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Viewpoint

Neurology of widely embedded free will

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ABSTRACT

Free will is classically attributed to the prefrontal cortex. In clinical neurology, prefrontal lesions have consistently been shown to cause impairment of internally driven action and increased reflex-like behaviour. Recently, parietal contributions to both free selection at early stages of sensorimotor transformations and perception of specifically self-intended movements were demonstrated in the healthy brain. Such findings generated the concept that 'free will' is not a function restricted to the prefrontal cortex but is more widely embedded in the brain, indeed including the parietal cortex. In this paper, a systematic re-interpretation of parietal symptoms, such as apraxia and reduced sense of agency, is given with reference to the consequences of reduced freedom of selection at early stages of sensorimotor transformation. Failed selection between possible movement options is argued to represent an intrinsic characteristic of apraxia. Paradoxical response facilitation supports this view. Perception of self-intended movement corresponds with a sense of agency. Impaired parietal distinction between predicted and perceived movement sensations may thus equal a restricted repertoire for selection between possible movement options of which intention is attributed to either oneself, others or an alien hand. Sense of agency, and thus perception of free will, logically fits a model of the parietal cortex as a neuronal interface between the internal drive to reach a goal and a body scheme required to select possible effectors for motor preparation.

1. Localization in clinical neurology

The interpretation of symptoms and signs in clinical neurology is based on the principle of localising functions in the nervous system (Tyler and Malessa, 2000). The consequence of a lesion in the brain is dysfunction, which may concern a wide range of sensory and motor modalities as well as cognitive abilities. The consistent association between specific dysfunction and a distinct lesion location provides an essential tool in reaching a neurological diagnosis. The presentation of an apparently localised function does, however, not necessarily mean that such a region represents a given function in isolation. Functional brain imaging in healthy subjects has increasingly demonstrated that the cerebral organization of functions is embedded in widely distributed networks (Friston, 2002; Bullmore and Sporns, 2009). The lesion of a crucial node in such a network determines the dominant presentation of distinct clinical deficit. The conceptual consequence of a distinct node participating in multiple networks is, however, that a single lesion may cause a gradual impairment in various functional domains while the capacity for possible compensation may be larger.

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Such new ideas on the functional organization of the brain may challenge the interpretation of previously well-described neurological symptoms.

The scope of this communication is to discuss whether the emerging concept of 'free will' being widely embedded in the brain is consistent with the presentation of neurological symptoms due to lesions outside the prefrontal cortex. In this respect, parietal symptoms will be particularly dealt with. As a starting point, 'free will' is pragmatically defined as the ability to generate self-intended action, independent from external cues. The concept of free will is further elaborated in this paper, treating distinction and coherence between (i) degrees of freedom in neuronal responses underlying free selection of possible actions and (ii) the perception of free will associated with a sense of agency.

2. Prefrontal cortex function

Planning goal-directed actions and making selections between them, not driven by external cues, is a function largely attributed to the prefrontal cortex and intrinsically linked to 'free will'. Free will implies the option to choose between alternative actions, taking in account the future consequences of such choice with reference to memorised experiences. The contribution of specific prefrontal regions to this coherent cluster of cerebral functions, and particularly involvement of the medial prefrontal cortex, has been described with increasing detail in recent years (Frith et al., 1991; Miller and Cohen, 2001; Lau et al., 2006; Koechlin and Hyafil, 2007; Mueller et al., 2007; Rushworth, 2008; Haggard, 2008). In neurological disease, the classical characteristic of prefrontal syndromes is the loss of initiative to undertake internally motivated action while responses to external stimuli are enhanced (Burgess and Shallice, 1996; Godefroy, 2003). The latter may vary from the simple grasp reflex to complex utilization behaviour (De Renzi and Barbieri, 1992; Lhermitte, 1983). Moreover, flexibility of problem solving is impaired and behaviour becomes increasingly stereotypic. In this sense, the richness of personality, with the presentation of its original behaviour, degrades as a result of frontal lobe dysfunction. The impoverished repertoire of internally driven actions and reflex-like responses to external events thus appear to reflect a reduction of free will. In this way, neurological symptoms provide fair arguments to link free will with prefrontal function.

3. Apraxia

Active motor interaction with one's environment, either driven by external cues or by internal motives, requires adjustment of movements to external circumstances. Such precise performance, e.g., in grasping an object, results from elaborate sensorimotor transformations. The parietal cortex, in functional concordance with premotor regions, is crucially implicated in providing the motor cortex the appropriate information to release final movement instructions to the spinal motor neuron (Wise et al., 1997; Binkofski et al., 1999; Matelli and Luppino, 2001; de Jong et al., 2001). Failure of such parietal function may result in apraxia, with sub-types depending of the lesion site (Heilman and Rothi, 1993; Leiguarda and Marsden, 2000; Goldenberg, 2009). A lesion around the posterior parts of the intra-parietal sulcus may e.g., result in optic ataxia, disabling the patient to direct the hand towards the target location (Perenin and Vighetto, 1988), while ideomotor apraxia due to a left inferior parietal cortex/angular gyrus lesion leads to failures in object manipulation (Buxbaum et al., 2003). At first sight, such parietal dysfunctions only points at impaired construction of a required motor plan, independent from the decision to select a preferred action. In recent years, however, experimental studies generated the concept that decision making is not restricted to prefrontal functioning but takes already place at early stages of visuomotor processing (Cisek, 2007). Neuronal recordings in monkey parietal and premotor cortex revealed response characteristics that indicated a stronger relation with the animal making free choices than with the condition in which invariant instructions were followed (Pesaran et al., 2008). With fMRI, the specific contribution of the (pre-) dorsal premotor cortex and inferior parietal cortex to free choice selection in visuomotor action has also been demonstrated in human (Beudel and de Jong, 2009). This raises the question how deficit in free selection manifests itself after parietal lesions.

4. Free selection in the parietal cortex

As argued above, movements aimed to achieve an external goal are limited by external constraints. On the other hand, in the context of 'free will' it should be considered that purposeful object manipulation, which is impaired in ideomotor apraxia, implicitly allows considerable degrees of freedom. E.g., in reaching for a glass of wine, without thought, either its upper convexity or the stem may be used to lift it. Moreover, a variety of finger positions may be similarly effective to accomplish the given aim of drinking its content. In this sense, a reduction in the degrees of freedom how to accomplish a task may be seen as an intrinsic component of apraxia, consequently linking the parietal cortex with particular aspects of free will. Such reduced freedom in selecting between possible movement options is consistent with impaired selection between motor programs as recently described by Coulthard et al. (2008). They provided plausible arguments to explain that in right posterior parietal lesions, paradoxical facilitation (speeding) of rightward movements in response to incongruent direction cues was due to unilateral release of mutual inhibition which normally takes place between early-stage competing motor programs.

A most basic restriction in the freedom of action concerns the inability to distinguish between the two options either to act or to refrain from action. This manifests itself in the 'alien hand syndrome', a disorder in which the patient's hand may reach for an object and start manipulating it without the patient wants to do so (Doody and Jankovic, 1992; Assal et al., 2007; Sala, 2009). The core symptoms of this neurological condition may arise from a lesion in either the anterior corpus callosum, the medial frontal cortex or the (non-dominant) parietal cortex (Scepkowski and Cronin-Golomb, 2003). In addition to behavioural characteristics resembling signs of frontal disinhibition as seen in the grasp reflex (De Renzi and Barbieri, 1992), patients report the experience of a hand acting