

A parietal-premotor network for movement intention and motor awareness

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It is commonly assumed that we are conscious of our movements mainly because we can sense ourselves moving as ongoing peripheral information coming from our muscles and retina reaches the brain. Recent evidence, however, suggests that, contrary to common beliefs, conscious intention to move is independent of movement execution *per se*. We propose that during movement execution it is our initial intentions that we are mainly aware of. Furthermore, the experience of moving as a conscious act is associated with increased activity in a specific brain region: the posterior parietal cortex. We speculate that movement intention and awareness are generated and monitored in this region. We put forward a general framework of the cognitive and neural processes involved in movement intention and motor awareness.

Conscious intention and motor awareness in cognitive neuroscience

In recent years, the neural bases of our conscious experiences have been extensively investigated using psychophysics [1,2], neuroimaging [3,4], anatomo-functional correlations [5,6], transcranial magnetic stimulation [7,8], electrophysiological analyses [9] and direct electrical stimulation of the brain [10,11]. All these approaches have led to the identification of a complex interconnected network underlying conscious experience. This network is organized around three major regions: the posterior parietal cortex (PPC), the supplementary motor area (SMA) and the premotor cortex (PMC). However, a general model articulating the functioning of these neural nodes is still lacking. Taking advantage of the most recent theoretical and experimental advances in the field, we propose here a general framework of the main cognitive and neural processes involved in generating the experience of conscious motor intention and movement awareness. This framework is based on our current understanding of the neural bases of: (i) conscious motor intention (the conscious desire to act), (ii) conscious motor awareness (the subjective feeling that we are moving) and (iii) veridical motor awareness (the objective knowledge that we are actually moving).

Although the emergence of movement intention into awareness is preceded by early unconscious processes taking place probably in prefrontal and parietal areas

[12,13] (Box 1), we focus here on the conscious component of movement and show that the conscious intention to move is independent of movement execution and that parietal areas are key in the generation and monitoring of movement intention and awareness.

Conscious motor intention

The establishment of conscious motor intention as a valid object of scientific investigation can be traced back to the pioneering work of Benjamin Libet and colleagues, 25 years ago. These authors asked human subjects to fixate a single clock hand rotating on a screen (Figure 1, top panel). The task was to press a button with the right index finger whenever the subjects ‘felt the urge’ to do so. After this movement, at a random time, the clock stopped and the subjects were required to report the position of the clock’s hand at the time they first became aware of their will to move (W-Judgment). The readiness potential (RP, an electrophysiological marker of early movement preparation) was recorded. The W-Judgment was found to precede movement onset by around 200 milliseconds. At the same time, the RP was found to precede the W-Judgment by about 1 second (Figure 1, middle panel). The latter latency strongly suggests that movement preparation anticipates the conscious intention to move. Similar results were provided by Haggard and Eimer [14] in a subsequent study which used a modified version of Libet’s paradigm. In this study, the subjects could choose whether to respond with the left or the right index finger. In addition to the classical RP, Haggard and Eimer also recorded the Lateralized RP (LRP), as a more specific marker of motor preparation (the LRP is thought to reflect the point in time at which response side – left vs. right – is determined) [15]. On average, the LRP was found to occur approximately 800 milliseconds before movement onset. Additional analyses also showed that the LRP began significantly earlier for early than for late W-Judgments, which was not the case for the RP. The authors concluded that conscious intention arises after the initial stage of motor preparation (linked to RP), at the time when a specific motor network is selected for action. This selection does not mean, however, that the elaboration of the actual motor command precedes conscious intention. Indeed, there is a 200–300 milliseconds duration between the W-Judgment and the actual motor command [2,14,16].

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Box 1. Prior intention

As shown by the seminal study of Libet and colleagues, preparatory motor activity, known as the 'readiness potential' (RP), starts at least 1 second before the emergence of any conscious intention to act [16]. Converging evidence suggests that this preparatory activity is not germinal. It is shaped by unconscious computations carried out in a wide network related to intentional actions [12,61]. To identify the key nodes of this network, researchers have investigated the neural bases of self-generated actions. They identified, as relevant, activations in a wide range of areas including the posterior parietal cortex (PPC), the anterior cingulate cortex, the supplementary motor area (SMA) and the dorsolateral prefrontal cortex (DLPFC) [62]. Activation in this latter region was the most likely to survive when self-generated actions were contrasted with externally-triggered responses (instead of a rest condition) [20,62]. Interestingly, the DLPFC receives important projections from the frontopolar cortex [63], a structure that has been shown to encode motor intentions up to 10 seconds before they become conscious [13]. In addition, the DLPFC projects to the SMA and PPC [64], two regions that have been shown to generate conscious intentions when electrically stimulated (see main text). Therefore, the early computations carried out by the prefrontal cortex seem to represent the first stage in the causal chain that renders our motor intentions available to consciousness.

In addition to the data above, it is widely admitted that the basal ganglia (BG) are important for producing intentional (self-generated) actions. However, evidence supporting this claim is rather weak. Neuroimaging studies have identified significant responses in the BG when the neural activations triggered by self-generated movements were compared to a rest state. However, no higher activation in the BG network was observed when self-generated movements were contrasted directly with externally triggered movements [20,62]. An absence of systematic involvement of the BG for self-generated movements was also reported in electrophysiological and inactivation studies in monkeys [65]. Finally, the idea that akinesia, in patients with Parkinson disease, concerns self-generated but not externally triggered movements has recently been rebutted [17].

This delay is similar to the time required to initiate simple reactive movements in response to visual or auditory stimuli [17–20]. This suggests that the motor output corresponding to the desired movement is not processed before, but after the time of conscious intention.

From an anatomical point of view, the supplementary and pre-supplementary motor areas (designated SMA hereafter) have been described as the most likely source for LRPs [15,21]. From this one may speculate that the medial motor regions play a critical role in the building of conscious intention. There is indirect evidence supporting this view. In particular, the SMA is activated when subjects attend to the time of their conscious intention to perform a movement [3]. Also, this structure is known to be a commonly injured region in patients suffering from the anarchic hand syndrome [22,23]: a pathological condition in which the executive and intentional systems are disconnected from each other, thus leading to the occurrence of arm movements without conscious intention [4].

However, the best evidence linking the SMA to conscious intention comes from an electrical stimulation study performed by Fried and colleagues [10]. Fried and colleagues stimulated the medial surface of the cerebral hemispheres of epileptic patients with subdural electrode grids [10]. The results indicated that stimulations delivered within the SMA region triggered a need or an urge to move that resembles a compulsive desire to act. Indeed,

patients felt as if they were not the agents of their movements. They reported that a movement 'was about to occur' or that the arm 'was going to move'. Slightly increasing the intensity of the stimulation above the urge threshold caused the evoked movements to actually occur. The proximity between the two events suggests that the urge to act experienced by these patients reflects the imminence of a movement. In agreement with this idea, stimulations of the SMA evoke very precise movement intentions such as an 'urge to move the right leg inward', 'to lift the right elbow' or to 'pronate the right forearm'. It has been proposed that the SMA triggers the movement by suppressing the inhibitory signal exerted on the primary motor cortex (M1) [24]. This suppression might be the neural correlate of the urge-to-move feeling experienced by epileptic patients during electrical stimulation of the SMA.

In addition to the data above, solid evidence also links the feeling of conscious intention to the activity of the PPC. It has been shown that selective lesions of this region can cause alien hand movements [4]. Also, it has been reported that patients with parietal lesions can lose the early subjective experience of wanting to move. To establish this result, Sirigu and colleagues [2] used Libet's paradigm in three groups of individuals: control subjects, patients with cerebellar lesions and patients with posterior parietal lesions (Figure 1, bottom). In agreement with previous results [3,14,16], the W-Judgement was found to precede movement onset by more than 250 milliseconds in control subjects and cerebellar patients. However, in parietal patients, the lag was only around 55 milliseconds. This short delay suggests that the patients did not know about their intention to move until movement release became imminent. It is tempting to relate this late consciousness to the claim that the urge to move experienced when the SMA is electrically stimulated reflects the imminence of a movement. One may speculate that healthy subjects rely on early activity within the PPC intentional system to be aware of their intentions to move, whereas parietal patients have to wait until the release of the motor command by the SMA to access this subjective experience.

Support for this view can be found in a recent study where direct electrical stimulation was applied over the parietal cortex in patients undergoing awake surgery for tumor removal [11] (Box 2). If the PPC is truly involved in the generation of conscious intentions, then electrical stimulation of this region should be accompanied by the subjective experience of 'wanting to move'. In accordance with this prediction, stimulation of the right inferior parietal lobule (Brodmann Areas – BA 40 and 39) triggered a strong desire to move the contralesional hand, arm or foot (Figure 2). In the same vein, stimulations of the left inferior parietal lobule (BA 39) provoked an intention to move the lips. Patients reported, for instance, 'a will to move the chest' or 'a desire to move the hand', which demonstrates the voluntary and endogenous character of the feelings they experienced. Interestingly, in most patients these intentions were much less specific than the precise intentions reported by the SMA patients (see above). Parietal (stimulated) subjects were generally unable to precisely describe the type of movements they intended to do, even when invited to do so. For instance, a typical exchange was

Box 2. Probing brain functions with electrical stimulations

Electrical stimulation has a long history in medical and fundamental sciences [66]. Today, this procedure remains strongly advocated for tumoral resections carried out in eloquent regions [67]. In these resections, the neurosurgeon stimulates the cortical surface while the patient performs various motor and cognitive tasks (e.g. opening-closing hand; naming objects) (Figure 1). Any reproducible functional disturbance induced by the stimulation provokes the interruption of the resection at the tested location.

The use of electrical stimulation for probing brain functions is not without controversy, however. A major issue concerns the tendency of electrical currents to spread through white matter bundles. This diffusion is inevitable, even for single pulse stimulations [68]. However, in contrast to a common view, it does not follow an anarchic path; the current spreads along physiologically meaningful pathways [69–72]. The resulting effect is assumed to mimic the normal function of the stimulated tissue [73]. In agreement with this hypothesis, it has been demonstrated, for instance, that the premotor neurons that trigger limb movements when electrically stimulated are the same as the neurons activated during goal-directed reaches [74]. Based on these data one might suggest that the spread of current along white matter tracts is not a difficulty that needs to be overcome, but a process that is essential to the expression of the investigated function.

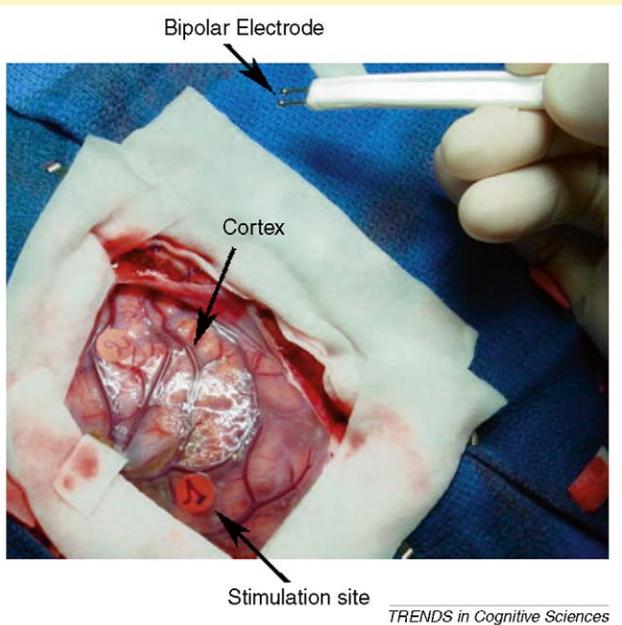


Figure 1. Peri-operative brain stimulation with a bipolar electrode during awake surgery for tumor removal (Image by courtesy of Dr Carmine Mottolese).

as follows [11]: Patient: ‘I wanted to move my foot’. Experimenter: ‘Which foot’. Patient (showing his left leg): ‘This one’. Experimenter: ‘How did you want to move it?’. Patient: ‘I don’t know, I just wanted to move it’. To account for these observations it was suggested that the PPC contains stored movement representations [25,26] and that electrical stimulations activate these representations, thus provoking a desire to move [11]. Under ecological circumstances, early unconscious computations carried out in the prefrontal regions might lead to the activation of these representations (Box 1). Note that increasing the intensity of the stimulations was never found to produce actual motor responses in parietal regions.

To summarize, parietal cortex stimulation generates conscious intentions to move. By contrast, stimulation of

the SMA triggers feelings of an urge to move that reflect the imminence of a motor response. This contrasting pattern of response suggests that intentions in the PPC are related to motor prediction and selection, whereas the feeling of an urge to move in the SMA is related to movement preparation [11,27].

Motor awareness

The issue of motor awareness amounts to a very simple question: how do we know we are moving? During the last decade, this question has received much less attention from researchers than the issue of conscious intention. Nonetheless, several important findings have emerged. At a phenomenological level, it was found that most of the basic functioning of the motor system occurs without awareness (for a review [28]). This means that the signal we are aware of when making a movement does not emerge from the movement itself, but rather from the predictions we make about the movement in advance of action. The best evidence supporting this claim comes from behavioral experiments in which a mismatch is introduced between the actual and perceived motor responses. This mismatch is typically within the margin of flexibility of the motor system: it is big enough to impose profound kinematic corrections to the ongoing movement but small enough to allow target acquisition. Under this type of protocol, despite large changes in hand path and joint trajectories, the subjects believe that they are executing the movement as originally planned and they do not take into account the sensory signals to update their conscious motor perceptions [28–30]. A study by Fournieret and Jeannerod illustrates this point [31]. Fournieret and Jeannerod instructed human subjects to trace sagittal lines on a graphic tablet. Visual feedback of the movement was available through a mirror positioned above the tablet. In some trials, this feedback was altered so that the line traced by the subjects deviated to the right or the left by a variable amount (from 2 to 10 deg). To perform a straight movement, the subjects had thus to produce a diagonal response. They were able to do so quite easily. However, they kept reporting that their movement was straight in the sagittal direction. In other words, they remained unaware of their large motor adjustments and ‘knew’ only about their original intention.

These observations are consistent with clinical reports in deafferented patients. As shown in recent studies, these patients exhibit normal motor awareness, even though they have no perceptual awareness [32–34]. They can report when they are moving and along which trajectory, but cannot detect, for instance, that their hand has been blocked at movement onset. The same type of dissociation is observed in hemiplegic patients with anosognosia. Typically, some of these patients fail to recognize or appreciate the severity of their motor deficit. Others try to ‘explain it away’ by arguing, for instance, that they are tired or not willing to move. Others finally, claim stubbornly that they are moving normally, despite their paralysis [35,36]. In a recent study, patients of this latter group were given false visual feedback of movement in their left paralyzed arm, through a prosthetic rubber hand [37]. Three conditions were tested: (i) the patients were instructed to raise their paralyzed arm, (ii) the patients were told that the

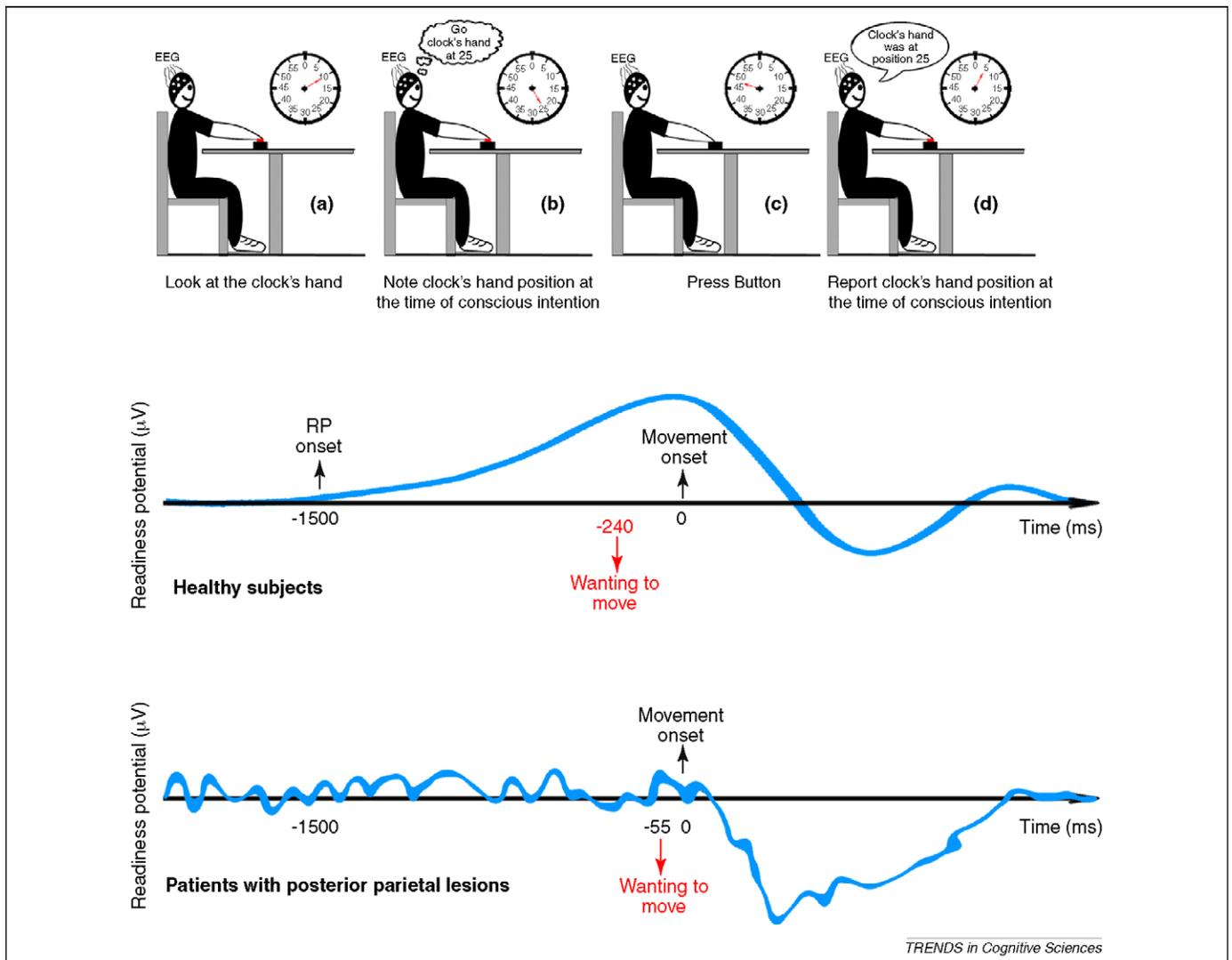


Figure 1. Top panel: Illustration of Libet's paradigm. The task is to press a button with the right index finger. (a) Participants watch a clock-hand rotating on a screen. (b) They have to identify the instant when they 'feel the intention to move'. (c) They actually press the button. (d) After a random delay, the clock stops and the subjects report the position of the clock-hand, identified in step (b). Middle panel: In healthy subjects, the Readiness Potential (an electrophysiological marker of early movement preparation) begins around 1.5 seconds before the conscious experience of wanting to move, which occurs itself around 240 milliseconds before movement onset. Bottom panel: In patients with posterior parietal damage, the Readiness Potential is absent and the conscious experience of wanting to move precedes movement onset by only a few tens of milliseconds. Data from [2].

experimenter would move their arm and (iii) no instruction. In contrast to hemiplegic patients without anosognosia, paralyzed patients with anosognosia disregarded visual information of their motionless rubber hand when they had the intention to move, compared with when they expected the experimenter to move the rubber hand, or had no movement expectation at all. These findings clearly support the idea that motor awareness derives from the processing of motor intentions. The reason why these patients cannot access a veridical awareness will be discussed in the next section.

Additional support for the idea that motor intention shapes movement awareness was recently provided by the Desmurget and colleagues' cortical stimulation study introduced in the previous section [11]. Two complementary pieces of evidence were reported. Electrical stimulations of the PMC (BA 6) evoked overt mouth and contralateral limb movements (Figure 2). However, in the absence of visual feedback, the patients firmly denied

that they had moved. This denial was not due to a low level of vigilance because patients during functional evaluations, when they were well awake, talked and moved in response to verbal commands. They also reported feelings of tingling or itching, indicating that their ability to introspect on stimulation-induced experiences was preserved. A contrasting pattern was identified for PPC when the sites initially identified as intentional (see above) were stimulated at higher intensities. In this case the subjects reported that they had actually performed the actions they had previously intended to do. However, no overt movements and electromyographic activity were present. To account for these findings it was suggested that higher intensities of stimulation did not just prime a motor representation to consciousness (giving rise to a movement conscious intention), but also recruited the executive network responsible for movement monitoring. This network is assumed to rely on forward modeling: a process that simulates the effect of the efferent output to estimate, in

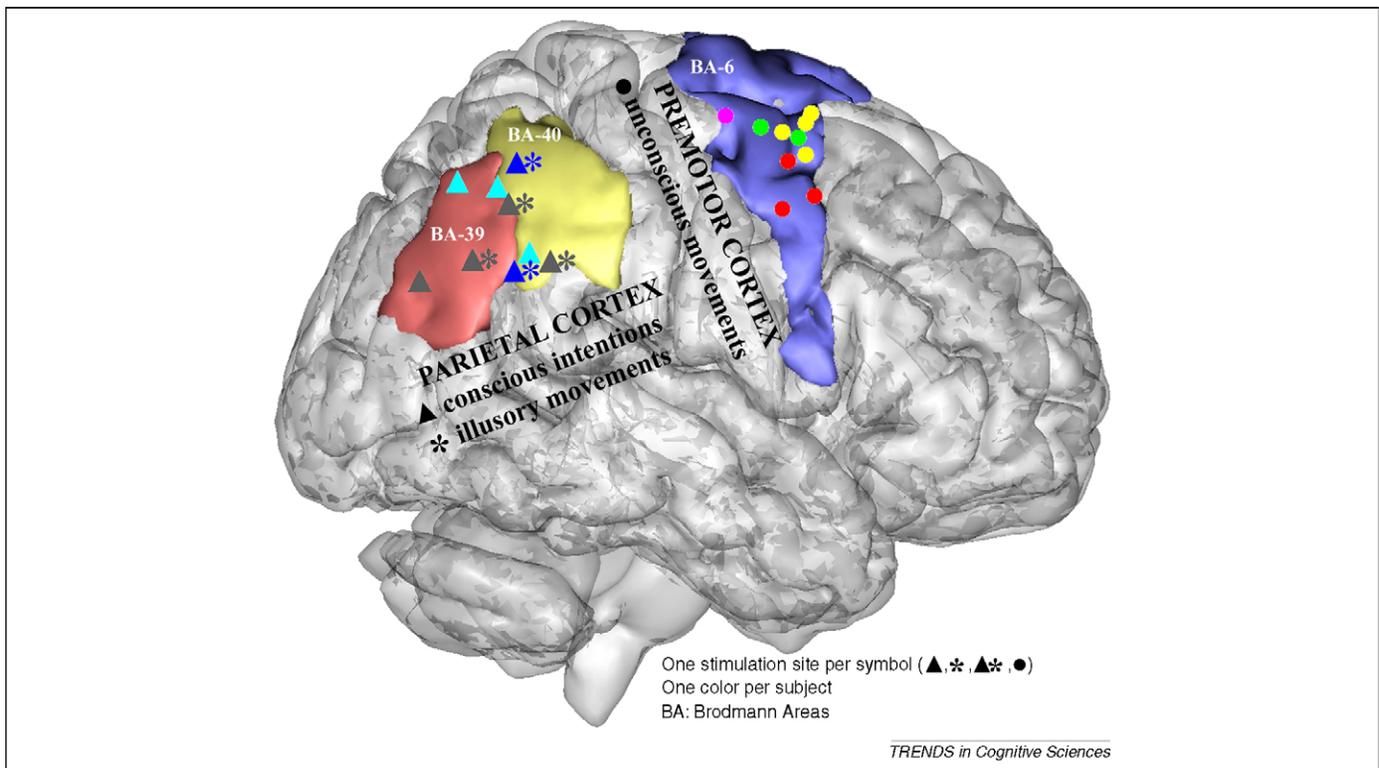


Figure 2. Premotor and parietal sites evoking conscious intentions, illusory movements and unconscious movements when stimulated with a bipolar electrode during awake brain surgery for tumor removal. Modified from [11].

real time, the state of the motor apparatus [38–40]. There is converging evidence that forward models are generated in the posterior parietal lobe [1,41–43]. It might be the case then that this structure mediates motor awareness by instructing motor regions that the movement has started, has stopped or is unfolding (Box 3).

To summarize, motor awareness does not emerge from the sensory signals generated by the movement, but from the predictions we make about the movement before action onset. These predictions are generated within the PPC, in the same regions where feelings of conscious intentions are evoked. Based on these observations, one may suggest that intentions and the prediction of what will result from carrying out these intentions create our conscious experience that we are moving. Indeed, what really matters when we initiate an action is the specific goal we have in mind. Whether this goal is reached through a straight or curved path, with a bell-shaped or asymmetrical velocity profile, on the basis of an open or closed loop response is of little importance [44–46]. Obviously, the neural mechanisms underlying consciousness have more important things to do than controlling the low-level executive details of our actions. It may even seem optimal, in terms of neural economy, to assume that a movement unfolds as planned when it reaches its goal.

Veridical motor awareness

In ecological conditions, our motor predictions are generally highly reliable. We rarely see our hand going rightward or downward when we move it leftward or upward. In the same vein, we seldom, if ever, face the surprise of seeing our arm not responding to a motor command. However, these unusual situations can occur as a result

of experimental manipulations [47–49] or brain lesions [35,36]. When this happens, the motor control system can no longer force the congruence between the desired and actual sensory reafferences, as it does continuously for errors of limited magnitudes [38–40,18]. In the presence of such large, unmanageable errors, the validity of our original predictions is challenged and we become aware of our movements as they actually unfold. For instance, subjects immediately detect strong force fields and large prismatic displacement applied to an ongoing point-to-point response. This motor awareness does not occur when the same level of perturbation is reached gradually [50,51].

Although the neural bases of veridical motor awareness remain largely unknown, recent evidence has emphasized the potential role of the PMC. In particular, Berti and colleagues [5] used magnetic resonance imaging to investigate the anatomical distribution of brain lesions in right-brain-damaged patients with anosognosia for hemiplegia (see above). Analyses identified the premotor cortex (area 6) as the most frequently damaged area related to this disturbance. To explain their result, the authors suggested that the brain mechanisms that normally compare the expected and actual peripheral reafferences are damaged in patients with anosognosia for hemiplegia, which prevents these patients from knowing that they are not moving [5,52]. Arguments favoring this hypothesis can be found in the observation that the PMC is involved in the computation of an expected sensory signal [53] and receives abundant peripheral inputs about the ongoing movement [54,55]. Additional evidence comes from a recent study in phantom pain [56]. As shown in this study, the PMC is the main area activated during the feeling of phantom pain, in agreement with the idea that this

Box 3. Forward models and motor awareness

Forward models predict the behavior of a body segment in response to a motor command. They are critical for solving fundamental problems in motor control, including sensory prediction, fast feedback corrections and state estimation [75]. During the past decade this latter process of state estimation has been suggested to mediate motor awareness [2,28,30]. The hypothesis is based on the assumption that movement-monitoring starts with the delivery of the motor command and stops at the end of the movement. This means that the brain has access to an internal signal indicating movement onset, movement end and movement accomplishment. Within this framework, motor awareness arises from the knowledge that we are moving and the assumption that we do so as initially expected. This model fits well with clinical and behavioral data showing that human subjects are good at determining the onset of their movement, poor at perceiving the actual kinematic details of their response and prone to consider that the movement was performed as planned (see main text).

Interestingly, strong evidence relates the process of state estimation to the functioning of the posterior parietal cortex [42,43,76]. On-line movement corrections that rely on forward computations are inhibited when a Transcranial Stimulation Pulse is delivered over the PPC at movement onset [77]. Following parietal damage, patients can experience feelings like losing their arm or foot [41] or they become highly inefficient at determining whether a movement is theirs or not [1].

sensation arises from a systematic mismatch occurring when a preserved efferent command is compared to an absent peripheral input [56].

Based on these data, one may wonder how PMC electrical stimulations can generate limb movements with no awareness [11]. A possible interpretation would be that the brain disregards the sensory inflow resulting from the movement because there is no expected signal with which to compare this inflow. However, such a model does not fit with the known ability of human subjects to perceive

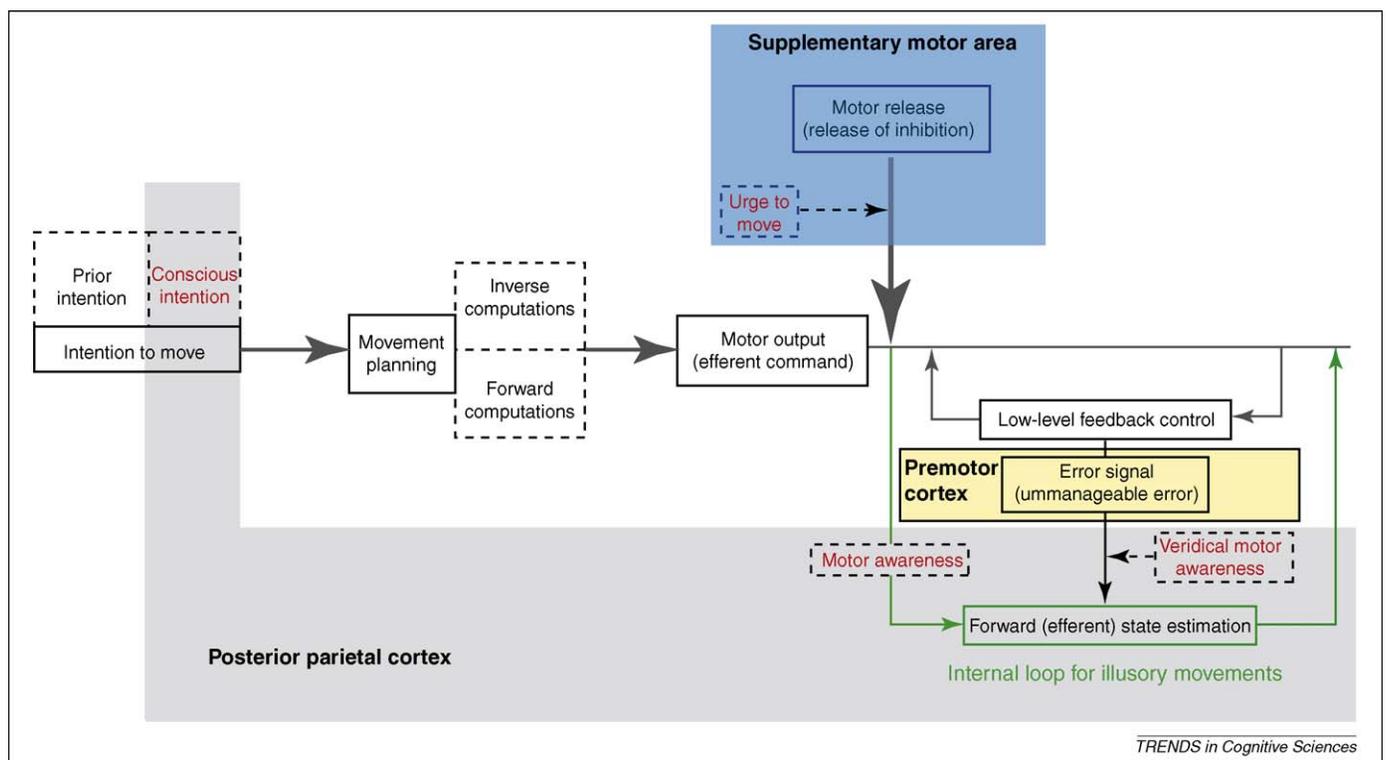
passive limb displacements [11,57] and experience movements in the context of tendon vibration [58]. One possible account for these discrepancies is that electrically-generated efferent outputs do produce corollary discharges to which sensory inflows can be compared [59]. Under normal circumstances the efferent outputs cause the limb to move as expected and no error signal is emitted. As a consequence, the PMC has no way of determining that a movement has occurred. However, in instances of peripheral stimulations, such as in the case of passive movement, an unexpected sensory inflow reaches PMC. This inflow information cannot be compared with an efferent (expected) signal since no motor command has been issued or no direct central stimulation has occurred. The discrepancy between the two sources of information may produce an error signal that, in turn, produces the conscious knowledge that the limb is moving.

To summarize, when a large mismatch exists between the expected and actual sensory signals, internal feedback loops become unable to ensure a correct match between the expected and actual sensory responses. An error is then generated; this leads the motor system to disregard the predictions made by the parietal cortex about the movement, in advance of action. As a result, conscious attention is drawn to the ongoing movement and the subject becomes aware, not of the predicted, but of the executed response.

A general model for motor intention and awareness

Based on the data above, it is possible to propose a general anatomo-functional model for motor consciousness (Figure 3).

Initially, there is an unconscious intention to act, a sort of *prior intention*, which emerges within a wide prefrontal-parietal network (Box 1). This prior intention causes an



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Figure 3. A general anatomo-functional framework for conscious intention and motor awareness.

unspecific activation of the motor system, as can be seen in the emergence of a RP within the precentral medial regions [15], around 1 or 1.5 seconds before the motor response [2,14,16]. Progressively, this RP becomes specific to the movement side. It starts lateralizing 800 milliseconds or so before muscle contraction [14]. Conscious intention (W-Judgment) comes last; it emerges around 250 milliseconds before movement onset [2,14,16]. We speculate that conscious intention arises during this period in response to an increased activity within the posterior parietal area. During the last 250 milliseconds before movement onset, the consciously selected response is planned within a parietal-motor network. When the efferent command is ready to be issued the SMA releases it by suppressing the inhibitory output exerted on M1 [24]. This release in turn triggers a conscious intentional urge to move. A few tens of milliseconds later, the movement actually starts. At this point a predictive signal is emitted within the posterior parietal cortex through forward modeling (Box 2). This signal monitors movement progression in real time and it might form the basis of our motor awareness. In parallel to this process, low-level premotor executive regions compare the actual sensory input with an expected reference. When an error occurs it is corrected automatically. Nothing reaches consciousness and the subject remains aware only of his/her intentions and the predictions of what will result from carrying out these intentions. However, when movement inaccuracy becomes unmanageable, an error signal is emitted causing the system to switch from predictive to veridical motor awareness.

Overall, this model offers a functional and anatomical framework for understanding how motor intentions and motor commands become available to consciousness. Through this framework, major abnormalities in the intentionality and awareness of action can be understood. For instance, alien hand movements have been shown to emerge following lesions of the posterior parietal (PPC) structures that bring motor intentions to consciousness [4]. Anarchic responses have been demonstrated to occur following damage to the medial frontal regions (SMA) that prevent M1 from releasing unwished motor commands [22,23]. Illusory movements have been reported after damage to the premotor cortex (PMC) [5]. This may be the effect of activations within the PPC, responsible for movement intention and monitoring, working in isolation and disconnected from premotor regions [11]; the latter being important for comparing actual and expected reafferent motor signals [5,53]. Of course further research is needed to confirm the validity and generality of this anatomo-functional model in healthy subjects and brain-damaged patients. Furthermore, it will be important to design adapted behavioral paradigms for studying these questions in non-human primates. It is probable that monkeys (and maybe other animals) experience some level of 'motor awareness' (they 'know' that they are moving). According to Searle [60]:

it is obvious that many of the important evolutionary functions of consciousness are intentional: For example, an animal has conscious feelings of hunger and thirst, engages in conscious perceptual discrimi-

Box 4. Outstanding questions

- Where in the brain does the subjective feeling that 'I want to move' emerge?
- Where in the brain is the conscious knowledge that 'I am moving' formed?
- How do we become aware of our intentions to move?
- What exactly are we aware of when making a movement and what sources of information does the motor system need to generate intention and consciousness of a movement?
- What is the evolutionary basis of conscious intentionality?

nations, embarks on conscious intentional actions, and consciously recognizes both friend and foe. All of these are conscious intentional phenomena and all are essential for biological survival.

These issues will need to be investigated if we want to fully understand the evolutionary origin and neural basis of consciousness.

Concluding remarks

We have presented evidence that the subjective feelings of conscious intention and movement awareness are mediated by a motor network involving the PPC, SMA and PMC. Based on a wide range of studies, we showed that we need intentions in order to be aware of what we are doing or, alternatively, that our intentions are what we are aware of. With respect to this point, an important message of the present article is that our conscious motor perceptions are built within the cortical areas that are responsible for movement planning and control. This suggests that motor awareness and conscious intention emerge as a result of neural computations carried out within the motor network in advance of action. Consciousness of our movements is therefore not an abstract mental process but a phenomenon deeply rooted in the neural system. Further research is necessary to assess how the brain regions, within the neural network described here, combine the different sources of information in time to allow conscious behavior to emerge. Illusion of movement without movement or real movement but without awareness illustrates that when specific cortical areas within this network are disconnected (because of lesion or artificial stimulation) the motor system holds wrong beliefs about its actual status. Verbal reports in human patients although introspective may prove a fruitful method to study the respective contribution as well as the limits of the different cortical nodes instrumental for such complex behavior that is intention and consciousness during the course of action (see Box 4 for a list of outstanding questions).

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