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### ORIGINAL ARTICLE



## Losing control: the hidden role of motor areas in decision-making OWEN P. O'SULLIVAN

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Decision-making has traditionally been viewed as detached from the neural systems of sensory perception and motor function. Consequently, motor areas have played a relatively minor role in discussions surrounding the control processes and neural origins of decision-making. Empiric evidence, catalysed by technological advances in the past two decades, has proven that motor areas have an integral role in decision-making. They are involved in the generation, modulation, maintenance and execution of decisions and actions. They also take part in a complex hierarchical assessment of multi-modal inputs to ensure that the most appropriate action is generated given the context presented. Clinical conditions such as, alien hand syndrome and utilisation behaviour exemplify the importance of these regulatory controls. This review charts the trajectory of our understanding of the hidden role of motor areas in decision-making and reflects upon the implications of our deepened understanding. The convergence of evidence from multiple modalities underpinning our current knowledge is discussed and the potential applications thereof considered.

Keywords: motor cortex, cingulate cortex, decision making, cognitive science, neuroanatomy, alien hand syndrome

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### INTRODUCTION

We like to think that our destiny is sculpted by the conscious decisions we make along the way. However, the simplicity of such a thought is as deceptive as it is alluring: humans tend to overestimate the degree of conscious control they wield over their decisions. Perhaps it is because of this fallacy that we are so taken aback by the blatantly irrational decisions we see ourselves and others make during times of turmoil, low mood or extreme anxiety. Simply put, it is all too easy to forget the degree to which we are governed by our emotions and instincts. We have a tendency to idealise ourselves as rational creatures capable of making clear, logical decisions - and ultimately, actions - based on the information at hand, the environmental context and our past experiences.

Decision-making refers to the cognitive process of evaluating a number of possibilities, and selecting the most appropriate thereof in order to further a specific goal, or task. This faculty is a fundamental component of executive function. The debate as to whether, or not we have the capacity to make free choices is neither new, nor settled. However, the cross-cultural experiential phenomenon in humans of a subjective sense of

control in volition is well-established (Sarkissian et al., 2010).

Traditionally, psychological theories have considered the process of decision-making to be distinct, higher and separate from the neural systems of sensory perception and motor function. Motor areas have thus played a relatively minor role in discussions surrounding the control processes and neural origins of decisionmaking. Research narratives and hypotheses were dominated by the prevailing dogma that decision-making was simply composed of two broad stages with a significant level of interaction between the two. The first stage, occurring in the orbitofrontal cortex (OFC), encompassed predominantly cognitive - or executive - features of decision-making. The second stage, originating from the limbic regions, concerned itself with the influential role of emotion (Bechara et al., 2000).

It is only in the past two decades that motor regions have begun to be afforded increased attention. They are, after all, known to be crucial in the planning, initiation and execution of movement. Action has traditionally been portrayed as representing the endpoint of cognition however, this

assertion is being challenged and consequently the lines between executive and motor functions are fading. Action is increasingly being viewed as a cognitive process in its own right. Researchers from various fields within cognitive neuroscience are actively striving to re-define the role of motor regions in the hope of gaining a deeper appreciation of their complexity and the extent of their involvement in the decision process. The nascent field of "decision neuroscience" has presented innumerate fascinating and challenging questions. Are these motor regions purely limited to a "back-seat" role of silent effectors, or do they have a more complex modulatory function? What role do these areas have in decision-generation? How does learning affect this role and what happens when they are damaged?

### **DISCUSSION**

### Classical views of cortical motor area function

In 1870, it was first demonstrated experimentally that electrical stimulation applied to the pre-central cortex was capable of eliciting limb movements (Fritsch and Hitzig, 1870). Fulton (1935) first proposed - and initiated the cascade of - subdivision of the motor cortex into primary and pre-motor regions. Intra-operative electrical stimulation later gifted neuroscience with the somatotopic map of the primary motor cortex, which famously became known as Penfield's homonculus (Penfield and Boldrey 1937; Penfield and Rasmussen, 1952). This was undoubtedly a watershed moment in the trajectory of our knowledge of motor function. The hierarchical and sensorimotor machine models later put forward by the prolific Hughlings Jackson (1958) were emphatically challenged by evidence from landmark anatomical studies on non-human primates in the 1990s demonstrating non-primary motor cortical areas with direct projections to the spinal cord (Dum and Strick, 1991).

### Division of labour - a brief overview of the motor areas

The primary motor cortex (M1) is responsible for the execution of actions and is somatotopically organised. Each side of the body is under contralateral hemispheric control. The premotor cortex is involved in action preparation. The lateral part of the premotor cortex is associated

with linking objects in the environment with a repertoire of specific actions. It does so by taking advantage of the structural affordances proffered by the object presented and uses these heuristically to help determine the most appropriate action in a given context. The medial premotor cortex is also known as the supplementary motor area (SMA). The SMA is associated with postural control, locomotion and the performance of well-rehearsed actions: these are movements which require minimal monitoring of the surrounding environment (Graziano and Aflalo, 2007). The anterior cingulate cortex (ACC) has connections with the motor cortex and spinal cord and is also closely connected with the pre-frontal cortex (PFC). A functional overlap is suggested to exist in the ACC and hence, a translative role - in converting intentions into actions - has been proposed for this region (Paus, 2001).

### Conceptualising the convergence of cognition and action

We are constantly making decisions in our lives. The sheer fluidity with which it comes to us is astounding. Optimal, and seemingly effortless, human behaviour belies continuous analysis of incoming multimodal sensory information. Contextual factors are then weighted in deciding between competing potential actions and the most appropriate behaviour is eventually selected (Bestmann, 2006). The physical parameters of the ultimate action must also be determined prior to execution. But how to possibly reconcile all of these processes into a feasible, integrated model for decision-making and action behaviour?

Cisek (2006) challenged the established notion that decision and action planning were serial processes spatially separate from one another. He proposed a computational model that sees potential decision and action alternatives competing simultaneously across multiple stages of the cortical hierarchy (Bestmann, 2006). The model he proposed was of a unified process, as distinct from previous "separatist" hypotheses. The experimental paradigm employed simulation of anatomically-informed neural networks to demonstrate evidence of the involvement of specific premotor areas (dorsal premotor cortex i.e., PMd) in actual decision-making. Spatial

features, salience and valence information were combined and weighted accordingly to ultimately determine which of the competing representations would come out on top. Decisions took place in an all-or-nothing manner once a certain "quenching threshold" has been met in the PMd (Grossberg, 1973; Bestmann, 2006). The model was supported by existing electrophysiological (Cisek and Kalaska, 2005) and behavioural data (Bock and Eversheim, 2000) based on similar suppositions.

### Connectional complexity of the cingulate cortex

The ACC's extensive (Barbas and Pandya, 1989) motor, spinal cord and PFC connections make it a likely candidate for having a role in the translation or, modulation of decisions into actions. The cingulate sulcus in particular exemplifies the high degree of connectional complexity observed in this area. It represents a confluence of inputs from the PFC, M1 and SMA in addition to giving rise to corticospinal projections (Dum and Strick, 1991). Paus' (2001) review article on the role of the ACC discussed the convergence of cognitive and motor processes with the processes involved in maintaining the arousal state. Positron emission tomography (PET) has been employed to discern if the ACC is involved in the willed control of actions (Paus et al., 1993). Paus et al. used a behavioural model to try to identify whether differential ACC engagement was observed based on the output system used to execute the response. In the experiment, simple responses were challenged by the presence of over-learned stimulus-response alternatives. PET findings confirmed differential activation based on whether the motor output was manual, oculomotor or verbal.

### Electrophysiological correlates

The error-related negativity (ERN) is an event-related potential (ERP) that peaks at approximately 100 ms after movement onset. It is characteristically associated with error detection and conflict monitoring. The ERN's neural origins have been localised in the area of the ACC (Dehaene et al., 1994). The PFC-ACC connections have been shown to be crucial for ERN generation (Gehring and Knight, 2000). This is

highlighted by the observation that patients with unilateral lesions to the lateral PFC display ERN in response to both erroneous and correct items; they are also less likely to demonstrate "corrective behaviour" (Paus, 2001). This evidence suggests a role for the ACC in corrective behaviour and judgement.

### Automatic motor responses

Saccades and visual grasp reflexes are examples of automatic activation of motor responses. In these cases, perceptual processing of a visual stimulus occurs which culminates in the execution of a motor action without the intention of the observer to act (McBride et al., 2012). Visual objects can automatically generate motor responses and they do so via their structural affordances. These affordances refer to facilitative features of the object suggestive of its function and manner of use. When an object is observed, potential motor plans are generated based on data presented. Functional neuroimaging studies have demonstrated the exquisite sensitivity of these visual systems by showing that motor areas are activated by simply looking at an object (Grèzes and Decety, 2002), without necessarily the intention to act upon its presence. We are told from a young age, "we learn by doing, not by seeing" however, this neuroimaging evidence raises intriguing philosophical questions which blur the boundaries of thought and action, hitherto perceived as categorically distinct from one another.

### Lessons from clinical neurology

Automatic activation plays a vital role in everyday life: facilitating desirable responses and inhibiting others is crucial for normal functioning in a dynamic environment rich in diverse visual stimuli. This ability to inhibit inappropriate responses is crucial: otherwise efficient goal-directed behaviour cannot occur (McBride et al., 2012). Its central role in ensuring day-to-day functionality is laid bare in conditions such as, alien hand syndrome and utilisation behaviour, wherein such behaviour becomes exceedingly difficult.

These striking conditions demonstrate what happens when the volitional restraints exerted to suppress these automatic actions in response to an object are released. Patients with alien hand syndrome reach and grasp for objects in their environment at random. They are aware that the movements are occurring and that they originate from their own body however, they do not experience any subjective feeling of control over these actions whatsoever. (Scepkowski and Cronin-Golumn, 2003). In utilisation behaviour, similar phenomena are observed except in this case the actions are usually purposeful (Boccardi et al., 2002). For example, an individual with this condition may be irresistibly drawn to repeatedly opening and closing the drawers in a desk as they walk past. The brain region affected in these conditions is predominantly the SMA however, damage to the corpus callosum, parietal lobes and basal ganglia can also be implicated in similar conditions (Boccardi et al., 2002).

### Decision neuroscience: fertile ground at the crossroads of research

Decision neuroscience is a relatively new field that has grown steadily over the past two to three decades. As the above examples have illustrated, it has firmly shed its reliance on purely psychological paradigms and now transcends disciplines and modalities: encompassing everything from single-neuron recordings to non-invasive functional neuroimaging and everything in-between. It is more intellectually accessible and less abstract than other areas in neuroscience and hence, its popularity and lure is unsurprising. Additionally, the potential for exponential growth in our understanding carries obvious immediate appeal and will certainly bear potential for wider interest outside of cognitive neuroscience. The study of economics, marketing, artificial intelligence, investment psychology and risk management are to name but a few of its many plausible applications. The psychology of decision-making has an undeniable philosophical legacy. And this inheritance has proved difficult to avoid, if not inevitable. However, rather than being disheartened by this spectre, decision neuroscience promises to provide the empiric evidence needed to aid us in addressing the neural basis of many perplexing questions regarding concepts of free will, conscious and unconscious volition, agency and individual culpability.

#### **CONCLUSION**

Motor areas have an integral role in decisionmaking. They are involved in the generation, modulation, maintenance and execution of decisions and actions. They take part in a complex hierarchical assessment of multimodal inputs with a view toward ensuring that the most appropriate action is generated given the context. The psychopathology demonstrable in patients with frontal lobe syndromes offers insight into the crucial need for executive controls for normal functioning. In order for humans to engage intelligently and efficiently with their environment, the integrity of these cortical connections must be ensured. Decision-making and action planning can however, no longer be considered as processes, for the most part, limited to the prefrontal cortices. Empiric evidence has proven otherwise and demonstrated that the increase in prominence of the motor areas in this regard is both timely and deserved. Furthering our understanding of cognitive systems such as this in a meaningful, cross-disciplinary and integrative manner remains an ongoing ambition previously precluded by technological limitations. Research into the applications of the neural basis of decision-making will no doubt prove to be a vibrant, highly competitive and potentially extremely lucrative pursuit.

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