



Research report

Subliminal modulation of voluntary action experience: A neuropsychological investigation

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ABSTRACT

Human voluntary actions are often associated with a distinctive subjective experience termed ‘sense of agency’. This experience could be a reconstructive inference triggered by monitoring one’s actions and their outcomes, or a read-out of brain processes related to action preparation, or some hybrid of these. Participants pressed a key with the right index finger at a time of their own choice, while viewing a rotating clock. Occasionally they received a mild shock on the same finger. They were instructed to press the key as quickly as possible if they felt a shock. On some trials, trains of subliminal shocks were also delivered, to investigate whether such subliminal cues could influence the initiation of voluntary actions, or the subjective experience of such actions. Participants’ keypress were always followed by a tone 250 ms later. At the end of each trial they reported the time of the keypress using the rotating clock display. Shifts in the perceived time of the action towards the following tone, compared to a baseline condition containing only a keypress but no tone, were taken as implicit measures of sense of agency. The subliminal shock train enhanced this “action binding” effect in healthy participants, relative to trials without such shocks. This difference could not be attributed to retrospective inference, since the perceptual events were identical in both trial types. Further, we tested the same paradigm in a patient with anarchic hand syndrome (AHS). Subliminal shocks again enhanced our measure of sense of agency in the unaffected hand, but had a reversed effect on the ‘anarchic’ hand. These findings suggest an interaction between internal volitional signals and external cues afforded by the external environment. Damage to the neural pathways that mediate interactions between internal states and the outside world may explain some of the clinical signs of AHS.

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1. Introduction

Voluntary actions can be functionally defined by two key properties: they are internally-generated, as opposed to triggered by external stimuli, and they are often goal-directed (Passingham, Bengtsson, & Lau, 2010). In addition, they are associated with two specific subjective experiences: an experience of volition, and an experience of agency. The experience of volition refers to pre-movement states and events such as desiring, intending, trying and initiating, while “sense of agency” refers to the experience that one’s voluntary actions cause outcomes in the external world.

On one view, the experiences of volition and agency are post-hoc inferences, triggered by monitoring one’s actions and their outcomes. In this case, preparatory brain events that precede action should not influence this experience (Wegner & Wheatley, 1999), although a “prior conscious thought” about acting may be necessary to trigger such inferences (Wegner, 2003). Alternatively, experience of agency could depend on a readout of brain processes in frontal (Fried, Mukamel, & Kreiman, 2011) and/or parietal areas (Desmurget et al., 2009) that precede voluntary action. Importantly, these two views make different predictions about how external stimuli might influence the experience of agency: If experience of agency is merely a reconstructive inference, interventions which influence brain processes preceding a voluntary action should have no influence on one’s sense of agency, unless those interventions generate some perceptual event which can figure in the inference. On the other hand, if experience of agency depends on internal precursor signals that drive voluntary action, any intervention that influences these signals may also affect experience of agency, whether the intervention is consciously perceived or not.

In neuroscience, voluntary actions are often linked to a medial frontal pathway associated with internally-generated movement, as opposed to a parietal-lateral frontal pathway for reacting to external stimuli (Passingham et al., 2010). Human experiments drawing on this tradition usually require participants to perform actions at a time of their own free choice, though this approach has been criticised for lack of ecological validity (Schüür & Haggard, 2011). Intervening on volition in such paradigms is methodologically difficult, because the experimenter cannot know when the participant will act. Further, any experimental intervention on precursor processes should preserve the ‘internally-generated’ aspect of voluntary action, rather than switching to a reactive mode of responding. Subliminal priming offers one potential method for studying volition. For example, subliminal visual primes have been used previously to manipulate the sense of agency by increasing the fluency of action selection processes (Chambon & Haggard, 2012). Priming can “nudge” the brain towards selecting one action rather than another (Eimer & Schlaghecken, 1998). Compatible priming also increases sense of agency, as if the prime had made the action more strongly intentional (Wenke, Fleming, & Haggard, 2010). However, subliminal visual priming paradigms require a precise temporal relation between prime and a supraliminal ‘go’ signal. They therefore involve externally-triggered rather

than internally-generated voluntary actions. Here, we used a novel design with subliminal electrocutaneous stimuli as a probe to influence brain processes preceding a voluntary action. We investigated how experimental manipulation of putative precursor signals can change the experience of agency in healthy adults and in an individual with ‘anarchic hand syndrome’ (AHS).

Healthy participants were asked to make voluntary key presses with their right index finger at a time of their own choosing. They occasionally received a mild electrocutaneous shocks on the same finger, and were instructed to press the key in reaction to such shocks as quickly as possible. This instruction aimed to set up a facilitatory association between shock and action. We reasoned that establishing a stimulus-response association between supraliminal shocks and actions would make the shock meaningful for action, and therefore more likely to prime action processing. Both voluntary and reactive keypresses were followed by a beep 250 ms later. Participants judged the time of the keypress using a rotating clock display. A shift in the perceived time of the action towards the following tone, compared to a baseline condition containing only a keypress but no tone, has been proposed as an implicit marker of agency (Haggard, Clark, & Kalogeras, 2002). Crucially, the shift in action awareness towards the subsequent tone appears to reflect volitional signals, since it is absent for involuntary movements (Cravo, Claessens, & Baldo, 2009), and increases with the amount of information that participants must generate internally (Barlas & Obhi, 2013).

Further, we delivered a train of subliminal shocks in some trials selected at random. We reasoned that the subliminal shocks might influence brain processes preceding voluntary action, because of the established association between shock and keypress. Because subliminal trials contained the same perceptual events as voluntary trials without subliminal shocks, any inferential processes should operate identically on both trial types. However, if sense of agency depends on a readout of brain processes that precede voluntary actions, and if these processes can be influenced by subliminal stimuli, we might expect subliminal shock trains to affect sense of agency, as measured by intentional binding. Since the classical effect of subliminal priming is to facilitate voluntary actions, and since we included other supraliminal shock trials specifically involving such a link, we predicted stronger binding for voluntary actions on trials with subliminal shocks, compared to trials without subliminal shocks.

We also tested the same paradigm with a single patient, TP, with AHS. AHS is a rare neurological disorder characterized by abnormal voluntary control over a limb (Kranick & Hallett, 2013). Three main variants of AHS have been distinguished in the neuropsychological literature: frontal, callosal and posterior. The most common pathologies underlying AHS is corticobasal syndrome, stroke and Creutzfeldt–Jakob disease (Hassan & Josephs, 2016). Patients often describe their affected arm as ‘alien’ or ‘having a mind of its own’. The movements are often goal-directed and triggered by external stimuli, but the patients are not able to control or stop them (Moore & Fletcher, 2012). Cognitive neuropsychologists have generally interpreted signs and symptoms of AHS using ‘object affordance theory’. Affordances are properties of objects in the

environment which promote or invite action (Gibson, 1986; McBride, Sumner, Jackson, Bajaj, & Husain, 2013). In healthy individuals, excessive reactivity to external stimuli is usually suppressed by endogenous control mechanisms within medial frontal cortex (Sumner & Husain, 2008). Accordingly, impairment of these control mechanisms in AHS lead to patients becoming excessively responsive to external stimuli, even when they do not intend or wish to respond to them (McBride et al., 2013; Riddoch, Edwards, Humphreys, West, & Heafield, 1998). In particular, the patients with AHS, including patient TP studied here, often involuntarily grasp external objects.

Cognitive neuropsychological accounts emphasise a form of “negative volition”, in which the lesioned cortex would have the normal role of ensuring tonic voluntary suppression of latent responses to environmental affordances. No studies, to our knowledge, have investigated how the damage underlying AHS influences the processes that generate voluntary action itself. One hypothesis, consistent with neuronal (Fried et al., 2011) and areal (Filevich, Kühn, & Haggard, 2012) evidence of intermingled action-promoting and action-suppressing representations in medial frontal cortex, predicts the damage that leads to AHS should also affect the generation, and experience of voluntary action.

2. Material and methods

2.1. Participants

47 healthy volunteers, aged 18–35 years of age (14 males, mean age = 22.4 years, SD = 3.9), were recruited from the Institute of Cognitive Neuroscience subject data pool. All participants were right handed, had normal or corrected to normal vision, had no history or family history of seizure, epilepsy or any neurologic or psychiatric disorder. Participants confirmed that they had not participated in any brain stimulation experiment in the last 48 h, nor had consumed alcohol in the last 24 h. Participants were paid an institution-approved amount for participating in the experiment. Experimental design and procedure were approved by the UCL research ethics committee, and followed the principles of the Declaration of Helsinki.

TP is a 54 year old, right handed woman. She is a former secretary with 11 years of education. Twenty-three months before the testing session, she had a ruptured aneurysm of the right anterior cerebral artery, resulting in subarachnoid haemorrhage, involving the genu and trunk of the corpus callosum (CC). After embolization, she had a vasospasm of the right middle cerebral artery. The most recent magnetic resonance imaging (MRI) (14 months before the testing session) showed damage in the CC (genu, body and splenium) and in the right anterior frontal and right basal frontal cortex, involving the anterior and middle cingulate gyrus (Fig. 1 & Table 1).

A complete neuropsychological examination (Table 2) at the time of the testing session showed residual attentional deficits (in the subtests “alertness”, “acoustical vigilance” and “divided attention” of the Italian version of the Test of Attentional Performance: Zimmerman & Fimm, 1992; Zoccolotti, Pizzamiglio, Pittau, & Galati, 1994), mild

impairments in perspective memory (Rivermead Behavioural Memory Test: Wilson, Cockburn, & Baddeley, 1985), abstract classification abilities (Wisconsin Card Sorting Test: Heaton, Chelune, Talley, Kay, & Curtiss, 2000) and executive functions (Tower of London: Culbertson & Zillmer, 2005; Phonemic and Semantic Verbal Fluency Test: Spinnler & Tognoni, 1987). No additional impairments were found in working memory (sub-test “Working Memory” of the Italian version of the Test of Attentional Performance: Zimmerman & Fimm, 1992; Zoccolotti et al., 1994), long-term and short-term verbal memory (Buschke–Fuld Test: Buschke & Fuld, 1974; Spinnler & Tognoni, 1987, Digit Span: Orsini et al., 1987) and spatial memory (Rey–Osterrieth Complex Figure Test: Caffarra, Vezzadini, Dieci, Zonato, & Venneri, 2014; Osterrieth, 1944, Corsi-Block tapping test: Spinnler & Tognoni, 1987), or logical and reasoning abilities (Raven’s Progressive Matrices: Spinnler & Tognoni, 1987). In addition, TP showed no sign of apraxia with either limbs or hands (Test of limb apraxia: De Renzi, Motti, & Nichelli, 1980; De Renzi, Pieczuro, & Vignolo, 1968). She had mild paresis with hypotonia of her left upper limb and hand. Both superficial and deep sensitivity were normal.

TP complained of her left hand behaving in an uncontrolled manner. For example, she reported that her left hand threw a towel into the bathtub full of water or that she blew her nose with a napkin that she held in her left hand, instead of using the handkerchief in her right hand. The episodes of uncontrolled behaviour of her left hand occurred on a daily basis in the first few months after the lesion and were characterized by groping movements, grasping, subsequent inability to release the grip, utilization behaviour and the persistent feeling of unresponsiveness of the left hand. At that time, TP also had frequent episodes of mirror movements (i.e., the anarchic left hand reproduced the movement of the unaffected right hand), and also reported the inability to coordinate simultaneous different movements of the two hands. At the time of the testing session, the frequency of the episodes of uncontrolled behaviour was reduced. Episodes of grasping behaviour and subsequent inability to release the grip occurred almost once a week. TP complained of the persistent feeling of unresponsiveness of her left hand and reported her attitude to restrain the actions of her left hand, by using the other hand to prevent it from moving. Despite the lack of voluntary control of her left hand, TP never denied ownership of the hand.

All experimental procedures were exactly the same in TP and healthy participants. The only difference is that all the data were collected from the right hand of the healthy participants, while for TP data was collected from both the right (healthy) hand and the left (affected) hand, in separate sessions.

2.2. Experimental procedure

After filling the consent form, the general experimental procedure was explained for the participants. Non-painful electrocutaneous shocks were delivered from a programmable Digitimer DS5 Bipolar Constant Current Stimulator (Digitimer Ltd., Welwyn Garden City, UK). Cloth electrodes (Biosense Medical, Chelmsford, UK) were placed on the proximal and medial phalanx of the right index finger and were connected

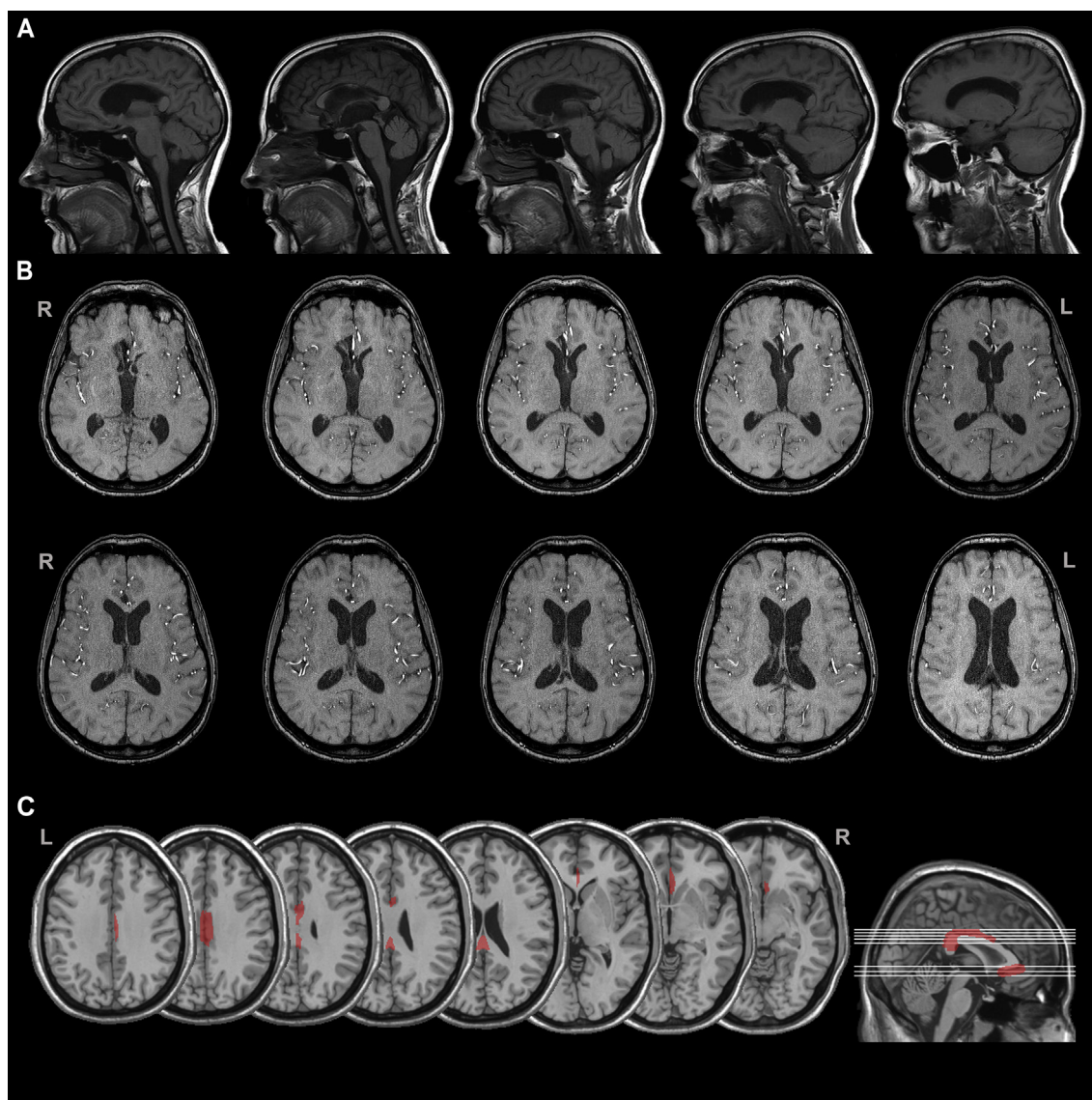


Fig. 1 – MRI scans of the patient TP in sagittal (A) and horizontal (B) view. C. Patient's lesion reconstruction. Mapping of the brain lesions was performed by MRICro (Rorden & Brett, 2000). Lesions, as documented by the most recent MRI, were traced on the T1-weighted template MRI scan from the Montreal Neurological Institute provided with the MRICro software.

to the anode and cathode cables, respectively. Intensity of the shocks depended on the trial type (see later). The duration of each shock was set at 10 ms.

The behavioural task started after setting up the electrodes. Each experimental session consisted of three tasks: First, a detection task was used to detect the lowest threshold level at which participants were able to detect the shocks. Then, supra- and subliminal levels of shock were calculated from the threshold measure and a signal detection task was administered to confirm perception of the shock stimuli. Participants who did not pass the signal detection task were excused and did not proceed to the next step. Finally, participants performed the 'intentional binding' task, which has been widely used as a proxy measure of sense of agency (for a review, see Moore & Obhi, 2012).

2.3. Threshold detection task

An ascending staircase approach was used to detect the lowest levels at which participants were able to detect the shock (Moore, Ruge, Wenke, Rothwell, & Haggard, 2010). Shocks started at .1 mA and increased in steps of .1 mA until the shock was detected, and then decreased in steps of .05 mA until the shock was missed, and then increased again in steps of .01 to find the detection threshold. A tone was played at the time of each shock and participants were asked to report if they felt a shock at the time of the tone or not. In this and all the later tasks, participants were instructed to report feeling a shock when they felt *any kind* of stimulus, not simply a *painful* shock. The level for supraliminal shock stimuli was set at 130% of the threshold level. The subliminal level was determined by reducing one step (.01 mA) from the threshold (e.g.,

Table 1 – For each brain region, the number (first column) and the percentage (second column) of lesioned voxels are shown. Quantitative estimate of the damaged brain regions and white matter areas was performed by superimposing the traced lesion reconstruction on the “automated anatomical labelling” template (AAL) (Rorden & Brett, 2000), and on the John Hopkins University (JHU) white matter labels atlas (Rorden, Karnath, & Bonilha, 2007).

Cortical areas	Voxels	Area %
Olfactory_R	347	15%
Frontal_Mid_Orb_R	13	0%
Cingulum_Ant_L	86	1%
Cingulum_Ant_R	589	6%
Cingulum_Mid_L	234	2%
Cingulum_Mid_R	1050	6%
Cingulum_Post_L	58	2%
Cingulum_Post_R	35	1%
White matter areas	Voxels	Area %
Unclassified	2281	0%
Genu of corpus callosum	111	1%
Body of corpus callosum	664	5%
Splenium of corpus callosum	714	6%

if the detection threshold was .45 mA, the subliminal level would be .44 mA). This strategy was chosen to ensure that subliminal shocks had sufficient energy to influence brain processes, while remaining imperceptible (see below).

2.4. Signal detection task

The estimated supra- and subliminal shock levels were then validated in a signal detection task. Each signal detection task consisted of four types of trials in a randomised order: 20 subliminal shock trials, 20 subliminal catch trials (with no shock), 20 supraliminal shock trials and 20 supraliminal catch trials (with no shock). In each trial participants heard two tones, 5 sec apart. They received a supraliminal shock at a random time between those two tones in supraliminal shock trials. No shock was delivered in catch trials. In subliminal trials, a train of subliminal shocks were delivered every 1 sec starting from the first tone and ending with the second tone. At the end of each trial participants were asked to report if they felt any shock between the first and the second tone or not. At the end of the task, participants' responses were used to estimate the sensitivity index (d') for the supra- and subliminal shocks. To proceed to the next step, participants were required to obtain a d' value within the range of .5–1.5 for subliminal shocks and a $d' \geq 3$ for the supraliminal shocks. The relatively high sensitivity index for subliminal shocks means that participants could sometimes detect the shock. We wished to ensure that the subliminal shocks were strong enough to influence brain processes. Those subliminal shocks that were detected by participants during the main task were discarded (see Section 2.5). If their d' did not match this criteria, the threshold detection task was repeated to find a new threshold followed by a signal detection task. If the desired d' was not achieved after four attempts, participant was excused and did not proceed to the intentional binding task.

2.5. Intentional binding task

We used intentional binding paradigm as an implicit measure of agency. The task was based on previous studies (Haggard et al., 2002), and was programmed in LabVIEW 2012 (Austin, Texas). Participants viewed a clock hand rotating on a computer screen, located 60 cm in front of the participants in a quiet room. The initial clock position was random. Each full rotation lasted 2560 ms. Participants made voluntary keypress by pressing the enter key with their right index finger. Participants chose for themselves when to make the voluntary actions. After each key press, the clock hand stopped at a random location, participants made a time judgement according to condition (see later). Each experimental session consisted of two conditions, presented in separate blocks. At the beginning of each block, brief instructions for the relevant condition were displayed on the screen. In the *baseline* condition, participants had to press the enter key at a time of their own free choice. The clock hand stopped after 1500–2500 ms (at random), and participants then judged the clock hand position at the time of their keypress. In this condition, participant's actions produced no sensory outcome and they received no shock. In the *agency* condition, participants were again asked to press the key at a time of their own free choice. However, this time each keypress produced a pure tone (1000 Hz, 100 ms duration) after 250 ms and they sometimes received a mild shock on their right index finger before pressing the key. At the end of each trial, participants made two subjective reports. First, they reported the clock hand position at the time of their keypress. Second, they reported whether they had felt a shock or not. Each block in the agency condition consisted of two types of trials in a randomised order: in two thirds of the trials a single supraliminal shock happened at a random time, drawn from an exponential distribution (min = 1 sec, max = 10 sec, mean = 5 sec) (Fig. 2A and B). In the other one third, a 1 Hz train of subliminal shocks occurred starting from a random time within 500 ms from the beginning of the trial and continuing for 10 sec (Fig. 2C). The train ensures that any keypress occurs within 1 sec of a shock. In all trials of the agency condition, participants were asked to press the enter key whenever they felt like but to press the key ‘as quickly as possible’ if they felt a shock. There were two possible outcomes in trials with a single supraliminal shock: either participants waited long enough, received the supraliminal shock and reacted (Fig. 2B), or they voluntarily pressed the key before the occurrence of the supraliminal shock, in which case the supraliminal shock was cancelled (Fig. 2A). The former trials were categorised as ‘reactive’ trials, if participants accordingly reported feeling the shock, and the later trials were categorised as ‘voluntary’ trials, if participants accordingly reported not feeling a shock.

Trials containing a train of subliminal shocks were also divided into two categories. First, if the participant reported perceiving any shock, the trial was discarded. If the participant did not report perceiving any shock, the trial was categorized as a ‘primed-voluntary’ trial.

The baseline condition was tested in two separate blocks of 15 trials each, at the beginning and end of the experiment. The agency condition was tested in four blocks of 40 trials each between the two baseline blocks.

Table 2 – Neuropsychological assessment. Asterisks denote a pathological performance. Patient's scores are reported in the left column, while cut-off scores are reported in the right column. SS: Standard Score. CS: Correct Score. T: T-value. ScS: Screening Score. ES: Equivalent Score. The ES ranges from 0 to 4, with 0 = pathological performance, 1 = borderline performance, and 2–4 = normal performance.

	Standard Score (SS)/Correct Score (CS)/T-value (T)/ Screening Score (ScS)	Cut-off/ Equivalent Score (ES)
Attention		
Test of Attentional Performance		
Subtest acoustical vigilance:		
- 0–5 min	T = 27*	T = 40
- 5–10 min	T < 20*	T = 40
Subtest alertness:		
- Without warning	T = 20*	T = 40
- With warning	T = 20*	T = 40
Subtest divided attention	T = 32*	T = 40
Executive Functions		
Tower of London		
- Total move score	SS = 84	SS = 70
- Total correct score	SS = 88	SS = 70
- Total rule violation	SS ≤ 60*	SS = 70
- Total time violation	SS = 92	SS = 70
- Total initiation time	SS = 98	SS = 70
- Total execution time	SS = 88	SS = 70
- Total problem-solving time	SS = 86	SS = 70
Wisconsin Card Sorting Test	SS = 81*	SS = 90
Verbal fluency test		
- Phonemic	CS = 25	ES = 2
- Semantic	CS = 52	ES = 4
Working Memory		
Test of Attentional Performance		
Subtest Working Memory	T = 40	T = 40
Memory		
Digit span	CS = 5	ES = 4
Buschke Fuld		
- Long Term Memory score	CS = 104	ES = 3
- Consistent Long Term Retrieval	CS = 83	ES = 4
- Delayed recall	CS = 7.75	ES = 3
Corsi-Block tapping test	CS = 4.75	ES = 4
Rey–Osterrieth Complex Figure Test	CS = 14.25	ES = 3
Rivermead Behavioural Memory Test	ScS = 8*	ScS = 9
Logical and reasoning abilities		
Raven's Progressive Matrices	CS = 30.25	ES = 4
Apraxia		
Test of limb apraxia		
- Right hand	Total score = 70	53
- Left hand	Total score = 70	53

2.6. Data analysis

In signal detection task the proportion of hits, correct rejections, misses and false alarms were calculated separately for supra- and subliminal shocks. These measures were then used to compute the sensitivity index (d').

In the intentional binding task, judgment error was defined as the difference between the judged clock hand position and the actual time of the keypress on each trial. A positive judgement error indicated a perceptual delay; a negative judgement error an anticipation. The mean and SD of the judgement errors across trials were then measured for each trial type. Action

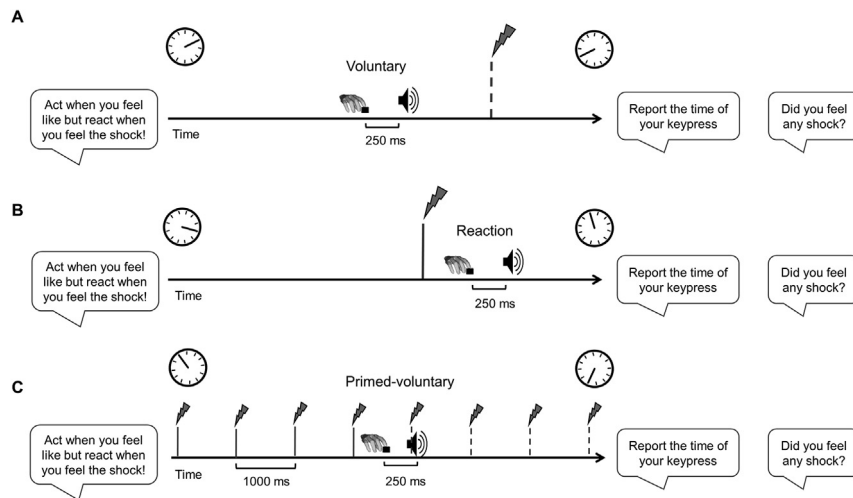


Fig. 2 – Timeline of an experimental trial. Participants were instructed to look at a rotating clock and to press a key at a time of their free choice or to react as soon as possible if they felt a shock. In voluntary trials participants pressed the key before occurrence of a supraliminal shock (large shock sign) (A). In reactive trials they pressed the key immediately after feeling the supraliminal shock (the supraliminal shock happened at a random time drawn from an exponential distribution) (B). In primed-voluntary trials a subliminal shock (small shock sign) was delivered every 1 sec till participants pressed the key (C). Each keypress was followed by a beep 250 ms later. At the end of each trial participants reported the time of their keypress and whether they received a shock. Dashed lines show hypothetical time of a shock.

binding was defined as the shift of reported time of action towards its outcome, and was calculated by subtracting each participant's mean judgement error in the baseline condition from that in the agency condition. Thus, perceptual association of an action with a subsequent tone would produce a positive value for action binding. We then used repeated-measures analysis of variance (ANOVA) and paired-samples t-test to compare action binding in voluntary trials with action binding in primed-voluntary trials. Multilevel models were used when comparing trial types with unequal sample size, using the *lme* function in R (R Core Team, Vienna, Austria). The main purpose of having supraliminal shocks was to establish a stimulus-response association between the shock and the action. We reasoned that this makes the shock meaningful for action, and therefore more likely to prime action processing. Finally, a Crawford test (Crawford, Garthwaite, & Porter, 2010) was used to compare TP's action binding scores from the healthy and affected hand with the action binding data in healthy participants.

We additionally checked whether subliminal shocks could influence behaviour, as well as sense of agency. The latency of each keypress from the immediately preceding subliminal shock was measured. These latencies were averaged across all primed-voluntary trials within each participant. We tested the null hypothesis that the action latencies in primed-voluntary trials are from a population with uniform distribution by using a separate Anderson–Darling test for each participant.

3. Results

3.1. Experience of agency in healthy participants

Of the 47 recruited participants, 27 met the d' criteria of the signal detection task and went on to do the intentional

binding task. Four participants did not finish the intentional binding task because their detection threshold was unstable during the task. Therefore, the final sample included 23 participants (16 females, mean age = 22.7, SD = 3.9). The average detection threshold was .5 mA (SD = .18 mA). The average supra- and subliminal shock levels were .64 mA (SD = .23 mA) and .49 mA (SD = .18 mA), respectively. The average d' for subliminal shocks was 1.03 (SD = .24). All participants had a $d' \geq 3$ for supraliminal shocks (Supplementary Table 1). On average, participants perceived 8% (SD = 11%) of the subliminal shocks. Importantly, there was no significant relationship between the frequency of perceiving subliminal shocks and the size of action binding effect ($r = -.21, p = .34$).

To investigate whether influencing precursor signals to a voluntary action with a subliminal probe could be reflected in one's experience of agency, we compared action binding in primed-voluntary trials and voluntary trials. The perceived time of action moved towards its outcome in both primed-voluntary ($M = 32$ ms, SEM = 7.60 ms, one-sample, $t(22) = 4.18, p < .01, 95\% \text{ CI } [16 \text{ } 47]$) and voluntary trials ($M = 18$ ms, SEM = 8.17 ms, one-sample, $t(22) = 2.24, p = .03, 95\% \text{ CI } [1 \text{ } 35]$) (Supplementary Table 2). However, this action binding was significantly stronger on trials with a subliminal shock train than on trials without shocks ($t(22) = 2.61, p = .016, d_z = .54, 95\% \text{ CI } [3 \text{ } 24]$) (Fig. 3A). This suggests that experience of agency towards an action and its effect is associated with precursor brain signals for that action.

Importantly, the effect of subliminal primes on intentional binding was not simply a reduced version of the effect of supraliminal shocks on time estimation. On supraliminal trials, we found that the perceived time of reactions moved away from the outcome tone towards the preceding supraliminal shock stimulus, in a reversal of the intentional binding effect ($M = -68$ ms, SEM = 23 ms, one-sample, $t(22) = -2.90, p < .01, 95\% \text{ CI } [-116 \text{ } -19]$). This reversal of intentional binding for

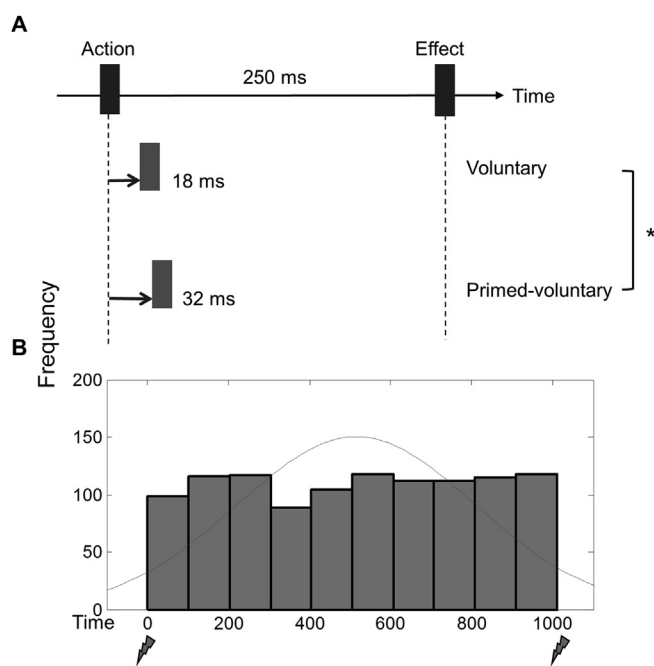


Fig. 3 – Data of healthy participants. A. Action binding in voluntary and primed-voluntary trials. $*p < .05$. B. Time histogram of latency of actions from their preceding subliminal shock (time 0), averaged across all primed-voluntary trials and all participants. Binding effects are drawn to scale and all values are in ms.

responses to a supraliminal stimulus has been reported previously: (Waszak et al., 2005). This finding suggests that the increase in action binding for primed-voluntary compared to voluntary trials could not be merely explained by the presentation of shocks.

Finally, to make sure that unbalanced number of trials is not confounding the results, participants' action binding data in each trial type was weighted by the ratio of number of trials in that condition to total number of trials. The significant difference between the conditions ($t(22) = 2.25, p = .03, d_z = .47, 95\% \text{ CI} [1\ 16]$) suggests that action binding is significantly stronger in trials with a subliminal shock even after controlling for unbalanced number of trials.

If subliminal shocks influence brain processes during action preparation, we might expect to find the effects not only on experience of agency but on some other behavioural measure such as action initiation. We therefore tested the hypothesis that the subliminal shocks influenced the latency of keypresses, by using the Anderson–Darling test to compare keypress latency on primed-voluntary trials to a uniform random distribution. The action latency distribution was significantly non-uniform in seven participants (Supplementary Table 3). The null hypothesis that this many tests being significant could happen by chance alone was examined using a binomial test. By the binomial distribution, the probability of getting seven significant non-uniform action latency distributions in a sample of 23 by chance is $B(.05, 7, 23) = .00009401$ (Fig. 3B). This suggests that subliminal shock has some influence on behaviour. However, the presence and

pattern of this effect differed across participants. While in some participants subliminal shocks facilitated action initiation, in others it delayed the time of the action (Supplementary Fig. 1).

3.2. Experience of agency in an individual with anarchic hand syndrome

TP was tested in two separate sessions, one session for the right (healthy) hand and the other for the left (affected) hand. Detection threshold in the first and second sessions was .65 mA and .84 mA, respectively. d' for subliminal shocks in the first and second sessions was .80 and .68, respectively.

When testing the healthy hand, perceptual time of action moved towards its outcome in both voluntary trials ($M = 58 \text{ ms}, \text{ SEM} = 23 \text{ ms}, \text{ one-sample } t(28) = 2.54, p = .017, 95\% \text{ CI} [11\ 105]$), and primed-voluntary trials ($M = 100 \text{ ms}, \text{ SEM} = 21 \text{ ms}, \text{ one-sample } t(36) = 4.82, p < .01, 95\% \text{ CI} [58\ 142]$) (Fig. 4A). In the second session, when testing the affected hand, actions did not bind to their outcomes in voluntary trials ($M = 35 \text{ ms}, \text{ SEM} = 20 \text{ ms}, \text{ one-sample } t(31) = 1.76, p = .088, 95\% \text{ CI} [-6\ 77]$), or primed-voluntary trials ($M = -45 \text{ ms}, \text{ SEM} = 40 \text{ ms}, \text{ one-sample } t(23) = -1.13, p = .27, 95\% \text{ CI} [-127\ 37]$) (Fig. 4A). Given the unequal number of trials in each condition, factorial repeated-measure ANOVA was performed in a multilevel model with the within subject factors of hand (healthy vs affected) and trial type (voluntary vs primed-voluntary). We found a significant main effect of hand ($X^2(6) = 9.66, p < .01$), but no significant main effect of trial type ($X^2(7) = .31, p = .58$). Importantly, the interaction between hand and trial type was significant ($X^2(8) = 5.80, p = .016$). Post-hoc analysis with Wilcoxon signed-rank test showed that the difference in action binding between the two hands was due to the primed-voluntary trial types ($p = .038$), not the voluntary trials ($p = .84$) (Fig. 4A & Supplementary Table 4).

The time histogram of latency of keypresses from their preceding subliminal shock in primed-voluntary trials is shown for the healthy (Fig. 4B) and the affected (Fig. 4C) hands of TP. Based on the Anderson–Darling test, the distribution of action latencies was not significantly different from a uniform distribution, in the healthy or the affected hand ($p > .1$). This finding, however, should be considered in the face of low number of trials from a single case.

3.3. Experience of agency in TP vs healthy participants

Finally, we tested whether subliminal shock effects on action binding were significantly different in TP and healthy participants, using Crawford test. This method tests whether a single patient's score differs significantly from that in a control group, and also provides a point estimate of the separation between the patient's score and the control group (Crawford et al., 2010). The effect of the subliminal shocks was measured by subtracting each participant's action binding in primed-voluntary trials from voluntary trials. The effect of subliminal shock on experience of agency, as measured by action binding, did not differ significantly between healthy participants and the healthy hand of TP ($t = 1.14, p = .27, Z_{cc} = 1.16$). However, while subliminal shocks enhanced action binding in healthy participants (subliminal shock

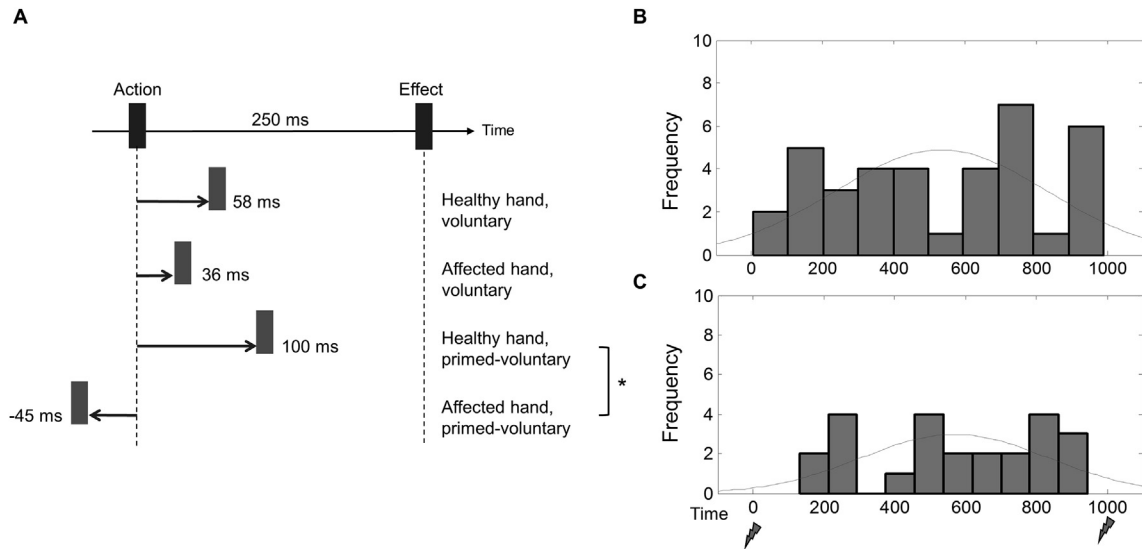


Fig. 4 – Data of TP. A. Action binding in voluntary and primed-voluntary trials for the healthy and the affected hand. * $p < .05$. B&C. Time histogram of latency of actions from their preceding subliminal shock, averaged across all primed-voluntary trials, displayed separately for the healthy (B) and the affected hand (C). Binding effects are drawn to scale and all values are in ms.

effect = 14 ms), they reduced it in the affected hand of TP (subliminal shock effect = -80 ms), hence showing an opposite effect ($t = -3.64$, $p < .01$, $Z_{cc} = -3.72$). Finally, we tested whether strong action binding in the primed-voluntary trials of the healthy hand of TP is also suggestive of an abnormal intentional binding. Crawford tests showed no significant difference between the action binding of the unaffected hand of TP and the healthy participants in the primed-voluntary ($t = 1.85$, $p = .08$, $Z_{cc} = 1.89$) or the voluntary trials ($t = 1.00$, $p = .33$, $Z_{cc} = 1.03$).

4. Discussion

Healthy subjects and an individual with AHS were exposed to subliminal electrocutaneous stimulus during the precursor period before performing internally-generated actions that produced an external outcome. We used an established implicit measure based on time perception to measure sense of agency. The perceived time of an action has been found to shift towards its outcome for voluntary actions but not for involuntary movements (Haggard et al., 2002). Using this ‘intentional binding’ index, we developed a new paradigm to investigate how sense of agency might be influenced by external subliminal stimuli. On one view, such stimuli might influence internal precursors of voluntary action, which in turn influence sense of agency. We investigated whether these subliminal shocks might influence sense of agency by boosting a putative ‘internal volitional signal’. On another view, sense of agency is based only on reconstructive inferences about perceptual events associated with action and outcome. Since the shocks were not perceived, this model cannot readily explain any effect of shock on sense of agency measures.

4.1. Subliminal primes boost sense of agency in healthy participants

The perceived time of endogenous actions moved towards their outcomes in both voluntary and primed-voluntary trials. Crucially, action binding was significantly stronger in primed-voluntary trials where actions were preceded by a subliminal shock, compared to when they were not. The direction of the effect, shifting action perception towards the subsequent outcome, rules out explanations based on P-centre phenomena (Morton, Marcus, & Frankish, 1976), or anchoring effects of the preceding shocks on time perception. Further, as participants could not feel the subliminal shocks, this difference is unlikely to reflect a conscious decision to control actions in a different way. Most importantly, the difference in action binding between trial types could not easily be explained by a purely post-hoc inference account of sense of agency, since the events perceived are identical in both conditions.

Previous studies showed that explicit agency judgements could be modulated by using visual subliminal priming (Chambon & Haggard, 2012; Chambon, Sidarus, & Haggard, 2014; Haggard & Chambon, 2012). Participants reported stronger experience of agency over action effects when the subliminal prime was compatible, compared to incompatible, with the selected action (Wenke et al., 2010). In those studies, as in our experiment, the prime influenced a stage of action preparation that necessarily precedes both action and its effect. This suggests that sense of agency cannot be purely retrospective. Rather sense of agency must depend, at least in part, on signals arising during action preparation. Of course, this does not rule out a further contribution from retrospective inference.

Additionally, given that subliminal shocks increased our measure of sense of agency, external stimulation facilitated putative precursor signals during action preparation. At first

sight, this may seem paradoxical, given the traditional dichotomy between brain systems underlying internally-generated and externally-triggered actions (Passingham et al., 2010). However, substantial cross-talk between the two systems exists. In one study, the reaction time to an external-trigger stimulus was reduced in the very final phases of preparation of a voluntary action (Obhi, Matkovich, & Chen, 2009; also see; Hughes, Schütz-Bosbach, & Waszak, 2011). We speculate that during action preparation, the subliminal shock is taken as an additional environmental cue. The subliminal shock may “nudge” the signal that generates voluntary action, facilitating a threshold crossing event (Schurger, Sitt, & Dehaene, 2012). In our paradigm, participants also occasionally reacted to supraliminal shocks. It remains unclear whether this prior association between shock and action is essential for the subliminal priming we observed. We hope to investigate this point in future experiments. Interestingly, we also found some statistical evidence for effects of shock on action initiation. However, this effect was not present in all participants, and the pattern of influence differed across participants. While in some participants subliminal shocks transiently facilitated action initiation, in others it delayed the time of the action. We note that inhibitory, as well as excitatory, time-dependent effects of subliminal shocks have been widely reported (e.g., Blankenburg et al., 2003). We speculate that subliminal shocks may not only sum with the precursor signals during action preparation but also change the threshold for the initiation of the voluntary action. The precise moment of action initiation thus depends on both signal amplitude and the current threshold.

4.2. Subliminal primes reduce sense of agency in an anarchic hand

Patients with AHS often complain of lack of agency for movements made by their affected hand. This was reflected in action binding data from the left (affected) hand of TP. While she perceived the time of the endogenous actions that were performed by her right (unaffected) hand as shifted towards their outcomes, this perceptual shift did not happen for endogenous actions of her affected hand. This finding based on our implicit measure of sense of agency is also in line with TP's subjective reports of episodes of lack of control of her left hand (see Section 2.1).

Interestingly, the significant interaction between hand and trial type showed that subliminal shock enhances sense of agency similar to healthy participants, but only when applied to the healthy hand. Subliminal shock had no statistical effect when applied to the affected hand. We suggest that, for the affected hand, a mechanism that uses precursor signals of voluntary action to compute sense of agency is now disrupted. The normal function of this mechanism would include integrating signals from the external environment and from internal states to construct a coherent subjective experience of action.

Normal behaviour is an outcome of active interplay between internal states and the external environment. Successful interaction of these two components is crucial for goal-directed behaviour and inhibition of unwanted

responses. Patients with focal damage in medial frontal cortex (though without signs of AHS) show disruption to automatic motor inhibition, as evident in a reversal of the normal negative compatibility effect in a masked-prime task (Sumner et al., 2007). Abnormal facilitation by priming, as well as the involuntary object-oriented actions that characterise AHS, could both be viewed as productive symptoms reflecting damage to a brain system that normally inhibits excessive environmental reactivity. Our results suggest a second aspect to AHS. The normal subjective experience of action is altered in AHS, and in particular the capacity to feel a sense of agency for voluntary actions that are appropriately interfaced to subtle cues in the external environment.

The brain lesions of TP mostly involved the right anterior cingulate cortex (ACC) and the posterior part of corpus callosum (CC) (Fig. 1 & Table 1). Lesions in these areas have been previously reported in patients with AHS (Hassan & Josephs, 2016). One fMRI study compared brain activity during alien hand and voluntary movements of a patient with AHS (Assal, Schwartz, & Vuilleumier, 2007). While alien hand movements were associated with isolated activity in contralateral motor cortex, voluntary movements of the same hand activated extensive networks including the ACC, suggesting a possible role of ACC in voluntary action control. Moreover, ACC has been shown to be active during self- and external-agency attribution tasks (Fukushima, Goto, Maeda, Kato, & Umeda, 2013; Nahab et al., 2011). Other case studies have associated lesions in the CC with volitional disorders of AHS (Della Sala, Marchetti, & Spinnler, 1991; Feinberg, Schindler, Flanagan, & Haber, 1992). CC connects the frontal and motor areas of the two hemispheres. Specifically, the body and splenium of CC, which are mainly damaged in TP, connect the premotor areas (Berlucchi, 2012). Damage to this area could thus lead to loss of transcallosal motor inhibition of the contralateral hemisphere (Kim, Lee, Lee, & Lee, 2014). Interestingly, Wolpe et al. (2014) found a relation between CC white matter loss and abnormal intentional binding in patients with alien limb due to corticobasal degeneration. This deficit was largely confined to anterior parts of CC.

Patients with AHS commonly report that their hand is not under their control or being controlled by an external agent (e.g., Assal et al., 2007). Our work suggests that this phenomenology may arise from two distinct sources. The first source, and the only one recognised in the current literature, is the positive symptom of the affected hand's performing undesired movements in response to the external world. We suggest here a second source of AHS phenomenology, namely a reduced sense of agency for one's own voluntary actions. In the normal brain, voluntary actions do not come “from nowhere”, but are aligned to subtle action possibilities suggested by the environment, akin to subliminal priming in laboratory experiment. Such priming increases explicit judgements of agency (Wenke et al., 2010), and increased intentional binding in healthy volunteers. However, this mechanism was absent for the affected hand of our AHS patient. To our knowledge, this is the first study to investigate a negative symptom of AHS by measuring the effect of the external world on experiences of voluntary actions.

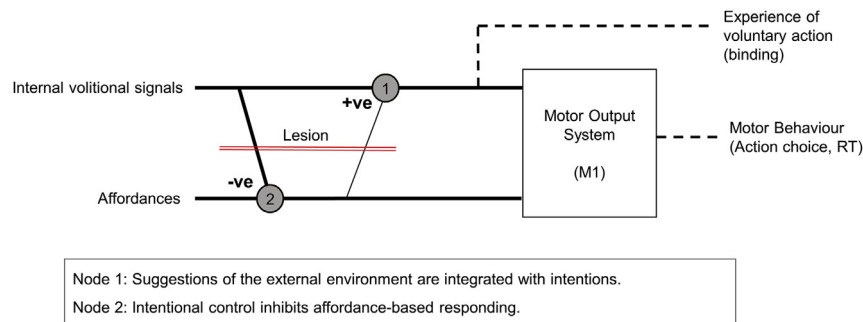


Fig. 5 – A cognitive framework for experience of voluntary action in healthy participants, and anarchic hand syndrome.

4.3. Sense of agency as a readout of internal volitional signals: a cognitive model

Based on our findings from healthy participants and TP we propose a cognitive model of the experience of voluntary action (Fig. 5). We suggest that one key input to the experience of agency is a readout of an internal volitional signal that precedes endogenous actions. This internal signal, however, could be influenced by externally-triggered signals from the outside environment (affordances): volition is not independent of the current environment and response space (Schüür & Haggard, 2011). In the case of healthy participants and the unaffected hand of TP, this external signal is integrated into the internal volitional signal to facilitate action preparation. Thus, the weak sensory evidence suggesting action that is provided by a subliminal prime is summed with the intention or predisposition to act provided by the task instruction. This integration is accordingly reflected in a stronger action binding and an altered distribution of acting. Thus, suggestions of the external environment are integrated with intentions, and the sense of agency depends partly on a metacognitive readout from the output of this ‘integrator’ (Fig. 5, node 1) (Fleming & Frith, 2014).

This interface between the will and the external world is damaged in AHS (Fig. 5). Classical descriptions of AHS suggest that intentional control no longer inhibits affordance-based responding – resulting in compulsive or utilisation behaviours (Fig. 5, node 2) (McBride et al., 2013; Riddoch et al., 1998). The affected hand sometimes reacts to the external world due to loss of the normal inhibitory signal of volition (Sumner et al., 2007). Accordingly, the patient's experience of actions is no longer driven by metacognitive readout of one's own intentions, but is instead driven by experience of actual motor outputs triggered by environmental stimuli. As a result, patients with AHS frequently describe movements of the affected hand as involuntary, even when they are well-formed and co-ordinated. For example, patients may report that their affected hand ‘has a mind of its own’, ‘is being ‘naughty’, ‘doing what it wants, not what I want’, etc.

This model contains the inhibitory link from the voluntary to the reactive motor system that is classically associated with AHS (Fig. 5, node 2). Our results here suggest that the interface also involves a second link, whereby the external environment, even in mild subliminal form, can gently nudge volition (Fig. 5, node 1). This nudge can lead to changed behaviour, as

in subliminal priming (Eimer & Schlaghecken, 2002), but also changed experience of volition, as in the altered sense of agency here. Damage to the interface area in AHS also weakens this second facilitatory link between the external environment and volition, preventing the normal subliminal facilitation of sense of agency. Taken overall, a healthy sense of agency requires that the voluntary motor system be responsive to appropriate external suggestions when these align with one's own wishes, while retaining the ability to suppress externally-driven actions when these are not desired. Our results suggest that the cingulate and the callosum participate in this bidirectional interaction.

5. Conclusions

We developed a novel paradigm to investigate the contribution of precursor signals of endogenous actions to sense of agency. We showed that experience of agency is a metacognitive readout of an interaction between internal volitional signals and the outside world, and not merely a post-hoc confabulation. Interestingly, this interaction was impaired in a patient with anarchic hand syndrome. These findings may help us better understand the mechanisms of volition and sense of agency and to better characterise the neurological disorders of volition.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2017.02.012>.

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