

## **Neural correlates of intention**

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### **Abstract**

At the behavioral level, we are constantly engaged in sensing the environment and performing ecologically relevant motor acts. The neural activity patterns that give rise to the initiation of such motor acts are still poorly understood. Early studies by Deecke and Libet have demonstrated robust changes in neural activity (as measured with scalp EEG), that begin several hundreds of milliseconds prior to the overt performance of a voluntary motor act. Interestingly these changes in neural activity start even before the subjective time point at which the subjects first feel the urge to move. These findings have set the stage for examining the neural underpinnings of volition, and initiation of voluntary actions over the past 40 years. Primate studies, neuroimaging studies in healthy human subjects, case reports of pathological conditions, and invasive electrophysiological data obtained from patients, all support a model in which the intention to perform an action results from coordinated pre-conscious activity of neuron assemblies in parietal and frontal circuits. In the current chapter, we discuss neurophysiological studies examining the relationship between neural activity and the emergence of the subjective feeling of intention to act.

## **Introduction**

At the core of human society is the belief that we are in control of our actions and are therefore held accountable for their consequences. A key element underlying accountability is the concept of intention. Stepping on the foot of the person in front of me when standing in line at the supermarket might seem as an act of aggression but if performed inadvertently the normative repercussion should be minor. The victim's assumption is that had I predicted in advance that moving my leg would result in stepping on his foot, I wouldn't have moved my leg in the first place. Thus, intention requires two elements: first, the volitional aspect of wanting to perform a certain action (moving the foot), and second the prediction aspect – the ability to foresee the consequences of the action (stepping on someone else). Young children are usually not held accountable for their actions since in many cases their ability to predict the consequences of their actions is not fully developed. At the judicial level, the presence or absence of intention determines the level of accountability which in turn evokes different penal codes even for identical action consequences.

Over the last several decades there has been a growing interest in the neural underpinnings of agency and volition since they carry special significance for judicial systems, various pathologies (e.g. anarchic hand, schizophrenia), and a wide variety of fields ranging from engineering to philosophy. For example, a better understanding of the neurobiology underlying agency and volition is relevant for building neural prosthetics for paralyzed patients who are unable to translate intentions into executable actions. Additionally, such knowledge is informative for philosophical debates about the concept of free will.

Several studies examining these issues have loosely used terms such as 'urge' or 'desire' to express the subjective feeling of 'wanting' to perform an action, as reported by the subjects. Throughout this chapter, we use the term intention to describe these subjective feelings. We define intention as awareness of an imminent execution of a voluntary motor plan aimed at achieving a certain sensory outcome. In particular we focus on intentions that are followed by actions within a relatively short temporal window (on the order of seconds) as opposed to long term intentions (e.g. the intention to take a hike on the weekend). We review human studies examining the neural correlates of intentions using various means including average evoked responses, changes in spectral power and firing rates of individual cells, clinical case reports, and electrical brain stimulation. We conclude by proposing a possible mechanism by which activity of sensory-motor neurons in medial frontal and parietal regions plays a role in the emergence of intention.

## **Physiological events preceding conscious intention**

We begin by discussing three markers of neural activity that have been demonstrated to precede voluntary actions: event related potentials, changes in spectral power of local field potentials, and changes in firing rate of individual cells. These markers correspond with different aspects of neural activity (see term box).

### Event-related potentials (ERP)

Early scalp electroencephalogram (EEG) studies by Deeke, Kornhuber, and Gilden (Deecke et al 1969, Gilden et al 1966, Kornhuber & Deecke 1965) reported the existence of a slow negative potential in the EEG signal that precedes the onset of voluntary movements (as recorded by Electromyogram; EMG). This slow potential, recorded over frontal and central regions of the brain, appeared as early as 850ms prior to onset of voluntary movement and was termed Bereitschaftspotential (BP) or readiness potentials (RP). In a seminal study by Libet and colleagues, the onset of this pre-movement potential was compared with the subjective time in which subjects first felt the urge to perform a quick voluntary flexion of the finger or wrist (Libet et al 1983). Subjects were asked to observe a rotating clock dial on a screen and make a movement at the time they chose. Following this movement, the subjects were asked to report the position of the clock dial at the moment when they first 'felt the urge' to move. This time point was termed 'W' and defined as "...the time of appearance of [the subject's] conscious awareness of 'wanting' to perform a given self-initiated movement" (Libet 1983, page 627). In agreement with the earlier studies, the RP preceded movement onset. However it was further found that the RP also preceded 'W' by several hundred milliseconds. The idea of a physiological marker that precedes the intention to move, has tantalized the field of neuroscience ever since. These studies provided the first realization that a subjective feeling such as intention can be explored empirically with physiological measures. Throughout the chapter, we use the term W, in reference to the time point at which intention emerges.

Further characterization of the readiness potential in relation to movement onset has revealed that it comprises of subcomponents including an early component (termed early Bereitschaftspotential) starting ~850ms prior to movement onset, a middle component (termed lateralized RP component) starting around ~400ms, and a very late component (termed motor potential MP) starting ~50 – 100ms prior to movement onset (Shibasaki & Hallett 2006, Yamamoto et al 2004). While the first component is bilateral, the latter two components are stronger in the hemisphere contralateral to the limb which is about to move. Although these studies demonstrate that the onset of readiness potential precedes movement onset, its temporal relationship to W is unclear. Haggard and Eimer examined this issue further and demonstrated that the onset of the middle RP component co-varied with how early the subjects reported W relative to movement onset (Haggard & Eimer 1999). The early RP component did not co-vary with W. This suggests that the onset time of the lateralized RP component (as opposed to the early RP component) is linked to the emergence of intention.

In another study, Sirigu and colleagues measured RP using scalp EEG from patients with lesions in the parietal lobe or cerebellum. Their experimental design was based on Libet's original experiment in which patients performed self-paced simple button presses (Sirigu et al 2004). At the behavioral level, the patients were not different from healthy controls in estimating the time of finger movement (~20 ms from actual time of button press). Similar to healthy controls in this and other studies, when estimating W, patients with lesions in the cerebellum reported an intention to press the button ~240ms prior to movement onset. In contrast, parietal patients estimated the onset of intention at 55ms prior to movement onset. Interestingly, these behavioral results were echoed by the onset time of RP over central and frontal cortical regions. In the parietal patients, the RP was drastically reduced when they had to report W, while in cerebellar patients and healthy controls, clear RPs starting ~1 second prior to movement onset were observed. The EEG studies described so far point to a neural event in the form of readiness

potentials originating from frontal/parietal regions that precedes and correlates with the temporal signature of intention (W).

Under certain circumstances, as part of a clinical evaluation, electrodes are placed directly (in an invasive manner) on the brain of human patients in order to record neural activity. In addition to the clinical importance, these circumstances provide a unique window of opportunity to gain a basic understanding of brain function in humans (Mukamel & Fried 2012). These invasive studies in patient populations have provided further invaluable insight into the anatomical localization of the cortical and subcortical sources of the readiness potential (See Fig. 1).

Using direct recordings from the brain (Electrocorticography; ECoG) various studies have examined the characteristics of the readiness potential in multiple regions within the motor system hierarchy. Ikeda and colleagues recorded a RP in primary motor area (M1) and the supplementary motor area (SMA) while patients performed voluntary movements with the finger, foot, or tongue, and also during vocalization (Ikeda et al 1992). They report a RP starting between ~500 and ~1500 ms prior to voluntary movement that originates in both regions. The RP in SMA was obtained during movements with ipsi (same side) and also contralateral effectors but was stronger for movements with effectors in the contralateral side. In M1, RP was found only for movement on the contralateral side. Regarding the selectivity of the RP in relation to the effector that is moved, converging evidence support a somatotopic organization of the RP in SMA (with a RP for hand movements more rostral than a RP for leg movement).

Yazawa and colleagues demonstrate that the RP can be recorded both from SMA and even more anteriorly in the pre-SMA (Yazawa et al 2000) although in the pre-SMA the RP is much less sensitive to effector type (Ikeda et al 1992, Yamamoto et al 2004, Yazawa et al 2000). Similarly, in the pre-motor cortex on the lateral side, Kunieda and colleagues report readiness potentials that are invariant to which effector performs the action (e.g. finger, foot, lips) (Kunieda et al 2004). It should be noted that in addition to RPs recorded from the cortex, subcortical sources have also been demonstrated in structures of the descending motor pathway including putamen, globus pallidus, the head of caudate nucleus and the posterior thalamus (Rektor et al 2001a, Rektor et al 2001b, Rektor et al 2001c).

The studies described so far demonstrate changes in brain potentials starting several hundred milliseconds prior to movement onset. These potentials are characterized by three components (early, middle, and late RP), with the middle component co-varying with the timing of intention. Invasive studies demonstrate that this potential is observed in a distributed network of cortical (primary motor, lateral premotor, SMA and pre-SMA – see Fig. 1) and subcortical regions, within the motor system hierarchy.

### Changes in spectral power

The RP described above corresponds to synchronized (evoked) neural activity which is phase-locked to a specific event (such as movement onset). Changes in neural activity can also be non-phase-locked (induced). Since these changes are not perfectly timed with an external event, they are hard to detect when examining evoked potentials averaged across multiple trials. Such non-phase-locked neural events are better observed by measuring changes in the spectral power of the

EEG signal in different frequency bands. These changes can manifest as either increases (event related synchronization; ERS) or decreases (event related desynchronization; ERD) in power at various frequency bands (Buzsaki et al 2012) (Neuper et al 2006). Both ERPs and changes in spectral power reflect activity changes of large populations of neurons.

Ohara and colleagues measured changes in spectral power of the ECoG signal while patients performed self-paced finger/wrist extensions (Ohara et al 2000). The authors found ERD in low frequencies (~10 – 22Hz) originating from SMA, M1 and primary somatosensory cortex (S1) that started between 0.5 and 3.4 seconds prior to movement onset. These power changes started earlier in SMA, and onset times did not depend on the laterality of the moving limb (i.e. ipsi or contralateral to the recording electrode). In M1 and S1, the onset of ERDs was later relative to SMA. In addition, ERD in these regions was more strongly lateralized in terms of latency and amplitude (i.e. ERD in M1 and S1 for contralateral movement started earlier and was stronger than ERD for ipsilateral movement).

In another study, Rektor and colleagues compared the anatomical distribution of ERDs in the alpha/beta range (~8 – 20Hz) and RP, while patients performed self-paced finger flexions with their right or left fingers (Rektor et al 2006). While in sensorimotor regions (such as S1/M1, and SMA) they found both RPs and ERDs preceding movement, ERDs were more widespread and could also be found in other regions in which RPs were not found (including orbitofrontal and inferior parietal cortices, and lateral and mesial temporal cortices).

Taken together, the temporal profile of ERDs and RPs are similar – preceding movement onset by up to ~3 seconds. While the anatomical distribution of ERDs is more widespread than that of RPs, there is large overlap of these two measures of neural activity in sensorimotor regions.

#### Changes in firing rates

The RP and changes in spectral power described so far pertain to activity changes across very large populations of neurons. However these measures do not allow discrimination of firing patterns of individual cells. In a recent study, we recorded extracellular single and multi-unit activity from 12 patients while they performed a variant of the task originally described by Libet (Fried et al 2011). The patients observed the dial of an analog clock rotate with a period of 2.6 seconds and were instructed to press a button on the keyboard ‘whenever they felt the urge to do so’. The timing of the button press was registered together with the neural activity, and the subjective time-point of urge to press (W) was calculated based on the patient’s post-hoc report of the location of the dial on the clock’s circumference. In agreement with previous studies, the patients reported the time of urge as occurring approximately 200ms prior to the actual time of button press (e.g Sirigu et al (2004)). We recorded spiking activity from neurons in frontal regions including the SMA, pre-SMA, and anterior cingulate cortex (ACC), and also from neurons in medial temporal regions. We found clear deviations from baseline firing rate of individual neurons that preceded W by several hundred milliseconds. These changes were more common in frontal regions (17% of recorded cells) compared with temporal regions (8%) and within frontal regions, the highest proportion of cells (23%) was observed in the SMA. This is in agreement with a previous study showing that the majority of cells in SMA and pre-SMA display increased firing rate (compared with baseline) during a 5 second delay period before execution of a finger-to-thumb apposition task (Amador & Fried 2004). In our study, changes in firing rates

were not uniform across neurons. Some cells displayed gradual increases in firing rate, while others (with more or less equal distribution) displayed gradual decreases in firing rate as W time was approached. Firing rate in both cell populations started to deviate from baseline ~1500ms prior to W. Interestingly 100 ms prior to W, firing rates started to return to baseline.

Both ERPs and changes in spectral power are measures that are based on averaged activity across multiple trials. On the level of individual trials, we showed deviations in firing rate of single neurons that allowed prediction (80% accuracy) of an upcoming intention 700 milliseconds in advance. These data suggest, that both increases and decreases in firing rate in frontal regions (predominantly in the SMA), might have a role in determining the time of intention.

The data reviewed so far points to a correlation between neural activity and the emergence of intention. This correlation is reported at the level of populations of cells (ERP and changes in low frequency spectral power), and also at the level of individual cells (changes in firing rate). These changes in neural activity are predominant in S1/M1, SMA/pre-SMA and also pre-motor cortex.

### **Physiological markers of intended movements**

Are the physiological markers discussed so far a hallmark of intended movements or are they associated with any movement type? The coupling between the presence/absence of various physiological markers and intention has been examined in various pathologies.

Patients with Gilles de la Tourette syndrome (commonly known as Tourette), suffer from uncontrollable motor and vocal tics. If the source of the RP is motoric in nature, and not linked to higher-level goals and intentions, one would expect a similar RP during voluntary and non-voluntary movements. In one study, five out of six patients showed no RP during endogenous tics but when the patients had to voluntarily mimic their tics, a RP starting ~500ms earlier was evident (Obeso et al 1981). In another study, similar results were obtained in 3 out of 5 subjects (Karp et al 1996). These results suggest that intention in controlled movement is coupled with the presence of a RP.

An additional pathology in which voluntary and non-voluntary movements were compared is anarchic hand syndrome (AHS). In patients with AHS, the affected hand occasionally performs meaningful goal-directed actions while the patients deny having an intention to perform these actions. As opposed to ballistic movements typical of Tourette patients, the actions performed by the anarchic hand are meaningful but inappropriate to the context. The patients are fully aware of their inappropriateness and often try to stop the action by using their healthy hand. This syndrome is often associated with lesions to the parietal or mesial frontal (SMA) regions (Della Sala & Marchetti 2005). In a case study, Assal and colleagues report a patient suffering from AHS in the left hand following stroke in the right parietal lobe. Using fMRI, they found increased activity in a network of motor regions (including right M1 and premotor cortex, and also left inferior frontal gyrus and frontopolar cortex) when the patients performed movements with their left hand experienced as voluntary. However, during left hand movements that were not experienced as being under conscious control, only activity in right M1 was found (Assal et al 2007). These results suggest that although activity in M1 is sufficient to evoke movement, it is

not sufficient for the emergence of intention which requires the recruitment of additional motor regions.

In addition to pathologies that involve improper intentions, such as AHS and Tourette discussed above, some patients suffer from the disorder of diminished motivation (DDM), manifesting clinically in abulia, apathy, or akinetic mutism. Symptoms include a poverty of behavior and speech output, and lack of initiative in generating movement, although the patients are capable of performing such movements. Anatomically, these disorders involve lesions in multiple regions including SMA, anterior cingulum, prefrontal cortex, and various subcortical regions (Bhatia & Marsden 1994, Manes & Leiguarda 2005, Marin 1997, Marin & Wilkosz 2005).

Initial fMRI findings in our lab support the involvement of right parietal cortex in the dissociation between intention and movement kinematics. Subjects had to perform hand movements in different directions across trials in order to obtain the same sensory goal. While primary and pre-motor regions were sensitive to the specific direction of hand movement, we found a region in the right parietal cortex that was sensitive to the intended sensory goal but invariant to the specific direction of hand movement that was performed to achieve it (Krasovskiy A. et al 2013)

These data further support the involvement of descending pathways controlling movement (at the anatomical level) and the presence of RP (at the functional level) in the emergence of intention.

### **Electrical stimulation and feeling of intention**

In some clinical settings, implanted electrodes in patients are used not only for recording ECoG or single unit activity but also to electrically stimulate and evaluate the functional role of the underlying tissue. This method allows assessing the causal role that specific brain regions might play in generating behavior.

As part of a functional mapping procedure conducted in epileptic patients, Fried and colleagues stimulated regions of the supplementary motor area (SMA) in 13 patients to determine the relation of the area of seizure onset to behavioral function (Fried et al 1991). In this procedure, different regions of the brain are electrically stimulated while clinicians look for overt motor responses. The authors reported the existence of a crude somatotopic map along the caudal-rostral axis of the SMA with the legs represented in caudal regions and the head and eyes represented more rostral. This somatotopic organization was also confirmed in later studies (e.g. Ikeda et al 1992, Lim et al 1994, Yazawa et al 2000). Surprisingly, stimulation of different sites in some of the patients, elicited the urge to move (as reported by the patients) even though no overt movement was observed. This reported urge was somatotopically organized and commonly corresponded with overt movement evoked when stimulation intensity was increased. For example, at low stimulation currents, the patient reported an urge to lift their right elbow, and increasing the stimulation current evoked overt right arm abduction.

In another set of 15 patients, Lim and colleagues confirmed the somatotopic organization of the SMA with the leg representation caudal (towards M1) and the head and upper extremities represented rostral (Lim et al 1994). Electrically stimulating the SMA evoked sensory responses including numbness, tingling or pressure sensation contralateral to the stimulating electrode. Importantly, occasionally some patients reported a sensation of movement or an urge to move their limbs in lack of overt movement. Invariably, the authors report that increasing the stimulation current evoked overt motor responses.

Recently, Desmurget and colleagues electrically stimulated the parietal and pre-motor regions of tumor patients as part of a functional mapping procedure designed to minimize postoperative sequelae following tumor resection (Desmurget et al 2009). Low current stimulation in inferior parietal regions evoked an intention/desire to move (as reported by the patients) with no overt movement recorded. Increasing the current level produced a sensation of movement although again, no electromyogram (EMG) activity was observed. In contrast, stimulation of lateral pre-motor regions did evoke overt movements at higher stimulation currents. In these conditions, the patients did not report a desire to move and in many cases they were not even aware of such movements.

These studies provide strong causal evidence for the involvement of mesial frontal and lateral parietal regions in the intention to perform a voluntary motor act.

## **Discussion**

In what follows, we discuss the findings reviewed above and conclude by suggesting a plausible neural mechanism underlying the emergence of intention to move.

Research over the past few decades detected physiological markers that correlate with the intention to move a specific effector. These physiological markers include slow changes in electrical potentials (RPs), changes in spectral power (ERD/ERS) that reflect changes in the degree of synchronization across large populations of neurons, and also changes (both increases and decreases) in firing rate of individual neurons. In some cases these physiological markers even allow prediction of an upcoming intention to move several hundred milliseconds in advance.

RP's have been commonly subdivided into different components including an early, middle and late component which start ~800, ~400, and ~100ms prior to movement onset, respectively. Since the time of movement onset and W are not independent, it is difficult to disambiguate the functional role of different RP components with regard to W or movement preparation. However, it has been shown that the onset of the middle component of RPs co-varies with the temporal report of W. Furthermore, the presence/absence of RP seems to co-vary with whether the movement is experienced as voluntary.

With regard to the anatomical distribution of these physiological markers, most evidence for RPs in humans is ascribed to frontal/parietal regions including S1/M1, SMA, and pre-SMA (predominantly on the mesial aspect of the cortex), and also the pre-motor cortex (on the lateral aspect of the cortex). Electrical stimulation studies further corroborate the involvement of



inferior parietal cortex and SMA in the emergence of intention to move (even in the absence of actual movement). In contrast, stimulation of the lateral motor regions has not been reported to evoke the sensation of intention. Stimulation in these regions has been mostly associated either with evoked movement or movement interference (such as speech arrest (Filevich et al 2012)). Further characterization of the different functional properties of these regions might shed light on their causal role in generating intention.

## **Model**

This chapter discussed a wide body of literature that described neural activity preceding intention of upcoming movement. However, the evidence we presented remained mostly correlational with regard to neural activation associated with movement and the emergence of intention. The fact that preconscious neural activity is observable across a wide variety of methodologies makes the absence of a mechanistic proposal with regard to its function all the more glaring. Our model aims to bridge this gap by proposing an underlying functional role for such neural activity in the emergence of intention and voluntary action.

We suggest that activation of a special class of neurons with visuomotor properties may hold functional significance for the emergence of intentions. We describe how these neurons, co-localized in the same brain regions in which we find RPs, may lay a framework in which intentions are translated into actions. This framework is supported by several lines of evidence including anatomical, behavioral, functional, and lesion data.

Neurons in various regions of the motor system, have been found to respond not only during overt action but also during passive observation of actions performed by others (mirror neurons; (Rizzolatti & Sinigaglia 2010)). Mirror neurons have been classified as either strictly congruent, responding to one type of action (either executed or observed), or broadly congruent - responding to one type of action during execution but to several types of actions during observation (Gallese et al 1996). It should be noted that typically, the various types of observed actions that broadly congruent mirror neurons respond to are logically related (e.g. different grips). Another type of cells with visuo-motor properties are ‘canonical neurons’. Like mirror neurons, canonical neurons respond during execution of goal-directed actions. However, while mirror neurons respond during observation of actions involving an agent interacting with an object, canonical neurons respond to the mere perception of graspable objects in the absence of an interacting agent.

Together, these various types of visuomotor neurons (strictly congruent, broadly congruent and canonical neurons) have the functional properties to represent possible actions based on perceived objects/actions in the environment. Their activity could represent the first step in generating an intention to act. For example, seeing a ball (or someone interact with a ball), evokes activity in several networks of visuomotor neurons corresponding to specific sets of possible actions – such as bouncing, throwing or kicking. Indeed visuomotor neurons in ventral pre-motor cortex of monkeys have been shown to respond in a differential manner to reachable versus unreachable objects (Caggiano et al 2009). At the behavioral level, observing actions performed by others is known to trigger an urge (and increased tendency) to perform similar actions (e.g. social contagion, the chameleon effect) (Chartrand & Bargh 1999). The activity of

mirror neurons and canonical neurons might play a role in such phenomena and constantly update the set of actions afforded by objects perceived in the environment (Cisek & Kalaska 2010).

We propose that the affordances discussed above (and the activity of mirror neurons) may be represented by the early phase of the RP. During the early RP phase, our model assumes that neural representations of multiple affordances are evoked (Figure 2A). Several lines of evidence support this assumption. The anatomical regions where RPs have been recorded, largely overlap with regions containing neurons with mirroring properties (including pre-motor, SMA, and primary motor cortex). Furthermore, decreases in spectral power (ERD) prior to voluntary movement are reported in the 8 – 20Hz frequency band. Decreased power of the EEG signal in the same frequency band is also associated with mirror neuron activity (mu suppression, (Pineda 2005)). Neurons with mirroring properties have also been demonstrated in parietal cortex, where electrical stimulation has been shown to elicit an urge to move. In addition, a large body of research from the monkey literature shows that frontal-parietal circuits simultaneously code the reaching direction of several movements (Cisek & Kalaska 2005, Cui & Andersen 2011, Klaes et al 2011). It should be noted that the early RP is not lateralized, in agreement with the computation of multiple affordances, possibly with different effectors.

At a certain stage the neural representation of a specific affordance crosses a selection threshold. This selection process is represented by the middle RP phase (Figure 2B). Unlike the early phase of the RP, the middle and also the late phases are lateralized in agreement with the interpretation that they represent the choice of a motor plan carried out with a specific effector. Interestingly, patients with parietal lesions or patients with Tourette, report feeling *W* almost concurrently with movement initiation. The absence of RP preceding movement in these patients, suggests that the middle phase RP might reflect the culmination of neural processes that give rise to intention. Taken together these findings suggest that *W* correlates with the point in time in which an affordance was selected. In essence, the earliest point in time in which the intention is felt (and subjectively reported), is tied to the point in time in which a selection threshold was crossed.

Once an affordance has been selected, the transition to the late phase of the RP occurs when an execution threshold is crossed (figure 2C). If observing a graspable object or observing someone else perform an action automatically evoked responses in motor cortex, there needs to be a “braking mechanism” in order to avoid automatic (and sometimes dysfunctional) imitation or uncontrolled manipulation of surrounding objects. What mechanism prevents the immediate execution/imitation of these actions? Evidence for such a putative braking mechanism comes from single unit recordings in monkeys and from epileptic patients which show that a subset of mirror neurons increase their firing rates during action execution but decrease their firing rates during action observation (Kraskov et al 2009, Mukamel et al 2010). Such functional properties might underlie the inhibition of unwanted actions. Interestingly, patients with frontal lobe lesions have been shown to suffer from compulsory imitative behavior (Chow & Cummings 2007) or utilization behavior (Gazzaley & D'Esposito 2007). The symptoms in these pathologies suggest a deficit in such a brake mechanism resulting in the inability of these patients to inhibit unwanted actions. It would be interesting to characterize RP in such patients.

Some testable predictions emerge from our model. If the early RP component represents action

affordances, an increase in the number of affordances should correspond with increased amplitude of the early RP. Moreover, interfering with the RP build-up at different stages (early/late) should modulate the subject's ability to report any experience of emerging intention.

Several questions regarding this putative mechanism remain unanswered. The functional role of each region within the fronto-parietal network underlying intention is not well established. RP has been shown both in pre-motor, SMA and parietal regions. However, only electrical stimulation in parietal regions and SMA elicits an urge to move. Increasing stimulation current evokes movement in SMA but not in parietal regions. These results point to functional differences between the regions that need to be elucidated. Furthermore, the temporal dynamics of activity between the different regions within the network are not known.

We note that our model does not account for actions that are 'internally generated', presumably originating from 'within' since they lack any discernable evoking stimulus. Actions are often classified along an axis ranging from internally to externally generated. Whereas externally generated actions are often in immediate response to an external stimulus (such as catching a ball), internally generated actions take place without any evident overt stimulus. We propose that the distinction between internally and externally generated actions corresponds with the temporal distance between the action-evoking stimulus and motor act. Within this temporal framework, internally generated actions are actions in which the temporal distance from the evoking stimulus is large (e.g. actions that are evoked by long term memory), whereas externally triggered actions have a shorter temporal window that separates them from their evoking stimulus. Much less is known about the processes by which internally generated intentions emerge. The study of spontaneous neural activity preceding voluntary action is currently an active field of research taking its first steps in addressing this issue (Rolls & Deco 2011, Schurger et al 2012).

The answers to some of these questions will have implications in various fields including pathologies (e.g. Tourette, and anarchic hand syndrome), brain machine interfaces, and may help the judiciary system decide the degree to which the defendant in a trial should be held accountable for his action consequences.

## **Term Box**

### **EEG (Electroencephalography)**

A noninvasive method for recording electrical activity from the brain by placing recording electrodes over the scalp. The measured signal corresponds to ionic current flow from large neural populations (mostly pyramidal cells). This technique provides high temporal resolution but suffers from low spatial resolution thus making exact anatomical claims regarding the source of the recorded signal difficult.

### **LFP (Local field potentials)**

Voltage changes resulting from both dendritic currents and action potentials of large populations of neurons. These signals are typically recorded invasively using thin (submillimeter) microwires or contact electrodes (~2mm) in the case of ECoG.

### **ECoG (Electrocorticography)**

An invasive method for measuring population neural activity. Multiple recording electrodes (typically ~2mm contacts) are placed during surgery directly on the surface of the brain of various clinical patients (e.g. epilepsy). These electrodes allow recording local field potentials (LFPs) from the underlying brain tissue.

### **fMRI**

A non-invasive method that measures changes in blood oxygen content. These changes are used as a proxy to estimate the underlying neural activity

### **ERP (Event-related potential)**

An EEG signal, locked to stimulus onset (or any other temporal event of interest). This signal is obtained by averaging the evoked EEG signal across many trials. This signal is typically divided into different components corresponding to various behavioral/neural aspects.

### **ERD/ERS (Event related desynchronization/synchronization)**

Changes in neural activity are not necessarily time-locked to an external event. Such changes often appear in the power of the LFP signal at specific frequency bands. These power changes infer an enhancement or reduction in synchronized neural activity across a population of neurons. ERD is interpreted as a correlate of enhanced cortical activity since neurons are not firing in phase with each other. In contrast, ERS is often interpreted as a deactivated cortical state in which neurons respond in phase with each other.

### **Single Unit Recordings**

These are extracellular electrical recordings of spiking activity, representing the firing rate of a specific neuron. In humans, such recordings are performed mostly in epileptic patients undergoing clinical evaluation for potential surgical treatment.

### **Affordance**

The set of possible actions that can be performed with an object. Many objects have multiple affordances - for example - a door knob affords twisting, pulling and pushing. The same object can have different affordances for different individuals depending on the set of skills within their motor repertoire.

### **Electromyogram (EMG)**

A measure of the electrical activity produced by muscles. This signal can be recorded by placing recording electrodes on the muscle.

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## Figure Legends

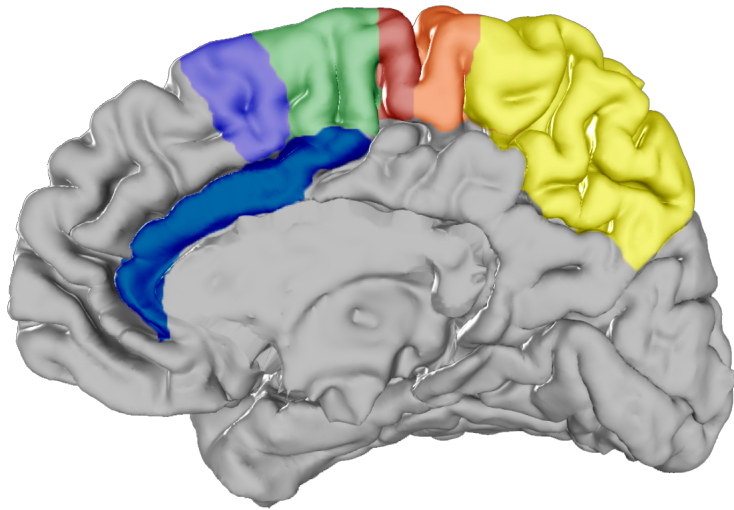
Figure 1:





Cortical regions from which RP was recorded. SMA – supplementary motor area; ACC – anterior cingulate cortex.

Figure 2:

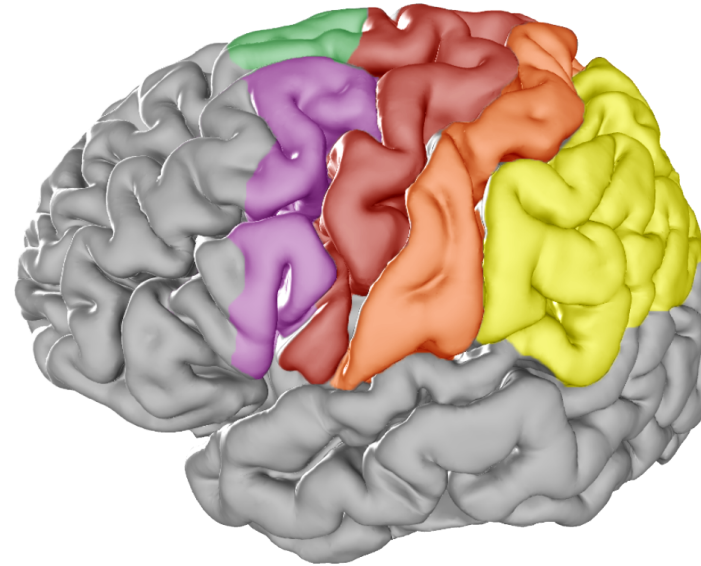
**Title: Model Scheme depicting the Functional Role of visuo-motor neurons in the Emergence of Intended Actions.** (A) Affordances Representations. Seeing an object in the environment evokes multiple affordances through the activity of visuo-motor neurons within various regions of the motor system hierarchy. The various affordances can be performed with different effectors and are represented by the early phase of the RP which is bilateral. (B) Action Selection. The neural representation of an affordance with a specific effector crosses a selection threshold. This selection process is represented by the middle RP phase and is lateralized to the contralateral hemisphere. During this phase the cognitive processes that give rise to W gradually evolve (represented in gray gradient) until W is finally reported. (C) The transition towards the late phase of the RP occurs when an execution threshold (between W and M) is crossed. The motor potential is evoked when the selected action is executed.




**Medial View**



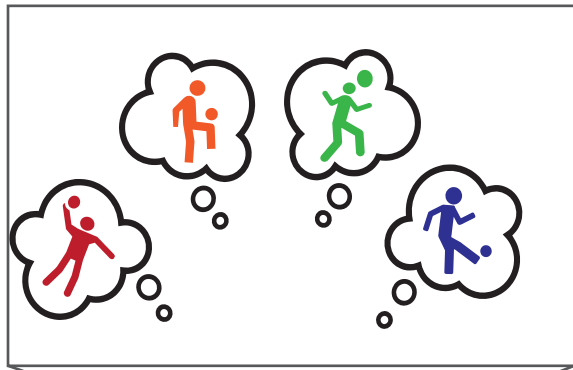
-  somatosensory cortex
-  posterior parietal cortex
-  SMA
-  pre-SMA

**Lateral View**

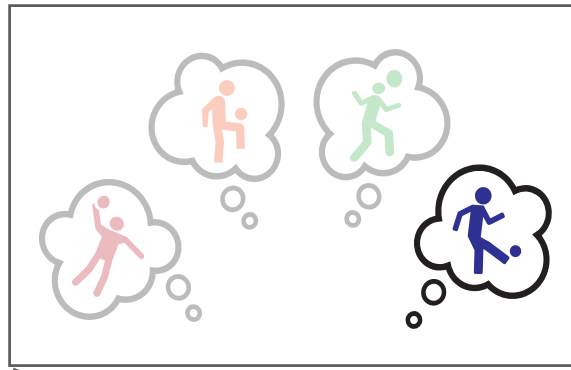


-  ACC
-  primary motor (M1)
-  premotor cortex

### A Affordances Representations



### B Action Selection



### C Action Execution

