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Research report

Feeling in control: Neural correlates of experience of agency

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ABSTRACT

The ability to control external events through our own actions is a fundamental aspect of human experience. Both the subjective experience of agency, and its neural correlates, remain poorly understood. Previous studies show that the angular gyrus is activated when participants explicitly judge that they *lack* agency. In contrast, the positive sense of agency over external events is associated with distortions of time perception. Here, we show that the perceived interval between actions and a subsequent tone is shorter than the perceived interval between a physically comparable passive movement and a tone, replicating the 'intentional binding' effect reported previously. We considered this as a potential implicit marker of agency, and investigated its neural basis, by using parametric analyses to identify brain areas whose activation correlated more strongly with the perceived action-tone interval in the action condition, than in the passive condition. Small volume corrections were used to test specific hypotheses about the contribution of the angular gyrus, and of the supplementary motor area (SMA), based on previous literature. We found no correlation between angular gyrus and our temporal measure of sense of agency. In contrast, we found that a lateral, caudal region within the SMA proper was more strongly associated with the perceived action-tone interval than with perception of a control interval following a passive movement. We suggest that the supplementary motor complex contributes to the subjective experience of temporal flow that accompanies goal-directed voluntary actions.

1. Introduction

Goal-directed action requires the ability to identify the consequences of our behaviour in the external world. We use the term 'agency' to refer to this fundamental aspect of human self-consciousness (Pacherie, 2008). Recent theoretical work distinguishes between two important aspects of agency (Synofzik et al., 2008a, 2008b). First, people can make explicit *judgements* about their agency ("I did that"). Second, there is a subjective feeling of control that accompanies one's own actions, even in the absence of any conscious awareness or reflective thought, known as *sense* of agency. The dominant experimental model for studying agency involves explicit judgements of whether a sensory event is caused by one's action, or by that of another agent. Several studies have used self-recognition paradigms to investigate this explicit sense of

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agency (Daprati et al., 2007; Tsakiris et al., 2005). In the typical design, the participant makes a manual action, and sees video feedback which may either show their own action or the action of another person. Participants judge whether they are viewing their own hand action or not. Other studies have extended this paradigm from recognition of one's own hand action to judging whether arbitrary effects, such as appearance of a symbol on a computer screen, are caused by one's own key press actions or another person's (Sato and Yasuda, 2005; Wegner and Wheatley, 1999). Spatial (Daprati et al., 2007) and temporal (Farrer et al., 2008; Wegner and Wheatley, 1999) congruence of one's own action and sensory feedback are key cues for self-attributing agency. Another prominent approach to investigate agency has been to manipulate agency as an independent variable by either giving participants control or not giving them control over some external event, and contrasting different levels of control (Metcalfe and Greene, 2007). Level of control is often manipulated by introducing a feedback delay.

Interestingly, recent neuroimaging studies failed to find any clear neural correlates for positive judgements of agency, but showed that the right angular gyrus plays a key role in *rejecting* agency based on lack of temporal congruence (Farrer et al., 2003, 2008). The importance of the parietal areas in general, and the angular gyrus in particular, in processing of agency was confirmed by patient studies. Lesions including this area were reported to produce a deficit in recognising visual feedback of one's own action (Sirigu et al., 1999). It remains unclear whether angular gyrus activation is linked to explicit judgement of agency, or whether automatic monitoring of action outcomes is sufficient. For example, Miele et al. found an extensive activation around the right temporoparietal junction (TPJ), including the angular gyrus, in a video game task when they introduced a distortion in the relation between participants' movements and the resulting displacement of an on-screen cursor (Miele et al., 2011) Farrer et al. (2008) found that angular gyrus activation increased when participants became aware of action–effect discrepancy, even when they were not required to judge agency per se. According to the simplest model, explicit judgements of agency would depend on a computation performed by the angular gyrus to match actions with effects, but it remains unclear whether this matching process is completely automatic, or requires explicit judgement of some kind, and whether the same matching process is also the basis of the subjective feeling of agency.

While explicit judgements of agency may be important in social contexts where any of several individuals might be responsible for an outcome, our everyday experiences of agency do not generally involve explicit judgement. We can, and frequently do, make instrumental actions where we have a definite background feeling or buzz of being in control. In such cases, we do have a phenomenal experience or sense of agency, even though we did not make any explicit judgement. We regularly experience a flow between the actions we make, and their external effects, for example when using a computer keyboard, driving a car or playing a guitar. Thus, we have an implicit feeling of agency, which is non-conceptual and subpersonal. Often, this implicit feeling of agency seems to run in the background of consciousness. Agency may only become truly salient when it is lost, for example when the keyboard on a computer jams, or the controls on a car fail. In the normal flow of experience, the sense of agency seems just to be part of what it is like to control one's action.

The neural basis of this background feeling of agency is not well understood. There is a general consensus that learned spatiotemporal association between actions and effects contributes to the background feeling of agency, in the same way as it contributes to explicit agency judgements. For example, the feeling of being in control over a car increases as we learn how to drive it. However, there is a general difficulty in *measuring* background phenomenologies of this kind. Several studies have used perceptual attenuation of sensory consequences of one's own actions (Blakemore et al., 1998; Chapman and Beauchamp, 2006) as an implicit measure of agency. In addition, several distortions of time perception can occur around the time of action. The pattern of these temporal distortions has lead to the suggestion that they could form a useful implicit marker of the sense of agency. For example, distortions of time perception occur for active, but not involuntary movements (Haggard et al., 2002), and do not occur when the effects of action are explicitly attributed to another person (Desantis et al., 2011). Here we use the attraction between the perceived time of actions and their effects as a putative marker of the subjective experience of agency. This perceptual attraction can be considered as a subjective consequence of the 'constant conjunction' of action and effect that underlies our experience of both agency and causation (Hume, 1763). A convenient measure of this associative aspect of sense of agency is the "intentional binding effect". When people make a voluntary action to cause a sensory effect a short time later, they estimate the interval between action and effect as shorter relative to a control condition where the same interval is used (Engbert et al., 2007; Buehner and Humphreys, 2009; also Haggard et al., 2002).

While explicit judgements of agency have been extensively investigated using functional magnetic resonance imaging (MRI) (see above), the implicit sense of agency has been much less investigated. Using positron emission tomography (PET), Elsner et al. (2002) asked participants to make voluntary actions, and followed these by an auditory effect. When participants subsequently listened to mixtures of these previously-caused tones and other, neutral tones, a caudal region of the SMA was increasingly active as the proportion of previously-caused tones grew. Re-presentation of previously-caused tones was assumed to reactivate associations between action and effect housed in the SMA. This result is consistent with a frontal contribution to sense of agency. However, no measures related to agency were obtained in the critical trials in their experiment. Miele et al. (2011) asked participants at the end of a video game task how much control they had experienced during that task. They found a positive correlation between pre-SMA activation and explicit judgements of "sense of control". However, it is unclear how such synthetic judgements relate to the underlying low-level experience of action events and consequences remain unclear. To our knowledge, the neural correlates of *temporal* association between individual instrumental actions and their effects have not yet been studied using neuroimaging. One transcranial magnetic stimulation (TMS) study (Moore et al., 2010) used independent estimates of time of action and effect to