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# The missing link between action and cognition

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### Abstract

The study of the neural correlates of motor behaviour at the systems level has received increasing consideration in recent years. One emerging observation from this research is that neural regions typically associated with cognitive operations may also be recruited during the performance of motor tasks. This apparent convergence between action and cognition – domains that have most often been studied in isolation – becomes especially apparent when examining new complex motor skills such as those involving sequencing or coordination, and when taking into account external (environment-related) factors such as feedback availability and internal (performer-related) factors such as pathology. Neurally, overlap between action and cognition is prominent in frontal lobe areas linked to response selection and monitoring. Complex motor tasks are particularly suited to reveal the crucial link between action and cognition and the generic brain areas at the interface between these domains. © 2007 Elsevier Ltd. All rights reserved.

Keywords: Motor control; Skill complexity; Motor learning; Attention to action; Neural plasticity

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*Abbreviations:* SMC, primary sensorimotor cortex; M1, primary motor cortex; SMA, supplementary motor area; pre-SMA, pre-supplementary motor area; PMC, premotor cortex; PMCd, dorsal premotor cortex; PMCv, ventral premotor cortex; pre-PMCd, rostral part of the dorsal premotor cortex; PC, parietal cortex; PFC, prefrontal cortex; ACC, anterior cingulate cortex; RCZ, rostral cingulate zone; RCZp, posterior division of the rostral cingulate zone; RCZa, anterior division of the rostral cingulate zone; CMA, cingulate motor area; IPS, intra-parietal sulcus; PD, Parkinson's disease; EEG, electroencephalography; MEG, magnetoencephalography; fMRI, functional magnetic resonance imaging

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### 1. Introduction

Skilled movement is an essential part of our daily life activities and covers a wide range in terms of intricacy. Furthermore, skill complexity can be characterized by two complementary components. Whereas objective complexity refers to the motor task structure and requirements, subjective complexity encompasses how the action plan is shaped by cognitive and emotional processes that drive the performer towards achievement of a particular goal (Fig. 1). We argue that these aspects of subjective complexity draw on brain structures that are not typically associated with motor control such as prefrontal areas. However, with the recent evolution towards the study of complex motor tasks and the manipulation of various factors, these brain structures have come to be seen as an integral part of a network involved in the organization of skilled movement. Identifying these brain regions and their associated functions is of importance for an enhanced understanding of human behaviour.

# 2. Motor skill complexity

Some motor tasks are performed with ease whereas others are complex, requiring considerable effort. Hence, which facets determine whether a motor action is experienced as complex or not? Picard and Strick (1996) specified that motor complexity co-varies with the pattern of brain activation, and thus the degree of information processing. Accordingly, it can be assumed that neural functioning will be affected by restrictions on information processing. One example refers to the postponed selection of a response when two stimuli occur in rapid succession. This delay known as the psychological refractory period suggests that response selection constitutes a critical processing constraint (Pashler, 1994) or a limitation on cognitive resources that relies on a supervisory system (Logan and Gordon, 2001; Schumacher et al., 2001).

While complexity is an often used concept, it is difficult to operationalize it in an experimental context. Some researchers have drawn on definitions developed in mathematics, information theory and physics such as entropy and randomness. Accordingly tools have been developed to quantify complexity, resulting in explicit measurements such as the Kolmogorov index that describes the length of an algorithm for generating a given number sequence (Tononi et al., 1998). Generally the dictionary defines complexity as "an entity that is composed of a number of interconnected parts". More complex implies more distinct components and/or more connections between them. Hence, the duality of component (sequential elements) and connection (coordinative elements) determines two key dimensions that underlie complex behaviour. In terms of movement regulation, complexity reflects a crucial concept as motor tasks with high degrees of intricacy are commonly performed. Indeed many aspects of our motor behaviour are embedded in a sequential or coordinative framework. In this respect, sequential complexity entails movement responses that vary along a spatial (ordinal) and/or temporal component, e.g., the number of responses



Fig. 1. Motor skill complexity. Whereas the motor dimension represents objective complexity, the cognitive and emotional dimensions refer to how complexity is experienced subjectively. The latter is influenced by external (environment-related) and internal (performer-related) factors, causing the subjective experience associated with the motor task to be variable and dynamic in contrast to the objective experience that is relatively fixed.

required, and the timing and order in which they occur. Harrington et al. (2000) have suggested that sequence complexity can be characterized by surface properties (such as the types of effectors and the number of movements) and a sequence-specific structure (such as the relations amongst the movements). Conversely, coordinative complexity involves the simultaneous performance of different effectors, giving rise to particular combinations of spatial and temporal association. Coordinative complexity has also been viewed in terms of deviations from basic coordination constraints that involve the egocentric principle (moving the limbs according to mirror symmetry) or the allocentric principle (moving the limbs in the same direction in extrinsic space) (Swinnen, 2002). Sequential or coordinative assignments can become very specialized and sophisticated as in sports, musical performances and work environments. Accordingly complex tasks typically entail a hierarchical organization, capturing the notion that their control does not involve decomposition into individual components or simple motor acts (Cordo and Gurfinkel, 2004).

In this paper, we propose that taking into account sequential and coordinative dimensions is valuable for understanding the neural processes that are recruited during complex motor tasks. We first elaborate on the neural networks that underlie sequential and coordinative complexity, followed by evidence of the changes in these circuits induced by external (environmental-related) and internal (performer-related) factors. We will demonstrate that these aspects play a significant role in determining the pattern of neural activity, exposing in large part the degree of cognitive control; the ability of the brain to organize processing in relation to goals (Miller and Cohen, 2001). Next, we discuss the allocation of cognitive resources, with a particular emphasis on attention, and discuss the prime frontal lobe areas that are implicated. In exploring these issues, we draw on observations from healthy controls as well as from neurologically impaired populations. We focus here in particular on motor control that entails limb movements rather than skills such as speech or handwriting that are closely associated with cognitive elements.

# **3.** Patterns of brain activation due to sequential and coordinative complexity

Two major and complementary approaches are generally adopted in explicating patterns of brain activity in neuroimaging studies: the study of regional activity and that of interregional interactions within networks. Whereas the examination of regional specialization is useful for understanding the organization of skilled actions, the multifaceted functions that underlie the planning and production of motor behaviour also require consideration of interregional connectivity (Serrien et al., 2006). So, task-related processes can be mediated not only by modulations in network activity, but also by differences in interregional couplings (Sun et al., 2004). Connectivity profiles can be inferred from fMRI as well as EEG/MEG methodologies, even though it is the latter that has received most consideration so far, depicted by spectral analysis techniques. In this respect, a valuable measurement of neural coupling is coherence that reflects interregional correlation of oscillatory activities across different frequency bands. To elaborate on the concept of skill complexity, data from both approaches will be incorporated next.

Skills that include sequential or coordinative complexity commonly require practice over an extended period of time. Hence, the acquisition process plays a crucial role in defining and redefining the experienced complexity as the learner progresses from an unskilled towards a skilled performance. Accordingly, the neural dynamics associated with the motor behaviour evolves in parallel with the degree of automatization. Besides the influence of the learning process, we will argue that external (environment-related) and internal (performer-related) factors are also important in tuning the subjective complexity of motor tasks and in shaping the neural activation patterns.

# 3.1. Learning

It is reasonable to assume that the computational demands, and thus the recruited neural resources vary with the complexity of the task, which is exemplified by increased functional connectivity patterns (Serrien and Brown, 2002; Rissman et al., 2004). As movements become more complex, the neuroimaging data point to: (1) increased activity in regions including those activated during simple movements, likely indicating intensified processing demands, (2) a shift from contralateral to bilateral activation, possibly due to the recruitment of specialized operations in each hemisphere or augmented control processes, and (3) increased involvement of prefrontal areas, presumably depicting cognitive processing in view of the goal requirements (Serrien et al., 2006).

As a function of training, the effect of sequential and coordinative complexity adjusts, resulting in corresponding changes in neural recruitment (e.g., Grafton et al., 2002; Doyon et al., 2003; Debaere et al., 2004; Puttemans et al., 2005). These include: (1) decreased activity because of improved neural efficiency or reduced functional requirements, generally observed in (but not restricted to) prefrontal areas (e.g., Jenkins et al., 1994; Passingham, 1996; Poldrack et al., 2005), (2)

increased activity due to expansion of cortical representations and/or intensified neural activity, as has been reported in primary and secondary motor areas as well as in subcortical regions (Grafton et al., 2002; Debaere et al., 2004; Floyer-Lea and Matthews, 2005; Puttemans et al., 2005), and (3) combined decreased and increased activity across regions as a result of neural redistribution (Hikosaka et al., 1999; Poldrack, 2000; Doyon et al., 2003; Kelly and Garavan, 2005). These changes occur dynamically over various time scales including the shortterm (minutes to hours), medium-term (days to weeks), and longterm (months to years). Practice-driven changes are also evident in the functional connectivity patterns that emerge and that become optimized during complex skill learning (Andres et al., 1999; Serrien and Brown, 2003; Sun et al., 2007). Here, a neural reorganization involves increases in some functional connections and weakening of others.

Because of these neural modulations, a reallocation of processing requirements takes place with learning. Most prominent is a transfer from a cognitive-demanding mode to one in which this need is reduced (Doyon et al., 2003; Meister et al., 2005; Puttemans et al., 2005). This process corresponds to a shift from controlled towards automatic functioning, and can be experimentally illustrated by the emergence of minimal interference during dual-task conditions in the latter as compared to the former performance mode (Passingham, 1996). After a skill has been mastered, cognitive resources may, however, be called upon again by task demands or instructions such as reattending to motor performance (Jueptner et al., 1997). In the literature various frameworks have been proposed that exemplify the difference in controlled vs. automatic processing demands, building on ideas such as working memory (Baddeley, 1992), a supervisory control system (Shallice, 1982; Posner and Petersen, 1990; Stuss, 2006), specialized processors that operate within a hierarchical system (Dehaene et al., 1998) or executive networks (cognits) that integrate information within and between distributed circuits (Fuster, 2006). A core feature of these models is that higher-order processing coordinates the flow of information across brain regions during multifaceted behaviour.

When performing well-learned or familiar motor configurations that involve sequential or coordinative complexity, the neural network commonly includes primary sensorimotor cortex (SMC), supplementary motor area (SMA), premotor cortex (PMC), parietal cortex (PC), basal ganglia and cerebellum (e.g., Sadato et al., 1997; Catalan et al., 1998; Fink et al., 1999; Tracy et al., 1999; Jäncke et al., 2000; Haslinger et al., 2002; Debaere et al., 2003; Haaland et al., 2004; Swinnen and Wenderoth, 2004; Verstynen et al., 2005). However, when the tasks comprise new or unfamiliar motor behaviour, the neural activation is tailored to the challenging requirements (Keele et al., 2003). For example difficult sequences that specify a temporal as well as ordinal component are associated with activation in pre-supplementary motor area (pre-SMA), the rostral part of the dorsal premotor cortex (pre-PMCd) and dorsolateral prefrontal cortex (dorsolateral PFC) (Sakai et al., 2002; Meister et al., 2005; Fig. 2A). For bimanual coordination tasks in which the two hands adopt complicated temporal and/or spatial task requirements, neural activation is (A) Complexity of sequencing



(B) Complexity of temporal coordination



Fig. 2. (A) Comparison of complex vs. simple sequences. The simple task consisted of key pressing in a fixed order whereas in the complex task subjects had to omit finger positions and start each sequence with a different key. The brain regions that showed increased activation were pre-SMA and pre-PMCd. It is noteworthy that the contrast of complexity did not show a differential activation in musicians. Figure reproduced from Meister et al. (2005) with permission from Wiley. (B) Comparison of polyrhythmic vs. isochronous performance. There were two polyrhythmic (3:2 and 2:3) and two synchronous (in-phase, anti-phase) tasks. The brain region that differentiated primarily the polyrhythmic from the isochronous sequence was pre-SMA. Figure used and adapted from Ullen et al. (2003) with permission from the American Physiological Society.

concentrated in frontal and parietal areas with a particular emphasis on pre-SMA (Ullen et al., 2003; Fig. 2B), the rostral cingulate zone (RCZ) of the anterior cingulate cortex (ACC) and precuneus (Wenderoth et al., 2005; Diedrichsen et al., 2006). Difficulties experienced in producing these complex patterns are usually manifested as tendencies towards temporal and spatial synchronization. In particular, people find it extremely taxing to move their limbs simultaneously at different frequencies (Serrien and Swinnen, 1997) or to generate concurrently distinct geometric forms with each limb (Franz et al., 1991; Wenderoth et al., 2005). These biases can, however, be overcome by integrating the responses into a unified organization, owing to conceptualization and/or training (Franz et al., 2001; Summers, 2002; Ivry et al., 2004; Swinnen and Wenderoth, 2004).

Motor skills are acquired during training but learning extends beyond the time period during which the performer

practices the task with consolidation evolving off-line between/following practice sessions (Robertson et al., 2004; Walker et al., 2005; Hotermans et al., 2006). During consolidation a motor memory may be stabilized during which it becomes resistant to interference, or, enhanced during which it associates with a higher level of performance (Robertson et al., 2004). Off-line improvements may result in goal- and movement-based changes, which develop over sleep and wake, respectively. This particular dissociation implies that consolidation is not a single process and that different facets of a memory will follow distinct rules (Cohen et al., 2005). In terms of skilled actions, evidence has indicated that off-line improvements depend on skill complexity and the computational requirements associated with learning (Spencer et al., 2006). For example, Kuriyama et al. (2004) observed marked overnight improvement for bimanual sequences involving the highest degree of complexity.

# 3.2. External factors

External factors arise from information provided by the environment or context within which a movement is produced. These elements affect the task settings and bias the cognitive demands or the adopted strategy towards realization of the motor goal. Within the study of motor control, one common manipulation has been to vary the mode of triggering that defines the required action. Moreover, the signal can be generated internally by the performer, or cued externally by a stimulus. Overall the functional connectivity diverges for both types of tasks, suggesting differences in processing demands (Gerloff et al., 1998). In particular, the greater degree of preparation during internally than externally generated movements becomes evident in pre-SMA and RCZ (Deiber et al., 1996; Ball et al., 1999; Cunnington et al., 2002) in addition to dorsolateral PFC and superior PC (Weeks et al., 2001). However, the preparatory demands of externally cued responses may also be subject to additional processing due to the particular task constraints. For example, it has been shown that synchronization on the metronome beat is easier to perform than syncopation when the movements must be produced off the beat (Mayville et al., 2001). This greater effort on central processing is reflected by activation in pre-SMA, lateral PMC and cerebellum (Jantzen et al., 2007). Furthermore, an increased activation of dorsolateral PFC and ACC can be observed when synchronization to the beat involves irregular as compared to regular rhythmic responses (Stephan et al., 2002). The impact of external cueing on processing requirements becomes further evident during conflict that arises during goal assignment. This is the case when bimanual movements are cued by means of symbolic (indirect) rather than spatial targets (direct), which induces activation of pre-SMA and RCZ during spatially asymmetrical movements (Diedrichsen et al., 2006).

Also feedback availability has a pronounced influence on the processing needs and becomes most evident when a discrepancy exists between the motor intention and the sensory consequences. For example, during early visuomotor or rotation adaptation, activation in (dorso-) lateral PFC and pre-SMA occurs that likely underlines a cognitive shift associated with the adjustment process (Krakauer et al., 2004; Della-Maggiore and McIntosh, 2005). Along a similar line when nonveridical visual feedback is provided during movement performance, dorsolateral PFC and superior posterior PC become strongly activated, with the former area being most crucial when spatial demands are emphasized (Fink et al., 1999). These observations suggest that a lack of congruence between intent and sensory outcome engages considerable cognitive resources beyond that simply required to correct the movement. Together these examples illustrate that distinct cognitive guidance is required when irregular, erroneous, or ambiguous signals are introduced during movement organization. Seemingly, this intervention helps to ensure the successful realization of the action goal.

#### 3.3. Internal factors

Internal factors refer to performer-related conditions that evolve from functional and/or structural changes in the neural architecture. These elements may be transient due to conceptualization, attentional or performance strategies (Fink et al., 2002; Rowe et al., 2002; Swinnen and Wenderoth, 2004), changes in arousal (Lorist et al., 2005) or performance-induced stimulants (Mattay et al., 2000). Alternatively, these factors may be more chronic and vary between positive and negative consequences such as long-term practice (high-level expertise) on the one hand, aging and neuropathology on the other hand.

Long-term practice can lead to an advanced degree of motor skilfulness as evident in the performance of musicians. Highlevel expertise correlates with improved neural efficiency and reorganization in various cortical and subcortical structures including SMC, premotor areas and cerebellum (Jäncke et al., 2000; Münte et al., 2002; Haslinger et al., 2004; Meister et al., 2005). These changes appear not only to depend on instrumental practice per se but also on the age at which training is initiated. In particular, musicians who start practicing before the age of seven show superior performance on complex motor tasks, even when groups are matched for years of experience. This observation supports the idea of a sensitive window in childhood for motor training (Penhune et al., 2005), and is likely due to structurally induced changes such as those noted in the corpus callosum (Schlaug et al., 1995).

As a result of aging and neuropathology (see below), two types of changes in neural activation pattern have been described: (1) reduced activity that is generally interpreted as resulting from neural dysfunction, and (2) increased activity due to inefficient functioning or compensatory operations related to intensified sensorimotor processing and/or augmented mental effort (Grafton, 2004; Reuter-Lorenz and Lustig, 2005). These neural modulations may differ for local and distributed networks, resulting in combined effects of dysfunction and compensation in view of performance (Rowe et al., 2006). This is supported from data that show decreased as well as increased interregional connectivity due to abnormalities in neural communication (Strens et al., 2004; Silberstein et al., 2005; Schnitzler et al., 2006; Uhlhaas and Singer, 2006). However, long-term adaptations due to expertise may offset any changes in the control processes that underlie behavioural performance (Krampe, 2002).

To understand age-related changes in neural activity, complex motor tasks can be particularly revealing. For example, during the production of sequential movements, neural activation is generally greater in elderly than younger



Fig. 3. (A) Age-related effects: overall neural changes. Brain areas that were more activated in elderly than in young subjects during well-practiced finger sequencing that included 12 movements within each unit of the sequence. Figure reproduced from Wu and Hallett (2005a) with permission from Blackwell Publishing. (B) Age-related effects: specific neural changes. Larger neural activation in elderly compared to young subjects during hand-foot coordination with two complexity modes (non-isodirectional, isodirectional). A pronounced effect was observed in brain areas such as pre-SMA, PMCd, RCZ, posterior PC and dorsolateral PFC. Figure used and adapted from Heuninckx et al. (2005) with permission from the Society for Neuroscience.

participants, with pre-SMA only activated in the former group (Wu and Hallett, 2005a; Fig. 3A). Along a similar line additional neural activation with age during coordination tasks is noted in areas such as pre-SMA, pre-PMCd, RCZ and PFC (Heuninckx et al., 2005; Fig. 3B). These observations indicate an increased involvement of brain regions that are strongly associated with cognitive functions. Furthermore, the expanded pattern of neural activity due to aging may parallel that observed in children (Casey et al., 2005; Durston et al., 2006), suggesting extra effortful processing (Crone et al., 2006). For example, when asked to continue producing a rhythmic pattern after a metronome was switched off, children recruited a common neural network as observed in adult participants in addition to pre-SMA and cerebellum (Rivkin et al., 2003). So, the children appeared to require increased cognitive control to support the internally generated responses.

Many forms of neuropathology produce impairments of motor control and these problems are usually amplified in conditions that require complex actions (Catalan et al., 1999). Disturbances of skilled movement are pronounced following damage to prefrontal (Luria, 1973), premotor (Freund and Hummelsheim, 1985) and parietal areas (De Renzi et al., 1983; Serrien et al., 2001) as well as to subcortical regions such as the cerebellum (Inhoff et al., 1989; Serrien and Wiesendanger, 2000; Diedrichsen et al., 2005), and basal ganglia (Harrington and Haaland, 1991; Agostino et al., 1992). Compensatory activation associated with neuropathology usually follows one of two paths: (1) increased activation in regions that support motor- and/or sensory-guided control such as premotor and parietal areas as well as cerebellum (Bartenstein et al., 1997; Rascol et al., 1997; Samuel et al., 1997), or (2) intensified activation in frontal lobe areas that reflect augmented cognitive operations (Wu and Hallett, 2005b). With some degenerative disorders, the changes can already be observed in presymptomatic states (Ghilardi et al., 2003; Feigin et al., 2006). To some extent these alterations in neural activity may be similar to those noticed in healthy controls when learning difficult tasks, implicating greater regional activation volumes and/or recruitment of additional brain areas (Mentis et al., 2003). This suggests that well-defined mechanisms respond to motor intricacy in order to support successful performance. Interestingly, changes in higher-order cognitive functions appear to predict deficits in complex motor behaviour better than simple motor performance in patients with Parkinson's disease (PD) (Fama and Sullivan, 2002). This signifies that the more complex a motor task, the more susceptible it is to the influence of cognitive abilities; a premise supported by observations from PD patients who experience difficulties in producing complex motor as well as cognitive tasks (Brown and Marsden, 1991). Also frontostriatal networks may be particularly important for cognitive functions required in the control of complex actions (Chudasama and Robbins, 2006) and as such contribute to developmental and individual differences in the recruitment of cognitive control (Liston et al., 2006).

Compensatory activity to support motor function is also observed following focal brain damage, as for example due to stroke. The form of this potentially widespread activation varies with numerous factors e.g., the extent and site of the lesion, the time span since the injury, the functional specialization of the damaged area(s), the viability of alternative processing pathways, the use of rehabilitation procedures, etc. However, data suggest that interhemispheric inhibitory interactions that are important for voluntary movement generation may be modified following neural damage (Murase et al., 2004) and accordingly influence functional recovery. In view of the level of cortical organization, the effect of disruption to higher-order processing is less obvious. In particular, a small lesion in primary motor cortex (M1) can have severe consequences for motor behaviour whereas a much larger lesion in PFC may be required to disrupt the representation and execution of plans (Fuster, 2006).

The research reviewed in this section emphasizes that neural activation patterns associated with complex motor behaviour are not fixed but undergo plastic adaptations. These may manifest themselves in sensorimotor or cognitive regions, include quantitative or topographical changes, reflect a fine-tuning or more permanent modification, and occur over varying time scales. Indeed, neural plasticity can be viewed as a fundamental process by which the most appropriate signals are generated according to the existing constraints, supporting the premise that the human brain exhibits significant re-organizational properties throughout life (Rossini et al., 2003).

# 4. Neural plasticity: neural reserve vs. neural compensation

The acquisition of complex motor skills, the adjustment to taxing environmental circumstances and the functional adaptation/recovery from neural damage all provide examples of neural plasticity at the systems level. A commonality across these situations is that effortful processing is considerable. In this respect two complementary concepts have been proposed; neural reserve and neural compensation (Stern et al., 2005). Neural reserve encompasses the ability to optimize performance in the healthy brain and reflects individual differences as well as modulations that occur due to task difficulty. As such it represents changes in neural recruitment due to efficiency or capacity. Conversely neural compensation during the performance of a particular task refers to the effort to maintain or improve performance in the aging or pathological brain and generally implicates brain structures that are not engaged in healthy, young individuals. Here, alterations in neural recruitment take place in order to overcome limitations due to functional and/or structural deficiencies. In the case of aging/ pathology, the effect of neural compensation likely superimposes on that of neural reserve when performing complex motor actions and accordingly accounts for the fact that elderly/ patients experience increasing problems as a function of task intricacy.

The analogous effect of neural reserve and neural compensation in the context of motor behaviour highlights a similarity in the response of the brain to increased skill complexity on the one hand and to adaptation due to aging or pathology on the other hand. In particular, it appears that in both conditions specific frontal lobe areas are recruited to join a core network. The involvement of these brain regions that are typically associated with higher-order cognitive functioning suggests a crucial link between levels of control for facilitating motor organization.

# 5. Dynamic modulation of skill complexity

#### 5.1. The impact of cognitive control

Tasks that involve minimal motor demands can prove useful in understanding how higher-order cognitive processes may be engaged during complex actions. This approach helps to illustrate the extent to which complicated behaviour, whether cognitive or motor, requires the involvement of similar generic functions. Consider two conditions that have been used to explore cognitive control: task switching and multi-tasking. Both cases necessitate rapid updating, evaluation and reconfiguration of task goals. That limitations exist in our ability to perform such operations is evidenced by substantial increases in response times when a switch in task-set occurs (Rogers and Monsell, 1995), or by cross-talk when two tasks are performed simultaneously (Pashler et al., 2001).

Functional imaging studies of task-switching or multitasking reveal a prefronto-parietal network (e.g., Schubert and Szameitat, 2003; Wylie et al., 2004; Brass et al., 2005), similar to what is observed for the production of complex motor tasks, at least during early stages of learning. A direct comparison of these conditions has shown that while certain higher-order areas such as pre-SMA are commonly activated, multi-tasking is strongly associated with activation in rostral ACC, whereas task switching correlates with activation in lateral PFC and intra-parietal sulcus (IPS) (Dreher and Grafman, 2003). This observation is consistent with a two-component system of cognitive regulation (Carter et al., 1998; Turken and Swick, 1999; Gehring and Knight, 2000; MacDonald et al., 2000) during which interactions between prefrontal and association areas lead to operations of response selection and monitoring. The output of the latter process can be used to increase topdown control, which becomes especially crucial during suboptimal performance (Botvinick et al., 2001; Garavan et al., 2002; Ridderinkhof et al., 2004). In terms of cognitive efficiency, poor performers tend to rely more on prefrontal circuits and directed interregional influences (Gevins and Smith, 2000; Rypma et al., 2006), suggesting an association between effective prefrontal organization and quality of performance. As such, interindividual differences between effortful and automatic processing (Hasher and Zacks, 1979) may be similar to intraindividual changes that occur with practice. The latter also hints at increased cognitive processing for those who experience the task as demanding, e.g., poor performing young or elderly subjects (Smith et al., 2001). Sometimes this neural intensification may already be present, even when it is not intrinsic to the task conditions (DiGirolamo et al., 2001). Efficiency is also affected when there is impaired functioning of frontal lobe or associated areas due to neuropathology. For example, in attention deficit hyperactivity disorder, a reduced ability to recruit task-related regions and to initiate new cognitive strategies gives way to increased effortful processing (Fassbender and Schweitzer, 2006).

As outlined earlier, the involvement of dorsolateral PFC along with pre-SMA and ACC is crucial for complex motor behaviour. The functional specialization of the dorsolateral PFC (Petrides, 2005), along with the functional heterogeneity of the pre-SMA and ACC (Rushworth et al., 2004; Nachev et al., 2005) allows higher-order cognitive processing in view of the goal specifications, encompassing selection and monitoring of the motor response. In particular dorsolateral PFC, caudal pre-SMA, and the posterior division of the rostral cingulate zone (RCZp) have all been linked with selection of the correct response representation (Rowe et al., 2000; Miller and Cohen, 2001: Picard and Strick, 2001: Schumacher and D'Esposito, 2002; Bunge, 2004; Nachev et al., 2005) whereas rostral pre-SMA and the anterior division of the rostral cingulate zone (RCZa) have been related to response monitoring and resolving of conflict (Picard and Strick, 2001; Nachev et al., 2005). Together these observations indicate a crucial role of prime frontal lobe areas in the decision making and guidance of complex actions, even though brain areas such as pre-PMCd and precuneus will also become involved depending on the task demands (Picard and Strick, 2001; Cavanna and Trimble, 2006).

The aforementioned suggests that cognitive processes that underlie complex behaviour involve relatively dissociable regions along the lateral and medial frontal axis. Thus, the neural mechanisms associated with cognitive control emerge in a similar way across domains, with recruitment of a broader network as the demand for such regulation increases (Shiffrin and Schneider, 1984; Posner and Petersen, 1990; Shallice and Burgess, 1996). It underscores common organizational principles for cognition and action. In agreement with this hypothesis, disorganization of behaviour across domains is a frequent outcome following frontal lobe damage (Duncan, 1986). In particular, these patients have difficulties in performing compound tasks, with their activities being characterized by basic forms or stereotypes, regardless of context (Luria, 1973). In this respect the problem to synthesize elements might be due to malfunctioning supervisory mechanisms (Shallice and Burgess, 1991) or impaired representational knowledge concerning task execution (Wood and Grafman, 2003). Further research is required to increase our knowledge about the sophistication of circuitry that operates across domains. Exposing commonalities and regularities are vital as they illustrate general principles of organization that enable coherent and adaptive behaviour.

#### 5.2. Attention and its relevance to action

The participation of specific frontal lobe areas in complex motor behaviour is likely directed through attention to action, or its associates such as intention or awareness (Jueptner et al., 1997; Dehaene et al., 1998; Rowe et al., 2002; Lau et al., 2004). In particular to activate rule-based representations, prefrontal regions help instantiate cognitive control via attentional mechanisms that interact with other networks (Posner and Petersen, 1990) or that are directly linked to the engaged sensorimotor regions (Rizzolatti et al., 1994; Eimer et al., 2006). As such selective attention guides processing priorities (Miller, 1999) which in the context of motor control serves to focus activity in brain areas that represent and regulate movement tasks. That attention to action truly impacts on performance (Rushworth et al., 2001; Rowe et al., 2002), becomes evident from mistakes or transient lapses when the person is distracted from the task (Passingham, 1996; West and Alain, 2000). This is in line with data that implicate lateral and medial frontal lobe areas for optimally steering top-down processing in favour of a particular action (Cunnington et al., 2006). Besides its prominent role in response selection, attention also exhibits a guiding role for maintaining the level of performance. In particular, an increase in attention is prompted by the desired outcome and arises in response to unfavourable events such as performance declines or errors (Sarter et al., 2006). This might occur when the movement parameters of the task diverge from the individual's preferred ones. For example, medial frontal areas such as pre-SMA and RCZ show increased activation when a motor task is performed at a tempo that deviates strongly from the preferred one (Kawashima et al., 1999) relative to processing in primary and secondary motor areas when movement rate or force is increased modestly (Dettmers et al., 1995; Sadato et al., 1996; Jenkins et al., 1997; Wexler et al., 1997; Turner et al., 1998; Debaere et al., 2004).

The previous indicates that the degree of attentional resources devoted to a task, conceptualized as the level of cognitive effort (Kahneman, 1973) has widespread implications for facilitating response selection and monitoring towards goal achievement. Failures to direct attention to the task demands may result in goal-neglect; the inability to transpose the requirements into a goal or to maintain it (Duncan et al., 1996). Such failures can be observed in aging and pathological conditions (Duncan et al., 1996; De Jong, 2001) but also in healthy young adults, especially under taxing circumstances (van der Linden et al., 2003). Also noteworthy is that attentional and emotional processes interact (Liotti and Mayberg, 2001; Pochon et al., 2002); a dynamic coupling that permits motivation to influence performance by shaping the direction and/or degree of attention (Kanfer et al., 1994; Sarter et al., 2006).

# 6. Network formation

#### 6.1. Anatomical considerations

Data from human and animal studies have been used to reveal principles of functional organization in the frontal lobe. This work has provided evidence that the basic architecture is quite similar across primate species (Geyer and Zilles, 2005; Petrides, 2005). Accordingly, a comparative approach seems legitimate to highlight organizational designs. One such fundamental principle is a hierarchical arrangement that follows a rostral-caudal axis along the frontal lobe, and which implicates a digression of regions that process abstract towards concrete aspects of movement. In particular, prefrontal signals are relayed to M1 via multiple motor areas (Picard and Strick, 1996, 2001; Rizzolatti and Luppino, 2001). Based on their connectivity profiles, these areas can be divided into anteriorand posterior-located motor structures. The anterior-located regions such as pre-SMA and pre-PMCd connect significantly with PFC (Luppino et al., 1993; Lu et al., 1994) and as such are apt to participate in higher-order cognitive processing, but they do not control movement directly (Picard and Strick, 1996, 2001; Luppino and Rizzolatti, 2000). Conversely posteriorlocated regions such as SMA, dorsal PMC (PMCd), and ventral PMC (PMCv) receive their main cortical input from the parietal lobe, and are strongly involved in sensorimotor processing related to movement generation. These motor areas form series of specialized circuits (Rizzolatti et al., 1998) and are under the control of prefrontal dependent pathways (Rizzolatti and Luppino, 2001; Dum and Strick, 2005).

Due to their involvement in cognitive control it is also relevant to consider the connectivity patterns of the cingulate motor areas (CMA). These regions have been classified into rostral (CMAr), ventral (CMAv) and dorsal (CMAd), with human homologues labelled as RCZa, RCZp and caudal cingulate zone (CCZ) (Picard and Strick, 1996, 2001). Although these regions project directly to M1 and spinal cord, CMAr has projections with dorsolateral PFC and pre-SMA (Luppino et al., 1993; Wang et al., 2001; Hatanaka et al., 2003), whereas CMAv (but not CMAd) interconnects with PFC (Lu et al., 1994; but see Hatanaka et al., 2003), permitting them to intervene in cognitive operations. Together these connectivity profiles suggest an essential contribution of specific frontal lobe regions in cognitive control, supporting the experimental data from complex motor behaviour.

# 6.2. Potential mechanism: synchronization of neural activity

As discussed earlier the functions that underlie the planning and production of motor behaviour necessitate the cooperation of distributed areas. The organizational structure of the brain suggests that this integration follows a hierarchical path. A potential mechanism for such large-scale information transfer might be the transient formation of dynamic connections that are mediated by synchronization of neural activity across frequency bands (Singer, 1993; Bressler, 1995; Engel et al., 2001; Varela et al., 2001). Moreover, neural oscillations can offer an effective means of communication among neural groups, allowing for the assembly of flexible networks (Fries, 2005).

Neural oscillations are characterized by various frequency bands. Whereas synchronized activity in the gamma band ( $\sim$ 30–100 Hz) has been largely associated with local processing, activity in the beta ( $\sim$ 15–30 Hz) as well as alpha (>8– 12 Hz) and theta (4–8 Hz) ranges has been more related to distributed processing. This suggests that low frequency processes might be more readily involved in top-down modulations that permit the integration of high frequency processes (von Stein and Sarnthein, 2000). Furthermore, activity in the theta, alpha and gamma bands has been largely linked to cognitive operations (such as memory, attention) whereas activity in the beta band has been most readily associated with motor regulation (Klimesch, 1999; von Stein et al., 2000; Serrien et al., 2003; Gross et al., 2005). Accordingly, activity in these various frequency bands may underlie distinct components of information processing, while transient coupling between them may provide efficient and flexible neural communication (Varela et al., 2001; Canolty et al., 2006).

### 7. Conclusion

When motor skills are well-learned, a network of primary and secondary sensorimotor areas as well as subcortical regions is engaged. Conversely during complex skill acquisition and when external (e.g., feedback availability) or internal (e.g., pathology) factors are altered, cognitive resources are recruited to ensure that the action is performed in accordance with the goal requirements. Such functions are primarily associated with frontal lobe areas. The key regions include dorsolateral PFC, pre-SMA and ACC, which are crucial for response selection and monitoring. These particular areas may be engaged transiently (e.g., as arousal fluctuates) or more permanently when the inherent status requires enhanced regulation at all times. This suggests that operations that reflect the degree of cognitive effort and that mediate the subjective experience of a motor skill are malleable, associating by some means to a selective marker of'conscious processing' (Dehaene and Naccache, 2001). Functional similarities across domains propose that the foundation of these cognitive adaptations is not specific to motor control requirements but rather represents higher-order abstractions that unfold via a hierarchical structure (Ivry et al., 2004), relying on efficient frontal lobe functioning. Although the significance of these cognitive processes is generally accepted, their underlying mechanisms and dynamic interaction with motor circuits are still far from clear.

This review emphasizes a deep-rooted connection between action and cognition that points to common circuits serving critical functions across both domains (Georgopoulos, 2002). An important goal for future research will be to refine the functional architecture of the core processes that underlie complex actions in order to establish how cognate loops are integrated with motor pathways to promote skilled behaviour. Furthermore, exploring the relationship between action and cognition will support the design of cognitive interventions that emphasize strategic and evaluative operations to improve behavioural performance after brain injury.

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