentions underlying other agents' actions.

Usually, the validation of a theoretical model of brain functioning implies the correlation of clinical deficits with focal brain damages or functional alterations of specific neuronal circuits, either in animal models or in human patients. Several studies on clinical populations with lesion in the parieto-premotor regions deemed to host MNs showed deficits in the subjects' capacity to reproduce and, in some cases, to recognize several types of gestures (Buxbaum, Kyle, & Menon, 2005; Heilman, Rothi, & Valenstein, 1982; Pazzaglia, Pizzamiglio, Pes, & Aglioti, 2008; Pazzaglia, Smania, Corato, & Aglioti, 2008; Rothi, Heilman, & Watson, 1985), but whether these patients are also unable to recognize the intentions underlying others' observed actions remains still unknown.

A more deeply investigated link is that between deficits of the basic mirror mechanism and some neuropsychiatric disorders, such as schizophrenia (Arbib, 2007; Burns, 2006; Enticott et al., 2008; Ferri et al., 2012) and autism (Gallese, Rochat, & Berchio, 2012; Iacoboni & Dapretto, 2006; Oberman et al., 2005; Williams, Whiten, Suddendorf, & Perrett, 2001), although only a few studies specifically dealt with the issue of altered recognition of others' motor intention. In particular, Boria et al. (2009) showed that autistic children appears to be capable of reporting "what" is the goal of an individual observed act, while they make errors in identifying "why" the act is performed (i.e. which is the underlying motor intention), particularly in the absence of functional information derived from the object's standard use. In another study (Cattaneo et al., 2007) typically developed (TDC) and autistic children (AC) were required to perform and observe grasp-to-eat and grasp-to-place actions. In TD in both execution and observation conditions there was an increase of the activity of a muscle (mylohyoid) involved in mouth opening before the hand touched the target, as to prepare the mouth to bite the food. In AC there was a delay of activation of the same muscle during grasping, and no activity was recorded during observation. These results suggest that these intention deficits found in autistic subjects might derive from a basic impairment in the cortical 'chain' organization of actions.

The findings here reviewed point to the idea that intentional actions can be envisioned at several, extremely different levels of complexity in the motor system, and the dedicated mechanisms for the neural organization of purposeful behaviour at all levels can be largely exploited to map and decode the intentional actions of others.

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