



Research report

Feeling in control: Neural correlates of experience of agency

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ABSTRACT

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

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1. Introduction

Goal-directed action requires the ability to identify the consequences of our behaviour in the external world. We use the term ‘agency’ to refer to this fundamental aspect of human self-consciousness (Pacherie, 2008). Recent theoretical work distinguishes between two important aspects of agency (Synofzik et al., 2008a, 2008b). First, people can make explicit

judgements about their agency (“I did that”). Second, there is a subjective feeling of control that accompanies one’s own actions, even in the absence of any conscious awareness or reflective thought, known as *sense of agency*. The dominant experimental model for studying agency involves explicit judgements of whether a sensory event is caused by one’s action, or by that of another agent. Several studies have used self-recognition paradigms to investigate this explicit sense of

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

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

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

a computer jams, or the controls on a car fail. In the normal flow of experience, the sense of agency seems just to be part of what it is like to control one's action.

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

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

measure intentional binding, rather than the interval estimation approach used here. Moore et al., found that disrupting the pre-supplementary motor area (pre-SMA) using theta-burst TMS produced a decrease in intentional binding. This result suggests that brain areas that underlie intentional action, such as SMA and pre-SMA, are also involved in the implicit sense of agency.

To summarise, previous brain imaging studies suggest that parietal regions may contribute to the explicit judgement of agency. However, existing data do not reveal whether the parietal regions, and the angular gyrus in particular, also play a role in the subjective experience of agency. While some neuroimaging studies suggest a contribution of the supplementary motor complex to the subjective experience of agency, these studies lack a clear perceptual measure of sense of agency. A recent TMS study using intentional binding as an implicit measure of agency also suggests a contribution of the supplementary motor complex (Moore et al., 2010). But that study was designed to test whether candidate areas were necessary for intentional binding, and could not draw strong anatomical conclusions about the precise location of the neural correlates of implicit agency. Indeed, the repetitive stimulation protocol used in such studies may have rather widespread effects in the stimulated region of cortex (Mochizuki et al., 2005), and can also produce remote effects via neural connections with the stimulated region (Stefan et al., 2008).

A recent meta-analysis of studies on the neural correlates of agency as identified in neuroimaging data has implicated the importance of parietal brain regions such as angular gyrus, TPJ and pre-SMA, but also found an association between agency and activation of the insula, dorsofrontomedian cortex and precuneus (Sperduti et al., 2011). However, this meta-analysis did not focus on low-level implicit markers of sense of agency.

We therefore aimed to identify brain regions associated with the implicit sense of agency, taking intentional binding as a proxy for sense of agency. We used an interval estimation task, in which participants judged the time between a button press and a resulting tone. In one condition this tone was elicited by the participant's active button press, in another condition the tone was elicited by a passive movement of the same finger (cf. Engbert et al., 2007).

In order to extract brain areas associated with the intentional binding effect we used a parametric approach in which we modulated each trial with its respective judgement error. Thus, trials with strong binding effects would have large and negative values for this regressor, since underestimation of an action–effect interval corresponds to a negative judgement error. The parametric regressor in the passive condition of the interval estimation task is assumed to capture all brain activation responsible for non-specific causes of variation in time estimation, such as arousal, division of attention etc. The parametric regressor for the active condition on the other hand was assumed to identify both these non-specific factors, and additionally the agency-related changes in time perception due to intentional binding. Contrasting these two parametrically modulated conditions – one that shows the attraction of voluntary action and tone, and one that does not – offers the possibility to extract brain regions that are related to intentional binding. We used this technique to investigate the specific contributions of the SMA and the

angular gyrus to sense of agency, given that these areas were repeatedly reported in previous studies of agency.

2. Methods

2.1. Participants

Seventeen healthy students (five males; age: mean = 22.4, ranging from 19 to 28) participated on the basis of informed consent. The study was conducted according to the Declaration of Helsinki, with approval of the local ethical committee. All subjects had normal or corrected-to-normal vision. No subject had a history of neurological, major medical, or psychiatric disorder. All participants were right-handed as assessed by the Edinburgh handedness questionnaire (Oldfield, 1971; mean score = 92).

2.2. Behavioural task

The experimental task was similar to the one reported in Engbert et al. (2007). It comprised an active and a passive condition. In the active condition participants saw a green hash on the screen and pressed a button with their right index finger at an (unsped) time of their own choosing. In the passive condition, a red hash was presented on the screen. The experimenter then pressed the participant's finger down onto the button, attempting to match the response time of the participants as precisely as possible. Each button press elicited the presentation of a tone after either 200, 300 or 400 msec. Immediately after hearing the tone, participants judged the duration of the interval between the button press and the tone onset using a visual-analogue scale operated with two keys in their left hand (index finger meant that the cursor moved to the left, middle finger meant that the cursor moved to the right and the middle finger of the right hand accepted the position of the cursor). Participants were given as much time as they needed for their judgement. The endpoints of the scale were 100 and 500 msec. Prior to scanning participants were trained to discriminate between two tones that were separated by 100 msec and separated by 500 msec for 10 min, with a further 10 min of identical training being given in the scanner prior to the experimental task itself. The trials were presented with a variable inter-trial interval ranging from 3000 to 5500 msec. The task consisted of two blocks each containing altogether 30 active and passive trials that were randomly presented. An equal number of trials in all six conditions were presented within each block.

2.3. Behavioral data analysis

Repeated-measures ANOVA with the factors agent (active vs passive) and tone delay (200, 300, 400 msec) was performed on the judgement error, namely the difference between judged time and actual tone delay.

2.4. Scanning procedure

Images were collected with a 3 T Magnetom Trio MRI scanner system (Siemens Medical Systems, Erlangen, Germany) using an

eight-channel radiofrequency head coil. First, high-resolution anatomical images were acquired using a T1-weighted 3D MPRAGE sequence (TR = 2530 msec, TE = 2.58 msec, TI = 1100 msec, acquisition matrix = $256 \times 256 \times 176$, sagittal FOV = 220 mm, flip angle = 7° , voxel size = $.86 \times .86 \times .9 \text{ mm}^3$). Whole brain functional images were collected using a T2*-weighted EPI sequence sensitive to BOLD contrast (TR = 2000 msec, TE = 35 msec, image matrix = 64×64 , FOV = 224 mm, flip angle = 80° , slice thickness = 3.0 mm, distance factor = 17%, voxel size $3.5 \times 3.5 \times 3 \text{ mm}^3$, 30 axial slices). Image volumes were aligned to AC-PC.

2.5. fMRI data pre-processing and general linear model (GLM) analysis

The fMRI data were analysed with statistical parametric mapping using SPM5 software (Wellcome Department of Cognitive Neurology, London, UK). The first four volumes of all EPI series were excluded from the analysis to allow the magnetisation to approach a dynamic equilibrium. Data processing started with slice time correction and realignment of the EPI datasets. A mean image for all EPI volumes was created, to which individual volumes were spatially realigned by rigid body transformations. The high-resolution structural image was co-registered with the mean image of the EPI series. Then the structural image was normalised to the Montreal Neurological Institute (MNI) template, and the normalisation parameters were applied to the EPI images to ensure an anatomically informed normalisation. During normalisation the anatomy image volumes were resampled to $1 \times 1 \times 1 \text{ mm}^3$. A filter of 8 mm full-width at half maximum (FWHM) was used. Low-frequency drifts in the time domain were removed by modelling the time series for each voxel by a set of discrete cosine functions to which a cut-off of 128 sec was applied. The subject-level statistical analyses were performed using a GLM.

To analyse the interval estimation task, we built a model with six separate regressors for active 200 msec, active 300 msec, active 400 msec, passive 200 msec, passive 300 msec, passive 400 msec. We also calculated the judgement error on each trial, defined as the judged interval duration minus the actual interval duration. Note that a strong intentional binding effect therefore corresponds to a large and negative value judgement error. We then parametrically modulated the above six regressors by the judgement error. Movement parameters were included to account for variance associated with head motion. All resulting vectors were convolved with the canonical haemodynamic response function (HRF) and its temporal derivative to form the main regressors in the design matrix (the regression model). The statistical parameter estimates were computed separately for each voxel for all columns in the design matrix. Contrast images were constructed for each individual to compare the relevant parameter estimates for the regressors containing the canonical HRF. Next, a group-level random effects analysis was performed. One-sample t-test was performed for each voxel of the contrast images. The resulting statistical values were thresholded with a level of significance of $p < .001$ ($z > 3.09$, uncorrected). To correct for multiple comparisons we applied small volume correction in the SMA and angular gyrus, based on previous neuroimaging findings that SMA houses action–effect links (MNI coordinate:

–4 –871, Elsner et al., 2002) and that angular gyrus is involved in explicit agency judgements (MNI coordinates: 58 –46 48; –48 –46 56, Farrer et al., 2008). The regions of interest (ROIs) were created using bilateral anatomical masks created based on the WFU Pickatlas (Maldjian et al., 2003) and the automated anatomical labelling (AAL) atlas (Tzourio-Mazoyer et al., 2002) of SMA, angular gyrus, insula, superior frontal medial cortex and precuneus.

The resulting statistical maps were overlaid onto a normalized T1-weighted MNI template (colin27) and the coordinates reported correspond to the MNI coordinate system.

3. Results

3.1. Behavioral results

The repeated-measures ANOVA revealed a significant main effect for agency [$F(1,17) = 5.96$, $p < .05$] with participants giving significantly shorter interval estimates in the active compared to the passive condition on the judgement error. There was an unsurprising significant main effect of delay [$F(2,34) = 16.49$, $p < .001$] with more pronounced underestimation of the action–effect interval at longer delays. There was also a significant interaction of both factors [$F(2,34) = 6.48$, $p < .01$] (Fig. 1). This interaction arose because the difference in judgement error between active and passive conditions increased with action-tone delay.

3.2. fMRI results

The interval estimation task was analysed by parametrically modulating the action onset with the judgement error of the action-tone interval. We then contrasted the active with the passive condition based on the fact that the active condition should involve a shortening of the awareness of the interval, whereas the passive condition should not. This analysis identifies brain regions that correlate with the compression of the action-tone interval more strongly in the active than in the passive condition. The previous literature gave strong

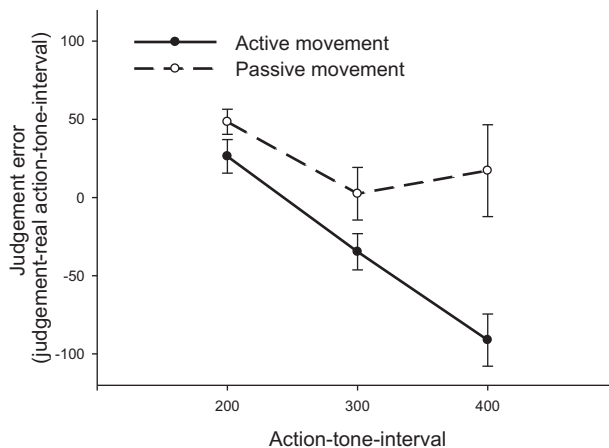


Fig. 1 – Behavioural results of judgement error in the interval estimation task (error bars indicate standard error of mean).

predictions about involvement of specific regions in the experience of agency: the angular gyrus and the SMA (see Introduction) but also insula, frontomedian cortex and precuneus. Therefore we used a small volume correction within anatomically defined mask of these structures of interest. We identified a significant cluster within the SMA ROI family-wise error corrected $p < .05$ after small volume correction at $-11, -8, 74$ (cluster size = 7 voxels) (Fig. 2). Closer inspection confirmed that the cluster was located in left BA6, effectively on the margin between the lateral portion of BA6 comprising the dorsal premotor cortex, and the medial portion comprising the SMA proper. We applied a similar small volume correction to the bilateral angular gyrus, insula, frontomedian cortex and precuneus ROI, but found no significant difference between the parametric regressors for the active and passive conditions (nor in the reverse contrast) surviving correction within these areas.

A whole brain analysis of the contrast between the parametric regressors for the active and passive condition with a statistical criterion of $p < .001$ uncorrected for multiple comparisons again revealed the same SMA cluster at $-11, -8, 74$, but no other significant clusters. Further, no significant clusters of activation were found in the reverse contrast.

4. Discussion

The present study reported neural correlates of a distortion of time perception following voluntary action, which is taken as a putative implicit marker of the sense of agency. The behavioural results replicate the findings of previous reports. We found shorter interval estimations in an active condition in which the participant caused the tone through their action, compared to a passive control condition (cf. Engbert et al., 2007; Wenke and Haggard, 2009). Ebert and Wegner (2010) recently showed that both implicit binding effects and explicit agency judgements show a similar sensitivity to

temporal delays. This suggests that our measure, though clearly implicit, does capture a core aspect of the phenomenology of agency.

We focussed on changes in time perception that accompany the sense of agency by using parametric analyses and a contrastive design. This analysis was designed to focus on the associative core of the implicit sense of agency, i.e., changes in perceived timing due to the ‘constant conjunction’ of motor and sensory events (Hume, 1763). Thus we parametrically modulated the BOLD response with the judgement error of the perceived interval between action and tone in the active condition, and then subtracted the similarly calculated parametric regressor in the passive condition. This procedure removes variations in time estimation due to non-specific causes, leaving only activations related to agency-related variability in time perception. That is, the contrast between the two parametric analyses is assumed to capture the variation in temporal experience that is specifically associated with the context in which the participant’s voluntary action caused the tone.

Our results highlight the involvement of SMA proper in agency-related intentional binding. We had a prior hypothesis that the posterior frontomedian cortex might underlie the association between action and effect from a previous PET study (Elsner et al., 2002) and a TMS study (Moore et al., 2010). However, the former study did not include a subjective measure of agency, and the latter study did not explore effects of stimulating different subregions within the SMA complex. Thus, our previous study may be the first aiming to find the specific brain areas correlating with the implicit feeling of agency. Our results showed a cluster in the left SMA proper, extending into the dorsal premotor cortex, whose activation correlated more strongly with judgement errors in the active than in the passive condition.

Some care is needed in interpreting this result, since it is based on a single neuroimaging experiment. However, the number of participants (17) in our study is roughly comparable

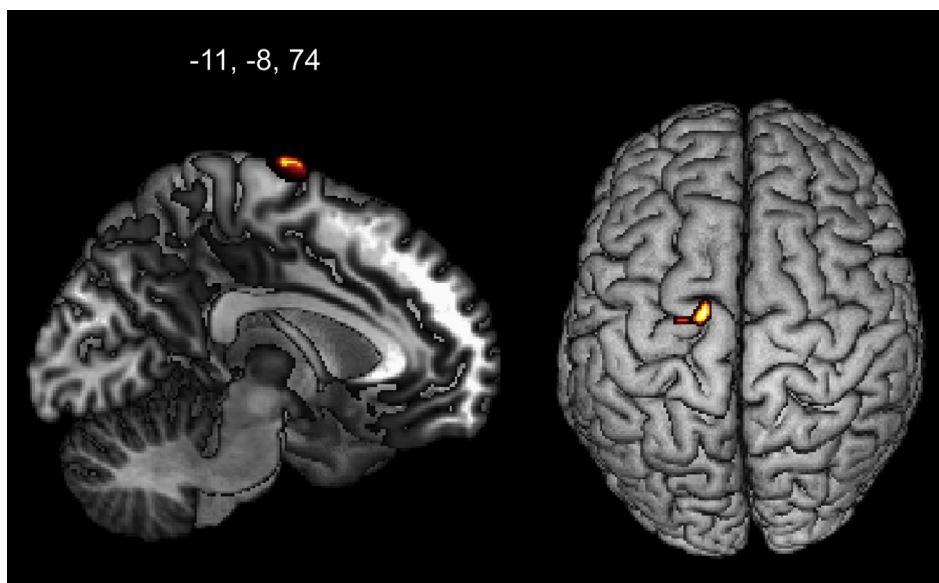


Fig. 2 – Brain area of the interval estimation contrast active condition > passive condition both parametrically modulated with the judgement error that reflects the subjective shortening of the interval between action and tone.

with other recent neuroimaging studies of agency and volition (De Luca et al., 2010: $n = 12$; Farrer et al., 2008: $n = 15$; Miele et al., 2011: $n = 11$; Nahab et al., 2011: $n = 20$). Moreover, dismissing a positive finding on the basis of a small sample does not follow the standard logic of statistical inference (Friston, 2012). Finally, our result can be interpreted in the light of convergent evidence from other studies about the role of this area. However, future studies with increased sample sizes should be conducted to confirm the reported results.

The SMA and pre-SMA have long been ascribed a crucial role in voluntary self-initiated action. Therefore, activation of the left SMA when making voluntary movements of the right hand is expected. Our results further show a correlation between activity in the left SMA and the subjective experience of binding between right hand actions and a subsequent tone. Other results are consistent with the SMA complex contributing to the experience of voluntary action, and not only to generation of voluntary action. For example, stimulation in the SMA/pre-SMA caused a feeling of “urge” to move a specific body part in neurosurgical patients, in absence of any detectable physical movement (Fried et al., 1991). More recent data suggest important distinctions between SMA and pre-SMA. The pre-SMA has been associated with the cognitive aspects of tasks and has been considered as a region of the prefrontal cortex (Picard and Strick, 2001). The SMA proper is thought to be more closely related to immediate action execution, and the pre-SMA to planning and initiation of actions, especially complex action sequences. Neurosurgical recordings from single units in humans suggest that activity in the SMA proper correlates more strongly with the experience of conscious intention immediately prior to voluntary action than does activity in the pre-SMA (Fried et al., 2011). In our study, the cluster activated in relation to the intentional binding effect was in the SMA proper territory, and was clearly caudal to the pre-SMA. These considerations suggest that the neural circuits responsible for intentional binding may be more closely related to immediate execution of voluntary action than to the planning and initiation of action.

The peak of the intentional binding cluster identified by our study was classified as being in the left SMA proper according to a standard automatic labelling technique (Tzourio-Mazoyer et al., 2002), but it was clearly more lateral and more posterior than the medial wall pre-SMA activations seen in some other studies of voluntary action and conscious intention (Lau et al., 2004). In fact, our cluster extended laterally into an area traditionally classified as dorsal premotor cortex. A widely-accepted view of Brodmann area 6 is based on a medio-lateral gradient, with medial portions being involved in internally-generated actions, and more lateral portions being involved in externally-triggered actions (Goldberg, 1985; Passingham et al., 2010; Kriehoff et al., 2011; Brass and Haggard, 2008).

The location of the neural substrate of intentional binding at the junction of areas for internal and external control of action may reflect the fact that our binding involves linking representations of intentional action to their external effects. Lesions in dorsal premotor cortex close to the cluster activated in our study have been associated with the denial of motor impairment in hemiplegic patients. These patients report that they perform intended actions, even though they are paralysed and unable to move (Berti et al., 2005). This anosognosia

was interpreted as showing that normal awareness of action is driven partly by both intentional signals, and by monitoring reafferent signals generated during actual movement. Dorsal premotor lesions appeared to impair the integration of actual reafferent information, leaving the patient with an experience of agency that relied only on their intentions, without any feedback from the affected limb's lack of movement. One might therefore interpret the dorsal premotor cortex as binding the sensory effects of action with the intentional action that caused them. This interpretation is also consistent with our data: stronger activation of this area was associated with stronger binding between action and effect.

Moreover, our activation was found in the left hemisphere, in a task where participants responded with their right hand.

Intentional binding may depend on both predictive processes (e.g., motor command signals, Blakemore et al., 2002; Wolpert and Ghahramani, 2000) and on post-hoc reconstruction (Dennett and Kinsbourne, 1992; Wegner, 2002). The prediction account suggests that compression of perceived time occurs because neural preparation for action already triggers anticipation of the effects of action. In contrast, reconstructive accounts suggest that the mind infers and constructs a narrative in order to explain bodily movements or their external consequences after the fact. Recent behavioural studies suggest that intentional binding includes both predictive and reconstructive components (Moore and Haggard, 2008). The current design does not allow us to formally separate the predictive and reconstructive components of sense of agency. We speculate that the computations within BA6 that underlie the sense of agency may recapitulate the medio-lateral gradient for the generation of action. Predictive contributions to sense of agency would rely on intentions and motor plans, and would be housed more medially, while reconstructive contributions to sense of agency would rely on integration of external sensory feedback, and would be housed more laterally. Therefore, the fact that our intentional binding cluster effectively straddles the intermediate zone between medial and lateral subdivisions may reflect the combination of both predictive and reconstructive processes. The two processes cannot be dissociated using interval estimation, but could be distinguished in future studies using estimates of action timing, and varying the probability that an action produces a tone.

We found no evidence that the angular gyrus was associated with our implicit temporal measures of sense of agency. Clearly, a null result in a single neuroimaging experiment must be interpreted with great caution: absence of a significant activation does not imply that angular gyrus plays no role in intentional binding. However, the lack of activation, even when applying small volume correction within the angular gyrus, may be surprising for several reasons. First, the angular gyrus was previously shown to be sensitive to delays in visual feedback of actions (Miele et al., 2011), and has been associated with explicit judgements of lack of agency. In particular, angular gyrus was also more strongly activated when participants judged that they were not responsible for visual feedback, relative to when they judged that they were responsible (Farrer and Frith, 2002). In several studies angular gyrus has been shown to be sensitive to delays and distortions in visual feedback (Farrer et al., 2003, 2008; Miele et al., 2011; Spengler et al.,

2009). The absence of parietal activations associated with intentional binding in our study may reflect our use of an implicit measure of agency, rather than an explicit judgement (Synofzik et al., 2008a, 2008b). We speculate that the frontal cortex is responsible for the implicit sense of control that accompanies normal goal-directed actions, while the parietal cortex is responsible for detecting deviations from expectancy by a comparison between predicted and actual consequences of action. On the other hand, neuropsychological and neurosurgical studies have confirmed that the parietal cortex also contributes to perception of intentions, as well as explicit judgements about action consequences (Sirigu et al., 2004; Desmurget et al., 2009). It thus remains unclear whether the parietal cortex contributes to the phenomenal experience of control. However, our data suggest that the characteristic experience of temporal flow between action and effect is frontal, rather than parietal in origin.

Furthermore we neither found evidence that the insula, frontomedian cortex or precuneus was associated with the implicit temporal markers of sense of agency. Moreover our results do not point to any subcortical involvement in the experience of intentional binding. Again, extreme caution is required in interpreting the null results from a single, averagely-sized neuroimaging experiment. However, it is worth noting that these areas have been strongly implicated in previous studies of agency (Farrer et al., 2003; Farrer and Frith, 2002; Ruby and Decety, 2001; Sperduti et al., 2011). Our finding of a premotor correlate of intentional binding suggests that the experience of agency may be dissociable from the subcortical processes underlying reinforcement learning of goal-directed actions. Sense of agency and reinforcement learning are clearly both important aspects of goal-directed action. Studies on reinforcement learning have stressed the importance of activation in ventral striatum. This area is involved in computations of reward and prediction error thought to underlie reinforcement learning (O'Doherty et al., 2003; Pagnoni et al., 2002; Pessiglione et al., 2006). Unlike reinforcement learning, our task involves no overt reward. Also unlike reinforcement learning, it emphasises subjective experience of action, in addition to action performance. These features may explain our finding that intentional binding involves cortical not subcortical brain regions.

To summarize, we have identified the neural correlates of an implicit measure of the sense of agency, namely the perceptual attraction between actions and their consequences, using fMRI. We found that activation of a lateral subregion of the SMA proper correlated with the strength of the 'intentional binding' between actions and their effects. This area may combine a read-out from the motor areas that control intentional action, with an integration of sensory information from areas that monitor external consequences of action.

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