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Voluntary control of a phantom limb

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ABSTRACT

Voluntary actions are often accompanied by a conscious experience of intention. The content of this experience, and its neural basis, remain controversial. On one view, the mind just retrospectively ascribes intentions to explain the occurrence of actions that lack obvious triggering stimuli. Here, we use EEG frequency analysis of sensorimotor rhythms to investigate brain activity when a participant (CL, co-author of this paper) with congenital absence of the left hand and arm, prepared and made a voluntary action with the right or the phantom "left hand". CL reported the moment she experienced the intention to press a key. This timepoint was then used as a marker for aligning and averaging EEG. In a second condition, CL was asked to prepare the action on all trials, but then, on some trials, to cancel the action at the last moment. For the right hand, we observed a typical reduction in beta-band spectral power prior to movement, followed by beta rebound after movement. When CL prepared but then cancelled a movement, we found a characteristic EEG pattern reported previously, namely a left frontal increase in spectral power close to the time of the perceived intention to move. Interestingly, the same neural signatures of positive and inhibitory volition were also present when CL prepared and inhibited movements with her phantom left hand. These EEG signals were all similar to those reported previously in a group of 14 healthy volunteers. Our results suggest that conscious intention may depend on preparatory brain activity, and not on making, or ever having made, the corresponding physical body movement. Accounts that reduce conscious volition to mere retrospective confabulation cannot easily explain our participant's neurophenomenology of action and inhibition. In contrast, the results are consistent with the view that specific neural events prior to movement may generate conscious experiences of positive and negative volition.

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1. Introduction

Some voluntary actions are accompanied by an experience of conscious intention, of initiating and controlling our actions. The basis of this experience of conscious intention is vigorously debated. Some stimulation (Fried et al., 1991) and recording (Mukamel et al., 2010) results suggest that the experience of conscious intention is associated with activation of specific structures in the medial frontal and parietal lobes (Desmurget et al., 2009). On an alternative view, the experience of conscious intention is not so much a direct read-out of any specific brain activity, but an inference about the causes of internally-generated actions. Thus, one might infer that one's own actions have some internal cause by

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http://dx.doi.org/10.1016/j.neuropsychologia.2015.06.032 0028-3932/© 2015 Elsevier Ltd. All rights reserved. general principles of causal reasoning. This cause would then be retrospectively inserted into the narrative stream of consciousness. Conscious intention would then not correspond to a mental state, in the normal sense, but to a reconstructive confabulation of action authorship (Wegner, 2002). The inferential or reconstructive view has received strong support from studies showing that attribution of agency (Wegner and Wheatley, 1999) and even primary experience of action (Moore et al., 2009) are strongly influenced by the context of action, and by the occurrence of events that might plausibly be caused by intentional actions.

Reconstructive inference raises a major methodological problem for studying action awareness. Most methods for investigating awareness involve a subjective report, which typically occurs *after* the event to which it refers. Even if there is a pure, premotor experience of intention that precedes action, most experimental reports of this experience are obtained *after* action. The experience of intention will then be altered by how the body actually moves. In fact, the entire experience of intention could be an invention by the mind to justify how and why the body moved. It







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has therefore proved difficult to access a pure experience of volition, independent of the bodily actions with which intention is associated (Fried et al., 1991).

The positions of "no volition, just inferential reconstructivism" and "direct access to conscious intention" may both be excessively strong. Recent work on consciousness suggests that all perceptions, not just conscious intention, are a form of synthetic inference based on integration of multiple neural activities over time (Dehaene and Changeux, 2011). Therefore, understanding how and when the experience of volition is generated in the human brain, and which circuits are involved in generating it, remains an important question in the understanding of consciousness. The case of volition may have particular applied importance, because most systems of law assume that an experience of willing an action, and/or failing to inhibit the action, is necessary for a person to be judged socially and legally responsible.

The everyday experience of action is strongly linked to the process of initiating actions (Libet et al., 1983). However, neuropsychologists have long recognised that a key element of behavioural control involves inhibiting actions that may be suggested by the environment, or by our previous experience (Della Sala et al., 1991). Accordingly, we recently suggested that the neural computations involved in voluntary action include a crucial decision regarding whether to act or not [the What, When, Whether (WWW) model of intentional action] (Brass and Haggard, 2008). This decision could act as a final point of control over behaviour (Filevich et al., 2012). The status of conscious processing in such inhibition is particularly controversial (Hughes et al., 2009; Libet, 2009). However, inhibition of action does not have any behavioural marker, by definition. This makes studying intentional inhibition of human action particularly challenging. We have previously shown that the conscious experience of intending to act can serve as a *subjective* marker for actions that are prepared, but subsequently inhibited (Brass and Haggard, 2007). In particular, we showed that the reduction in beta-band EEG power that precedes voluntary action was replaced, in trials where participants freely chose to inhibit their actions (Walsh, E., et al., 2010).

Here we have tested an individual with congenital absence of the left arm in a voluntary action and voluntary inhibition paradigm. CL is a 37 year old (at time of testing) performance artist, born without a left hand and arm. She is a co-author of this paper. CL experiences occasional but vivid phantom sensations related to the "left hand". The experiences include strong urges to move and control her phantom left limb. Her participation in the experiment offered a unique window into the neurophenomenological mechanisms of voluntary action and voluntary inhibition. First, we wished to investigate whether preparation of movements with the phantom hand might be accompanied by a subjective sense of volition, and by the normal neurophysiological markers of voluntary action. A further scientific reason for studying CL's performance is the opportunity for a novel comparison between voluntary action and voluntary inhibition of action. In the normal case, the comparison between action and inhibition inevitably involves body movement in the former case, but not the latter. Thus, sensory feedback from the body movement may confound any contrast between action and inhibition conditions. In principle, neurophysiological measures of preparation prior to action may avoid this confound, because physical body movement has not yet begun. However, any difference between action and inhibition conditions could still reflect differences in predicted sensory feedback, rather than an active process of inhibition confined to the inhibition condition. In the case of a phantom limb, in contrast, action and inhibition are physically identical, and are presumably predicted to be physically identical. Therefore, any difference in neurophysiological markers must reflect a central neurocognitive process of inhibition. In line with CL's subjective

experiences of command over her phantom left hand, such volitional control might arise from innate core cortical mechanisms. Alternatively, CL might acquire volitional control over her phantom left hand via a process of generalisation or interhemispheric transfer from motor representations for her right hand; in which case pre-movement ERD before actions made by her phantom left hand might appear as "weak echoes". Finally, the results could contribute to the understanding of phantom limb phenomena per se. To our knowledge, no previous study has investigated either the preparation or the inhibition of voluntary actions of a phantom limb.

2. Methods

2.1. Procedure

The method was essentially similar to a previous experiment performed with a group of 14 two-handed volunteers, and previously reported elsewhere (Walsh, E., et al., 2010). Briefly, in the previous study participants performed self-paced voluntary keypresses with the right hand in one condition. Using the "Libet method", participants reported the time at which they experienced the conscious intention to make the voluntary action. Participants were asked to act within the first revolution of the clockhand, in order to avoid ambiguities regarding whether their subjective reports referred to the first or to subsequent rotations of the clock-hand. Further, the clock rotation period was set to 5120 ms (Walsh, E., et al., 2010), rather than the 2560 ms used in previous studies (Haggard et al., 2002), to ensure an adequate period for freely choosing when to act. In further blocks of trials, they were given the additional instruction to inhibit the action at the last possible moment on some trials that they freely chose, while still reporting the time of intending the action, the so called "W time" (Libet et al., 1983), whether they actually cancelled it or not. Here, CL performed the same task in the same conditions as the control participants. In a first session, she used her right hand (see Fig. 1). In a second session, conducted some 10 weeks later, she performed the same tasks with her phantom left hand. In the "left hand" inhibition block, CL reported after each trial whether she had acted or inhibited on that trial, since there could be no behavioural marker of this decision in the absence of a physical left hand. In each session, there was an initial practise block of "action-only" trials. This was followed by two further action-only blocks, and then four blocks in which the participant freely chose on each trial whether to act or inhibit action ("act-or-inhibit" trials). Each block comprised 40 trials. Testing was performed with the permission of the local ethics committee, and in accordance with the principles of the Declaration of Helsinki.

2.2. EEG recording and analysis

EEG data were recorded from sites F3, Fz, F4, FC3, FC2, FC4, C3, Cz, C4, P3, Pz, P4, O1 and O2. EEG was sampled at 500 Hz, bandpass filtered between 0.1 and 250 Hz, and re-referenced to linked mastoid electrodes. The EEG power in the upper alpha- and lower beta- bands, previously associated with motor preparation and execution (Pfurtscheller and Lopes da Silva, 1999), was computed. Our analyses focussed on established EEG markers of volition: the event-related desynchronisation (ERD) prior to voluntary action, and post-movement beta rebound. We were also interested in whether CL would show an event-related synchronisation (ERS) associated with action inhibition, similar to that reported previously. The time and frequency windows used for each planned analysis are reported with the results. CL's data were compared between her actual right hand and phantom left hand as a withinDownload English Version:

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