

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

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 key-presses 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 clock-hand, 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, FCz, FC4, C3, Cz, C4, P3, Pz, P4, O1 and O2. EEG was sampled at 500 Hz, band-pass 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 within-

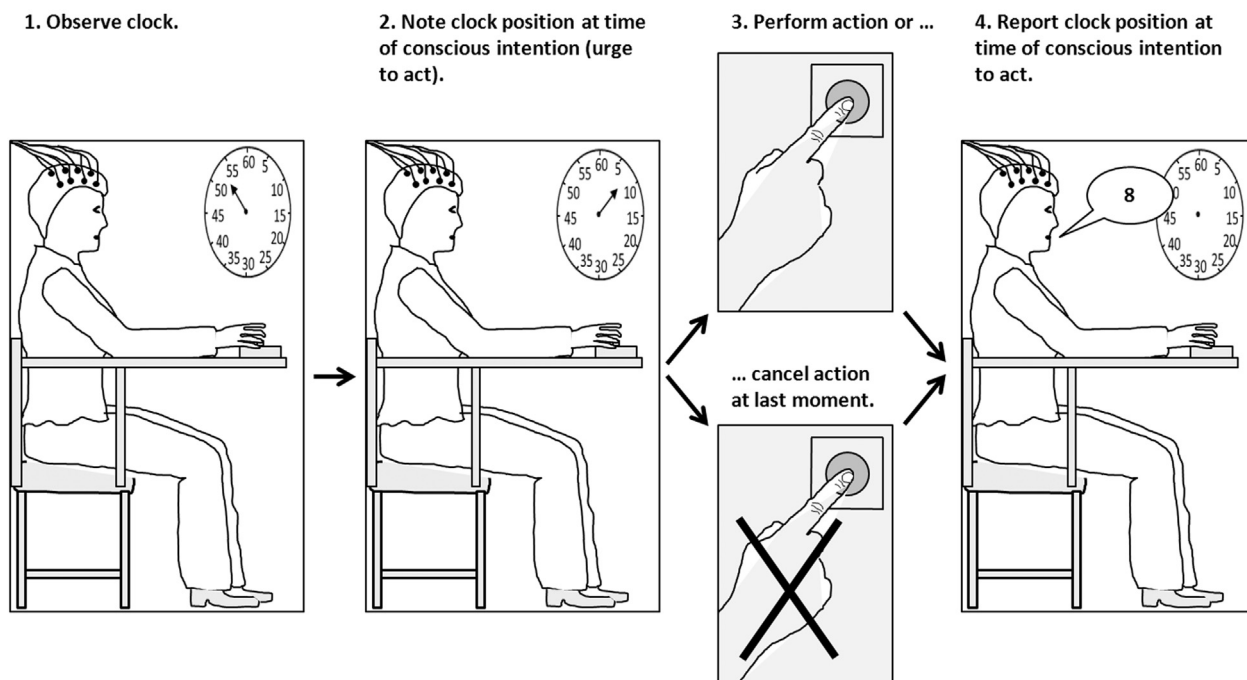


Fig. 1. Measuring conscious intention regarding the decision to act, on trials where actions were executed or cancelled at the last moment.

participant comparison. Further, CL's performance with each hand was compared with previously-published data from a group of two-handed volunteers (Walsh, E., et al., 2010).

The EEG processing followed standard methods used in the previous study (Walsh, E., et al., 2010). Briefly, artefacts and blinks were excluded by rejecting epochs containing signals greater than $+120 \mu\text{V}$ or less than $-120 \mu\text{V}$; for the phantom left hand, 28% of epochs were rejected and 19% for the right hand. Epochs were extracted from 1000 ms before to 500 ms after each event relative to CL's average, baseline corrected using a window from 1000 to 800 ms prior to the locking event. Separate averages were obtained for each of the following trial types: action-only trials, action trials in act-or-inhibit blocks, and inhibition trials in act-or-inhibit blocks.

3. Results

CL reported no particular difficulty performing the Libet task. In the session where she used her phantom left hand, she reported a sensation of preparing and commanding the keypress action of the "left hand". Interestingly, in blocks where she had to prepare but then sometimes inhibit the action of the "left hand", she spontaneously reported the phantom "left hand" as wilful, and difficult to control. She reported having to make a particularly strong effort to inhibit the actions of the "left hand" on selected trials, because of the compelling urge for the "left hand" to make keypress actions.

3.1. Behavioural results

In the condition where CL could freely choose to inhibit on certain trials, she chose to do so on 53% of trials for the right hand, and reported doing so for 46% of trials for the "left hand". In contrast, in the control dataset published previously, participants inhibited on 49.7% (range 41.2–60.4%) of trials. We also compared the perceived time of intention with the actual time of the keypress for right hand actions only. In action-only blocks, CL reported an experience of intention, or "W judgement" (Libet et al., 1983), of

–76 and –116 ms for each of the two action-only blocks, yielding a mean W judgement of –96 ms (SD across trials = 164 ms) before the keypress. In action-only blocks, the control group participants had a mean W judgement at –283 ms (SD across participants = 164 ms) before the keypress. In the four act-or-inhibit blocks, CL reported a mean experience of intention –38 ms (range –21 to –53 ms for the 4 blocks; SD across trials = 104 ms) before the keypress. The control group participants had a mean W judgement at –408 ms (range: –580 ms to +11 ms across individuals; SD = 415 ms) before the keypress. W judgement times generally show considerable variation across individuals (Trevena and Miller, 2002). We used the procedure of Crawford and Garthwaite (Crawford and Garthwaite, 2002; Crawford et al., 2010) for comparing a single case with a control population, and for calculating effect sizes. In action-only blocks, CL's W judgements for the right hand, compared with those of the controls (Walsh, E., et al., 2010), and showed no significant difference: $t=1.102$, $p=0.291$. Likewise, in act-or-inhibit blocks, CL's W judgements for the right hand also did not differ from those of the control sample: $t=0.861$, $p=0.405$.

3.2. EEG results

CL's EEG data were inspected to test three specific predictions based on previous studies. First, we predicted a premovement ERD in motor rhythms during action preparation (Pfurtscheller and Lopes da Silva, 1999). Second, we predicted a post-movement beta rebound (Neuper and Pfurtscheller, 2001). Third, we predicted an ERS associated with the decision to inhibit (Walsh, E., et al., 2010). In each case we compared CL's phantom left hand with her right hand, and with previously-published data from two-handed controls (Walsh, E., et al., 2010). As before, we restricted our search for neural activity relative to intentional inhibition to a time from 340 ms before to 340 ms after the W judgement and a frequency range of 8–24 Hz (alpha- and beta-bands). In addition, we restricted our analyses to induced, rather than evoked activity, because induced activity does not imply precise event-related time-locking captured by evoked analyses. We used subjective time

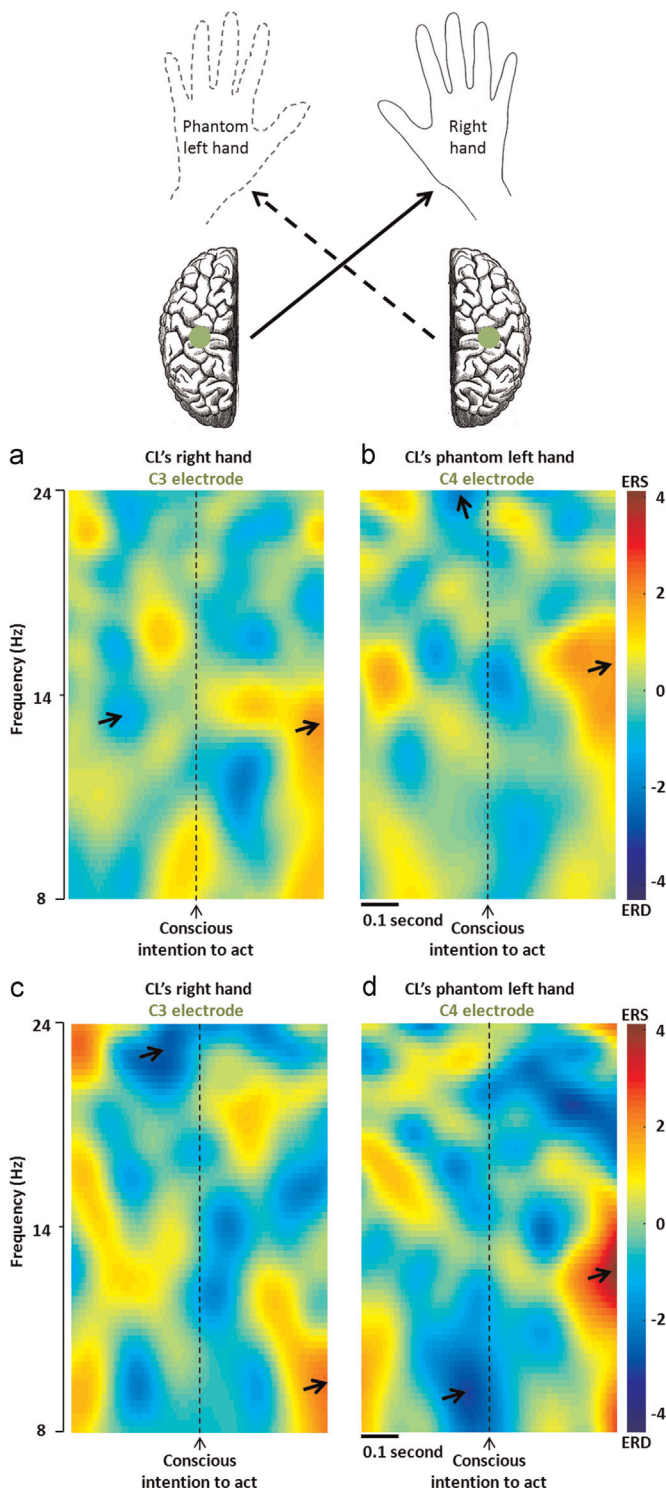


Fig. 2. Spectral power for action trials in the mu- and beta-bands around the time of conscious intention, contralateral to the acting hand. The data are shown time-locked to the average time of conscious intention to act (W judgement, dashed vertical line). (a, b) Action-only blocks and (c, d) action trials in the act-or-inhibit condition. Note the contralateral mapping between the scalp electrodes and the hands. Blue colour indicates event-related desynchronisation (ERD). Red indicates event-related synchronisation (ERS). Note mu-ERD prior to and during movement, followed by ERS (beta rebound: BR) after movement. Arrows show peak values of ERD prior to, and ERS after the moment of conscious intention. For actions using CL's phantom left hand, the contralateral right motor cortex EEG is shown (electrode C4, b, d). For actions using the right hand, electrode C3 is shown (a, c). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

estimates for time-locking, and the temporal precision of these is generally rather low.

We thus investigated whether CL showed an ERD during action preparation, and a beta rebound, on action trials. We separately considered the blocks consisting only of actions (action-only blocks), and the action trials from act-or-inhibit blocks. Fig. 2 shows the classic, clear pre-movement ERD, shown as blue colour in the 8–24 Hz region in both CL's data. For CL, pre-movement ERD is visibly greater preceding actions of the phantom left hand (Fig. 2d) than in the physically-present right hand (Fig. 2c). Fig. 2a and c also shows a clear rebound ERS for the right hand. This rebound ERS occurs in the same frequency range as pre-movement ERD, beginning immediately after the average W judgement. This rebound ERS is more visible for the phantom left hand (Fig. 2d, see arrow) than the physically-present right hand (Fig. 2c, see arrow). The full results are shown in Table 1.

Fig. 3 shows the EEG data for trials in act-or-inhibit blocks where CL chose to inhibit action. In previous work (Walsh, E., et al., 2010), we had found an increased oscillatory power in the low beta range linked to this event. CL's data also show a clear ERS peak in the same frequency range, both for the physically-present right hand, and for the phantom left hand (Table 2).

We wanted to address statistically the hypothesis that a phantom limb can support neural processes of voluntary action preparation, and of voluntary action inhibition. We statistically assessed (Crawford and Garthwaite, 2002; Crawford et al., 2010) whether CL's pre-movement ERD, rebound ERS, and inhibition ERS differed from those in the control group. Pre-movement ERD and rebound ERS were tested separately for action-only blocks and for action trials in act-or-inhibit blocks. We applied this test to the time, frequency and amplitude of CL's data for the contralateral hemisphere, for each of these three events of interest. In each case we compared CL's phantom left hand and her right hand with the previously-published data from two-handed controls (Walsh, E., et al., 2010). As in the previous study, we restricted our search for neural activity relative to intentional inhibition to a time from 340 ms before to 340 ms after the W judgement and a frequency range of 8–24 Hz (alpha- and beta-bands). In all of the 36 tests performed (see Supplementary material), CL's EEG peaks lay within the 95% confidence interval for the control group, when corrected for multiple comparisons (Bonferroni corrected; McDonald, 2009). Importantly, all the amplitudes of pre-movement ERD, rebound ERS and inhibition-related ERS fell within the confidence interval for the controls. Thus, the timing, frequency and amplitude of CL's EEG activities did not reliably differ from controls, and were present for both the physically-present right hand and for the phantom left hand.

4. Discussion

We show that a participant (CL) with congenital absence of the left hand and arm showed three classic central markers of volition with respect to simple movements of the left hand. We asked CL to perform simple voluntary keypress actions with her physically-present right hand, or with her phantom "left hand", in the context of the Libet experiment (Libet et al., 1983). By using the reported time of intention to act as a subjective marker of volition, we were able to examine the neural correlates of volition for a phantom hand, for the first time. The pre-movement decrease in oscillatory power in the alpha and beta bands is a classic central signature of the preparation of voluntary action (Pfurtscheller and Aranibar, 1979; Pfurtscheller and Lopes da Silva, 1999; Stančák et al., 2000). CL exhibited this pre-movement event-related desynchronisation (ERD) to an extent that was indistinguishable from normal controls, both with the physically-present right hand,

Table 1

EEG results from action trials for participant CL and a control group (Walsh, E., et al., 2010). The results show the spectral power (dB) in the motor rhythm range (8–24 Hz) around the time of conscious intention (–340 to 0 and 0 to +340 ms relative to mean W judgement). For the pre-W time window, the time, frequency and amplitude of EEG minima are shown as a measure of ERD. For the post-W time window, the time, frequency and amplitude of EEG maxima are shown as a measure of post-movement beta rebound. For the control group data ($N=14$), standard deviation across participants are given. Data for CL do not have an associated measure of variability. The electrodes of interest (channels) are based on a previous study (Walsh, E., et al., 2010). * indicates a value significantly different from the control sample ($p < 0.05$), using the method described by Crawford and Garthwaite (2002).

Trial type	Channel	Pre-W time –340 to 0 ms			Post-W time 0 to +340 ms		
		Time (ms)	Frequency (Hz)	Amplitude (dB)	Time (ms)	Frequency (Hz)	Amplitude (dB)
CL: right hand							
Action-only	C3	–190	13.3	–1.2	334	12.8	2.0
Action trials (act-or-inhibit blocks)		–100	21.9	–2.6	340	9.1	2.3
CL: phantom left hand							
Action-only	C4	–70	24.4	–1.9	340	15.3	2.0
Action trials (act-or-inhibit blocks)		–52	8.8	–2.8	340	12.3	4.1
Control group: right hand							
Action-only	C3	–220 (126)	14.1 (3.5)	–2.5 (1.2)	245 (93)	13.7 (3.3)	2.5 (1.1)
Action trials (act-or-inhibit blocks)		–184 (100)	15.2 (6.0)	–2.3 (1.6)	293 (65)	15.5 (4.5)	2.5 (1.1)

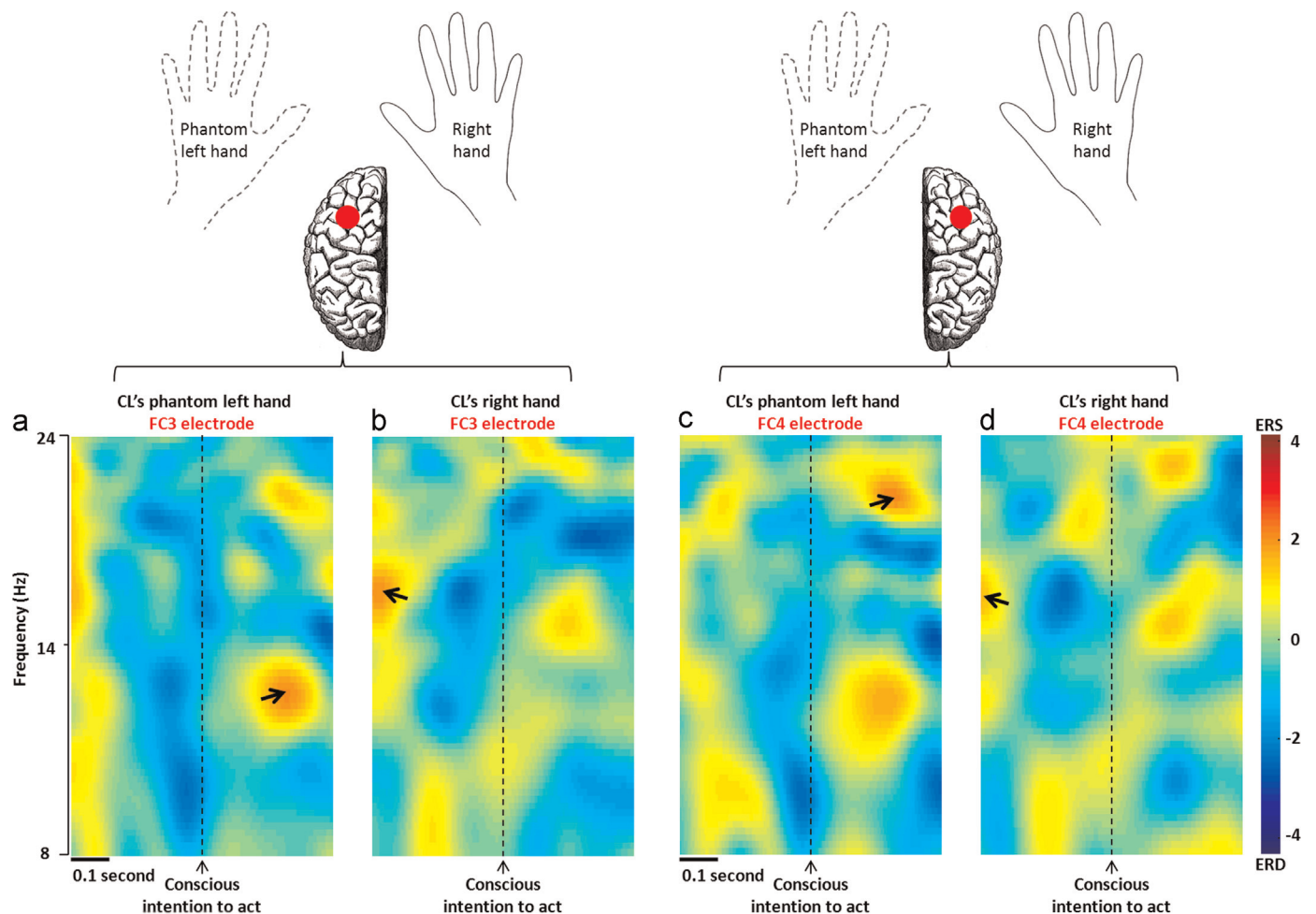


Fig. 3. Spectral power in the mu- and beta-bands around the time of conscious intention on inhibition trials from the act-or-inhibit blocks. The data are shown time-locked to the average time of conscious intention to act (W judgement, dashed vertical line). Data are shown for inhibition of phantom left hand actions (a, c) and right hand actions (b, d). Based on previous results, the FC3 (a, b) and FC4 (c, d) electrodes were analysed, for movements of both the right and left hand (Walsh, E., et al., 2010). Blue colour indicates event-related desynchronisation (ERD), and red indicates event-related synchronisation (ERS). Note ERS occurs around the time of W judgement (arrows indicate peak ERS values: see text). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and with the “phantom” left hand.

We also investigated the post-movement rebound phenomenon. Post-movement rebound is often attributed to the proprioceptive feedback generated by a voluntary movement. In that case, CL’s phantom hand should show a reduced post-movement rebound. Our data did not support this hypothesis, as a clear beta rebound can be seen (Fig. 2b and d). Beta rebound has also been

noted after withholding of a motor response, though in this case it is weaker and shorter than after termination of movement (Solis-Escalante et al., 2012). However, since our finding of beta-rebound within normal range is a null result, further research is necessary to understand the origin of the post-movement rebound. Finally, in some blocks, we asked CL to choose to inhibit some actions at the last possible moment. We had previously shown that such

Table 2

EEG results from inhibit trials in act-or-inhibit blocks. The time (ms), frequency (Hz) and amplitude (dB) of a spectral peak are shown. The time window is -340 to $+340$ ms relative to W judgement, and the frequency window is 8 to 24 Hz. The electrodes of interest (channels) are based on a previous study (Walsh, E., et al., 2010). Data for participant CL and the control group ($N=14$; mean and standard deviation across individuals) are shown. * indicates a value significantly different from the control sample ($p < 0.05$), using the method described by Crawford and Garthwaite (2002).

W time \pm 340 ms				
	Channel	Time (ms)	Frequency (Hz)	Amplitude (dB)
CL's right hand	FC3	-324	16.1	2.0
CL's right hand	FC4	-336	15.9	1.6
CL's phantom left hand	FC3	224	12.3	2.1
CL's phantom left hand	FC4	214	20.7	2.1
Control group, right hand	FC3	165 (171)	15.0 (5.0)	2.0 (0.8)
Control group, right hand	FC4	45 (233)	16.3 (4.8)	2.0 (0.9)

intentional inhibition of voluntary action is associated with a transient increase in EEG power (ERS) in the low-beta band. Again, CL's performance was within normal limits, both for the physically-present right hand, and for the "phantom" left hand, and the inhibition-related ERS was clearly visible in her data.

One previous study has investigated the neural basis of action control in phantom limbs following amputation. Raffin et al. (2012) investigated the brain networks associated with instructed sequences of finger-thumb opposition movements. When patients were instructed to execute these movements with the phantom hand, activation of sensorimotor cortical areas was found using fMRI. Our pre-movement ERD data are broadly consistent with these findings (Fig. 3a and c). Interestingly, merely imagining making such movements with the phantom hand did not activate the sensorimotor cortex (Raffin et al., 2012), suggesting a dissociation between imagining and executing movements of a phantom limb.

The ability to form and inhibit intentions is the basis of human voluntary control, and also plays a fundamental role in the social and moral responsibility. Intentional action and intentional inhibition of action involve specific brain processes within the motor system, and also specific conscious experiences (Brass and Haggard, 2007; Fried et al., 1991; Ridderinkhof et al., 2014). Our data suggest that these processes may function in the cortex even when the body does not have the effectors for the intended action. Our EEG measures were consistent with a full range of intentional control over a phantom limb being possible. Importantly, CL showed classic EEG signatures of both the positive volition required to initiate action, and of the negative volition required to inhibit an action that is about to be performed.

The results obtained with CL's phantom left hand have several important implications for current discussions of volition. First, they point to volition being a purely central phenomenon, independent of actual motor behaviour. We found that CL's attempts at intentional control over the phantom left hand were associated with specific neural events, which were time-locked to a conscious experience of intention. Since she had never had any experience of moving a left hand, and since there was no detectable movement in any effector during these attempts, we suggest that these neural events are entirely central, rather than peripheral. Our result therefore supports the view that voluntary action is a distinct process of the motor areas of the cerebral cortex, and that this process produces a characteristic conscious experience of volition.

Importantly, the location of our EEG activations suggests that intentional inhibition of action is also an identifiable process within the frontal lobes.

Strongly reconstructivist accounts of volition might struggle to explain these results. Reconstructive theories suggest that the experience of volition is based largely on post-hoc inferences derived from the observable results of our intentional actions, such as the body movements and outcomes they produce (Wegner, 2002). In the case of CL's left arm, however, there was no physical output in either action or inhibition trials. Nevertheless, a conscious experience of intention was present in each case. More interestingly, the neural activities were quite different when CL prepared and then "executed" a voluntary movement of the phantom left hand, and when she prepared but then inhibited the voluntary movement. These neural activities further corresponded to those of a control group, both for intentional action, and for intentional inhibition. In the control group, intentional actions and intentional inhibitions differ because physical body movement is present in the former but not the latter case. The presence, or even the expectation, of this physical event could potentially explain differences in neural activity in the control group. However, CL's attempts to move her phantom left hand, and her attempts to inhibit its movement, both appear to be purely central events, without any identifiable bodily motoric expression. Therefore, the characteristic neural signatures of action and inhibition need not be linked to the presence or absence of a physical hand movement. Instead, they may reflect purely central mechanisms of generating, and of inhibiting, the voluntary motor command.

Our inhibition-related ERS result may be particularly important. Intentional inhibition is difficult to study experimentally, due to the lack of behavioural markers (Filevich et al., 2012). Intentional inhibition was hypothesised to reflect active inhibition of a prepared action, occurring entirely within the cerebral motor system. However, previous results (Walsh, E., et al., 2010) could potentially be explained if participants made a slight anticipatory muscle contraction without pressing the response key (Leuthold et al., 1996), and then "inhibited" by aborting this incipient muscle contraction. Indeed, cessation of muscle activity is known to produce a post-movement beta rebound (Pfurtscheller, 1981; Salmelin and Hari, 1994). Therefore, cessation of partial activity could potentially explain previous reports of inhibition-related ERS. However, CL's data seem to rule out this possibility of a peripheral origin of inhibition-related ERS, because the neural activity was present when CL inhibited actions prepared with the phantom left hand, just as much as when she inhibited actions prepared with the physical right hand.

CL therefore, in line with her subjective experiences, appears to have full volitional control over her phantom left hand, using a neural mechanism comparable to volitional control of her physical right hand. How might volitional control arise in the case of a phantom hand? We see two possibilities. First, key elements of volition might not be experience-dependant. The central generators for voluntary motor commands, and for inhibiting voluntary motor commands, may exist even when the peripheral motor apparatus does not develop. Importantly, these volitional activities must support a conscious experience of intention, since we detected them by temporally aligning them with conscious intention in a Libet paradigm. Despite never having consummated a voluntary motor command for a left hand, CL's right hemisphere generated both volition-related activity and volition-related experience. On one view, the core cortical mechanisms of volition might be innate. CL may then not have needed to *learn* the volitional control of the phantom left hand through experiences of successful voluntary motor control. However, we cannot exclude other possible alternative explanations, including interhemispheric transfer.

A second possibility exists. CL might have acquired volitional control over the phantom left hand by a process of generalisation or transfer from other motor representations. For example, as the voluntary control of her right hand developed during childhood, an interhemispheric coupling may have transferred the plastic changes associated with acquisition of voluntary control from the left hemisphere, controlling the contralateral physical right hand, to the right hemisphere, controlling the phantom left hand. Importantly, we found that pre-movement ERD before actions of the phantom left hand was stronger in the contralateral right hemisphere than in the ipsilateral left hemisphere (Fig. 2c and d). Volition-related processes in the right hemisphere were not merely weak echoes of a stronger process in the hemisphere contralateral to the intact hand. Thus, any interhemispheric transfer of volition must be sufficient to establish an *independent* voluntary control mechanism in the hemisphere controlling the phantom limb. The transfer of volition account implies that one voluntary control module is sufficient to provide “neural scaffolding” for other voluntary control modules, and that actual peripheral movement and feedback are not necessary. In this case, the voluntary control of the right hand by the left hemisphere could provide sufficient neural organisation to underpin volitional control of the phantom left hand by the right hemisphere, in the absence of any left hand movement or sensation.

The interhemispheric transfer view makes the further interesting prediction that the sense of voluntary control over a congenital phantom should increase during development, as children progressively develop voluntary control over other body parts. We are not aware of any autobiographical memory study of the age at which phantom sensations appear. This seems an interesting area for future research. However, phantom sensations are rather rare in congenital amelia (Brugger, 2012). Of course, innateness and total interhemispheric transfer of volition are extreme positions. A more plausible alternative may involve a combination of an innately-specified neural substrate in the cortical motor circuits, supplemented by a developmental maturation of that pathway, guided by experience transmitted through other cortical representations. CL's volition with respect to her phantom left hand could reflect a combination of a preserved, possibly innate, cortical motor map (Longo et al., 2012), and a generalisation of voluntary action mechanisms in the left hemisphere that control her intact right hand, to the right hemisphere representing the phantom left hand.

We acknowledge a number of limitations of this study. Our investigation is confined to only one case of voluntary control over a phantom limb. Comparison between the phantom left hand and the intact right hand is based on individual averages, and lacks any associated measure of variability or error term. Therefore, for example, our finding of stronger pre-movement ERD contralateral to the phantom left hand, rather than ipsilateral, was not evaluated statistically. Observed differences in ERD/ERS frequencies in alpha and beta bands (Figs. 2 and 3) might reflect distinct processes (Buchholz et al., 2001), motor system reorganisation (Walsh, L.D., et al., 2010), or shifts in locations of cortical movement representations following from motor commands being sent to a physically absent phantom hand (Giraux et al., 2001; Reilly et al., 2006). Thus, differences in ERD/ERS frequencies, and their timing, should be interpreted with caution. Caution is also required when interpreting the relation between the time of conscious intention and specific brain activities. Self-generated actions can be triggered by any of a number of reasons, including habit (e.g., grooming behaviours), prospective management of future sensations (e.g., drinking water before you begin to feel thirsty), exploratory foraging, and improvisation (Hebb, 2005). The brain mechanisms involved in these different situations are likely to be diverse (Charles et al., 2014; Schurger et al., 2012).

We did not directly compare our EEG measures for CL's “executed” and “inhibited” left hand movements. Indeed, the inferential value of doing so could be questioned, since the neural measures themselves were defined by similar contrasts in our previous study. However, for the phantom left hand, ERD prior to movement followed by beta rebound was clearly visible (Fig. 2b and d). ERD followed by ERS was clearly visible on inhibition trials (Fig. 3a and c). Arguably, the inhibition-related ERS could be interpreted as a form of postmovement beta rebound. Beta rebound is thought to reflect the deactivation or “idling” of motor cortical networks (Neuper and Pfurtscheller, 2001; Pfurtscheller and Neuper, 2001), or the resetting of previously activated motor networks (Pfurtscheller et al., 2003), and is also present after motor imagery and median nerve stimulation (Neuper and Pfurtscheller, 2001). However, beta rebound lasts for approximately 2 s, with the peak in its oscillatory power occurring approximately 1 s after the end of motor tasks (Pfurtscheller et al., 2005). The beta synchronisation observed on inhibition trials for CL's phantom left hand was relatively short-lived, lasting approximately 150 ms (see arrowed ERS peaks in Fig. 3a and c). The onset, duration and frequency band range of CL's inhibition-related ERS thus visibly differs from postmovement beta rebound. In addition, we have reported largely null results: CL's neurocognitive mechanisms of volition fell within the range of 14 control participants. Interpreting null results is always problematic. The scientific interest of this study lies in the fact that apparently normal brain mechanisms of volition may exist despite congenital absence of the associated body part.

In conclusion, a single participant with congenital absence of the left hand and arm showed EEG activities during voluntary action and inhibition that resembled those of a healthy control group. This suggests that the neurocognitive mechanisms underlying voluntary action and voluntary inhibition may be central, and do not require either efference to the target body part, or efference from it. The ability to command voluntary actions, to inhibit them, and to experience conscious volition, all appear to be intrinsic to the brain's cortical motor networks. Moreover, these abilities can develop without direct sensorimotor experience, perhaps through transfer from cortical events linked to other voluntary actions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.neuropsychologia.2015.06.032>.

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