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An Online Neural Substrate for Sense of Agency

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"Sense of agency" refers to the feeling of controlling an external event through one's own action. On one influential view, sense of agency is inferred after an action, by "retrospectively" comparing actual effects of actions against their intended effects. In contrast, a "prospective" component of agency, generated during action selection, and in advance of knowing the actual effect, has received less attention. Here, we used functional magnetic resonance imaging to investigate prospective contributions of action selection processes to sense of agency. To do so, we dissociated action selection processes from action–outcome matching, by subliminally priming responses to a target. We found that participants experienced greater control over action effects when the action was compatibly versus incompatibly primed. Thus, compatible primes facilitated action selection processing, in turn boosting sense of agency over a subsequent effect. This prospective contribution of action selection processes to sense of agency was accounted for by exchange of signals across a prefrontal–parietal network. Specifically, we found that the angular gyrus (AG) monitors signals relating to action selection in dorsolateral prefrontal cortex, to prospectively inform subjective judgments of control over action outcomes. Online monitoring of these signals by AG might provide the subject with a subjective marker of volition, prior to action itself.

Keywords: action selection, agency, angular gyrus, dorsolateral prefrontal cortex, fMRI

Introduction

Imagine you are the manager of a busy factory. You should experience a strong feeling that your actions profoundly influence what happens throughout the factory. But where does this feeling come from, and when does it occur? Do you infer your degree of control only retrospectively, when you see the finished product ready for shipping or even the quarterly sales figures? Or is it prospective? Does the ease and clarity with which you make strategic decisions already give you a feeling of control before you see actual results?

This everyday example illustrates the contrast between 2 neuroscientific views of what has often been called "sense of agency," that is, the subjective experience of controlling one's own actions and, through them, events in the outside world (Haggard and Tsakiris 2009). Much current research emphasizes this sense of control arises when external events are consistent with internal predictions of action outcomes (Blakemore et al. 1998; Farrer et al. 2008; Moore and Haggard 2008; Sato 2009; Nahab et al. 2011) or are generally consistent with our intentions (Wegner 2002; Wegner et al. 2004). For, example, if I intend to turn on the light by pressing a switch, and the light then happens to come on, I am likely to feel that I caused the light to come on. On this view, agency is inferred "retrospectively," after an action has been performed, based on the external consequences of the action. On a neural level, many studies suggest that the angular gyrus (AG) computes sense of agency by retrospectively matching the predicted effects of action against its actual effects, resulting in a perturbed sense of agency when a mismatch occurs (Farrer and Frith 2002; Farrer et al. 2003, 2008).

An alternative possibility, that sense of agency might be based on "prospective" processes relating to actions one "will" shortly perform, has received less attention. Yet, there is some evidence that people can prospectively judge agency by monitoring their performance online, whilst doing the task, and irrespective of whether subsequent intended outcomes occurred, or did not occur, as predicted (Metcalfe and Greene 2007). Here, we explore whether this prospective sense of control may depend on internal processes of action selection and preparation occurring "before" movement, even when participants make retrospective judgments of agency. In line with this assumption, we investigated whether AG, which has been shown to compute "retrospective" agency by monitoring action outcomes (Farrer et al. 2003, 2008), may also code for a prospective sense of control by monitoring action selection processes in advance of the action itself and independently of action outcomes.

To do this, we dissociated the processes of action selection from the match between actions and outcome, by subliminally priming responses to a target. Previous research has shown that action selection is easier (faster and less error prone) when preceding subliminal primes are compatible with a motor response to a target stimulus than when they are incompatible (Vorberg et al. 2003). Interestingly, this fluency of action selection is also relevant to sense of control. Thus, in one recent study (Wenke et al. 2010), participants reported stronger sense of control over action outcomes when their responses to a target cue had previously been subliminally primed by a compatible, as opposed to an incompatible, prime. Importantly, this was not simply due to the predictability of the action outcomes, since outcome stimuli (colored patches in this experiment) following compatible and incompatible primes were equally predictable. Rather, the stronger experience of control when subliminal prime and target cue were compatible could only be explained by the "fluency" of action selection processes—that is, by an internal signal influenced by subliminal priming, and experienced before the action was made. Thus, compatible primes facilitated action selection processing by making selection processes "fluent." Increased fluency of selection in turn boosted sense of agency over action effects (Wenke et al. 2010).

We adapted this experimental paradigm for functional neuroimaging (fMRI) in order to investigate the neural basis of this prospective sense of control (Fig. 1). First, we identified areas coding for the fluency of action selection, by comparing trials where prime and target were compatible versus incompatible. Second, we predicted that participants would feel more control when action selection was fluent (Wenke et al. 2010). We therefore sought to identify brain activations whose correlation with sense of control differed between prime–target compatible (i.e., fluent) and incompatible (i.e., dysfluent) trials. Finally, we used psychophysiological interaction (PPI) analysis to investigate whether the relation between subjective sense of control and objective fluency of action selection processes was associated with changing connectivity between the areas identified by these contrasts.

Materials and Methods

Participants

Twenty-eight right-handed participants (15 females and 13 males aged 19–31 years), with normal or corrected-to-normal vision, were recruited to participate in the study. They provided written informed consent prior to the experiment and were all paid €17 for their participation. None of them had a history of brain trauma, seizure disorder, mental retardation, affective disorder, substance abuse, or substance dependence within the past 6 months nor any medical condition which would interfere with MRI studies (e.g., extreme obesity, claustrophobia, cochlear implant, metal fragments in eyes, cardiac pacemaker, neural stimulator, metallic body inclusions or other metal implanted in the body, pregnancy). Of these 28 participants, 6 were excluded because of: technical issues (1; the presentation program crashed during the scanning session), excessive motion (4; more than one translational displacement of 3 mm or greater), or high sensitivity to subliminal primes (1; for more details about the prime visibility test, see Supplementary Information and Fig. S2). The study was approved by the local ethics review board at the University of Leipzig, Germany.

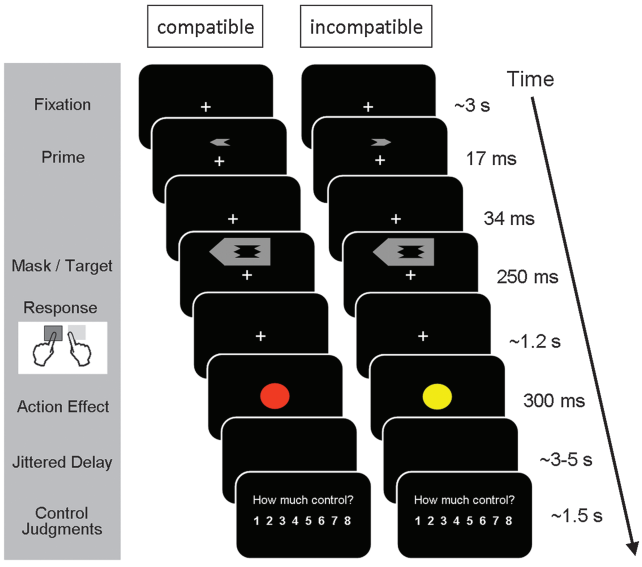

Figure 1. Schematic of trial procedure and stimuli. Example trials from the 2 possible combinations of the prime-action compatibility (compatible: left panel; incompatible: right panel). Participants were instructed to respond to the target stimuli and were not informed of the presence of the arrow primes. Primes and masks could appear randomly above or below fixation on each trial. The appearance of the effect was randomly jittered 100, 300, or 500 ms after the keypress to avoid ceiling effects in perceived control. After a jittered delay varying from 3 to 5 s, participants were asked to estimate how much control they felt they had over the action effect.

Design and Procedure

The participants' task was to find out, by pressing the left or right keys, how much control they had over color-effect stimuli that followed their keypress actions. The metacontrast masks that served as targets consisted of arrows that unambiguously pointed to the left or to the right. Subliminal primes also consisted of left or right pointing arrows. Participants were required to press the key that corresponded to the direction of the mask/target (see Fig. 1; more detailed information about apparatus and materials can be found in the Supplementary Information).

On half of the trials in each block at random, the prime and the mask/target (and therefore also the manual response) were "compatible," while on the remaining trials, they were "incompatible." On prime-response compatible trials, the direction of the prime corresponded to the direction of the mask/target and hence signaled the same response. On incompatible trials, prime and mask/target pointed in different directions.

Action effects consisted of colored circles that appeared on the screen 100, 300, or 500 ms after the response. This jitter was introduced in order to avoid potential ceiling effects in perceived control resulting from high temporal predictability (Haggard et al. 2002; Wenke et al. 2010). The distribution of jitter was the same for all conditions and thus orthogonal to the manipulation of prime-response compatibility.

Colored circles were of 4 different colors (red, green, blue, and yellow). The color that participants saw on each trial depended whether the trial was prime–target compatible or prime–target incompatible. In each block, 2 colors (one for each hand) were assigned to prime-compatible responses, another 2 colors to prime-incompatible responses. Compatible effect-colors consistently followed compatible prime–target combinations (e.g., the color red was shown when a left mask/target followed a left-pointing arrow prime). Incompatible effect-colors were consistently mapped to targets that did not correspond to the direction of the prime (e.g., the color yellow was shown when a left mask/target followed a right-pointing arrow prime). Colors were rotated through compatibility conditions via a Latin square such that, across all 4 blocks, each color appeared in each compatibility condition for each hand. After the effect was displayed, participants judged how much control they felt they had over the color effect by using a scale ranging from 1 (no control) to 8 (complete control).

Timeline

Primes were presented for 17 ms, followed by the mask after a Stimulus Onset Asynchrony of 34 ms. Mask/target duration was 250 ms. The response window was set to 1200 ms. If participants failed to respond within this time window, or made an incorrect response to the mask/target, they saw a black × instead of a colored circle. The colored patches showing action effects remained on the screen for 300 ms. After a jittered delay (gray background) varying from 3 to 5 s, a rating scale appeared for 1500 ms, allowing the participant to judge the level of control she felt over the color patch. Once the participant made her control judgment, the rating scale was replaced by a fixation cross until the end of the 1500 ms response window. The fixation cross persisted for a 3000 ms intertrial interval.

Each block ended with a pause lasting 30 s. The experiment consisted of 4 blocks of 48 trials each. When an error occurred in a trial, the corresponding trial was repeated at the end of each block (up to 5 error trials per block). Repeating error trials ensured that all colors were seen equally often, even if participants made response errors.

Data Acquisition and Preprocessing

Images were collected using a Bruker 3.0 T whole-body and radio frequency coil scanner. The fMRI blood oxygenation level–dependent signal (BOLD) was measured using a T_2^*-weighted echoplanar sequence (repetition time, 2000 ms; echo time, 30 ms; flip angle,

90°). Twenty-six contiguous slices (thickness, 4 mm; gap, 0.4 mm; matrix size, 64 × 64; voxel size, 3 × 3 × 4 mm^3) were acquired per volume. A high-resolution T_1-weighted anatomical image (repetition time, 1300 ms; echo time, 3.93 ms; 256 × 240 image matrix; field of view, 256 mm × 240 mm; slab thickness, 192 mm; spatial resolution, 1 × 1 × 1.5 mm^3) was collected for each subject prior to functional acquisition.

Image preprocessing was performed using SPM5 (Wellcome Department of Imaging Neuroscience, University College London, UK, http://www.fil.ion.ucl.ac.uk/spm/). For each subject, each of the 4 scanning sessions contained 220 functional volumes after the first 5 scans were rejected to eliminate the nonequilibrium effects of magnetization. All functional volumes were realigned to the first volume to correct for interscan movement. Functional and structural images were coregistered and transformed into a standardized stereotaxic space (Montreal Neurological Institute template) (Evans et al. 1994). Functional data were then smoothed with an 8-mm full-width-at-half-maximum, isotropic Gaussian kernel and temporally processed using a high-pass filter with a frequency cutoff period of 128 s. Serial correlations were accounted for by use of an autoregressive model of the first order. To control for possible noise artifacts in the data, we used a weighted least-squares approach, in which we downweighted images with high noise variance (Diedrichsen and Shadmehr 2005).

fMRI Data Analysis

We computed brain activations using standard statistical procedures. Statistical parametric t score maps were obtained from local fMRI signals using a linear multiple regression model with conditions (modeled as boxcar functions convolved by the canonical hemodynamic response function) and scanning series as covariates.

For compatible and incompatible conditions, we defined the "action selection" phase as the interval between prime onset and participant's response to the mask/target stimulus and the "control judgment" phase as the period from the scale onset to participant's rating of their level of control (see Fig. 1). Thus, 4 distinct event-related regressors modeled correct trials associated with compatible and incompatible conditions at both time of action selection and control judgment.

Each participant's control ratings in each compatibility condition were divided into tertiles to define low, medium, and high levels of experienced control (for details, see Supplemental Information). We entered the tertiles into the model to identify brain regions in which the BOLD signal recorded at 1) time of action selection and 2) time of control judgment was modulated by judgments of control. We examined regression coefficients separately for compatible and incompatible conditions. Additional event-related regressors factored out participants' motor response and response times for the action selection phase in both compatible and incompatible conditions (see Supplementary Information and Fig. S1). Finally, scanning series and head motion parameters estimates (translation in x, y, z; roll, pitch, yaw) were included as covariates of no interest in the design matrix.

Regression parameters were estimated in every voxel for each subject, and then parameter estimates were entered in a between-subject random-effect analysis to obtain statistical parametric maps. We identified brain activations showing significant contrasts of parameter estimates with a voxelwise (T = 3.68, P < 0.001, uncorrected) and clusterwise (P < 0.05, uncorrected) significance threshold. All reported activations survived false discovery rate correction for multiple comparisons (P < 0.05) (Genovese et al. 2002).

Results

Behavioral Performance: Prime Visibility Test

One subject was excluded from both behavioral and fMRI analyses because her d' in the prime d' visibility test was sufficiently high (0.98) to suggest conscious perception (greater than one standard deviation above the mean). For all remaining subjects, signal detection analyses confirmed that primes were below the threshold of awareness, with mean d' not significantly different from zero (mean d' = 0.077 ± 0.24, P = 0.21) (for more details about the prime visibility test, see Supplementary Information and Fig. S2).

Action-Effect Experiment

Behaviorally, participants' responses to arrow targets following compatible primes were faster than following incompatible primes (two-tailed t-test, t_{21} = −3.08, P = 0.005). Participants also experienced higher levels of control over action effects following compatible prime–target associations (t_{21} = 2.89, P = 0.008), consistent with previous results (Wenke et al. 2010). For error rates, we only found a marginal difference between conditions, with participants tending to make more errors in incompatible than in compatible trials (t_{21} = −1.81, P = 0.08) (Fig. 2; see also Supplementary Fig. S3 that provides frequency histograms for control ratings made under compatible and incompatible conditions). We used linear regressions analyses to investigate any possible relation between RT and control ratings in each subject. These analyses did not reveal any significant correlations between RT and control ratings, neither on compatible (all R's < 0.172, all P's > 0.09) nor on incompatible (all R's < 0.192, all P's > 0.064) trials (see Supplementary Table S1 and Fig. S4). On average, RT explained less than 1% of the variance in sense of agency.

Main Effect of Action Selection

Regions involved in action selection were identified by contrasting compatible and incompatible trials. In order to identify pure effects of action selection, independent of sense of control, we excluded regions which varied with sense control at time of action selection, by exclusively masking action selection activations with a parametric contrast of {compatible × control} versus {incompatible × control}, or {incompatible × control} versus {compatible × control}, as appropriate (see Supplementary Information for details, and Fig. S1). This procedure identifies regions reflecting the objective fluency or dysfluency of action selection, but whose activity was independent of subjective control experienced by subjects.

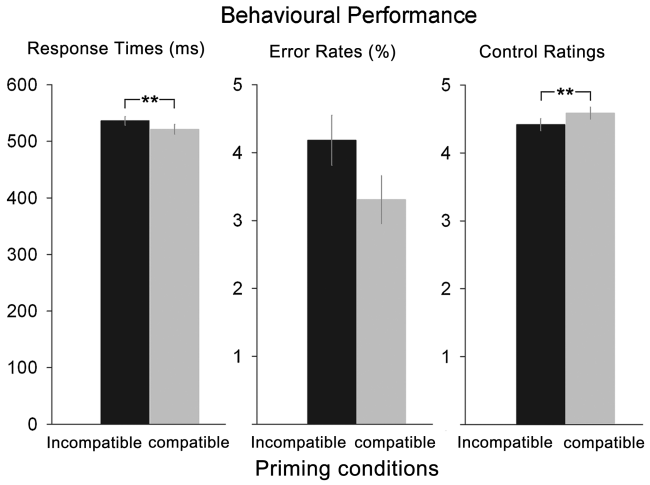

Figure 2. Action-effect experiment. Left to right, graphs show: mean response times (536.3 vs. 521.1), % of errors (4.2 vs. 3.3), mean control ratings (4.4 vs. 4.6). All error bars indicate standard error of the mean. $^{**}P < 0.01$.

fMRI responses on compatible trials relative to incompatible trials revealed a set of regions including left (x, y, z = –45, 12, 42, T = 4.32) and right (x, y, z = 45, 18, 39, T = 4.62) dorsolateral prefrontal cortices (DLPFCs) and left putamen (x, y, z = –26, –3, 0, T = 3.77) (Fig. 3 and Supplementary Table S2). Compatible trials also elicited stronger activations in left and right orbitofrontal cortices, but these activations did not survive the clusterwise P < 0.05 threshold. We did not find any stronger activation in incompatible trials than compatible trials, even when data were visualized at P < 0.05, extent threshold 10 voxels.

Interaction between Action Selection and Sense of Control

We identified regions whose activation, at the time of action selection, was differentially modulated by levels of control (low, medium, high) according to the condition of action selection (compatible, incompatible), using a parametric contrast of {compatible × control} versus {incompatible × control}, or {incompatible × control} versus {compatible × control}, respectively.

Left AG activation was modulated by levels of experienced control in incompatible but not compatible trials (x, y, z = –36, –69, 45, T = 4.47; Fig. 4*a* and Supplementary Table S3; for additional results, see also Supplementary Information and Fig. S5). Specifically, activation of AG increased as sense of control became weaker in trials where prime and target were incompatible. In contrast, AG activation did not vary significantly with control on compatible trials. We did not find any regions whose activity increased with "greater" control in incompatible trials, even when data were visualized at P < 0.05, extent threshold 10 voxels.

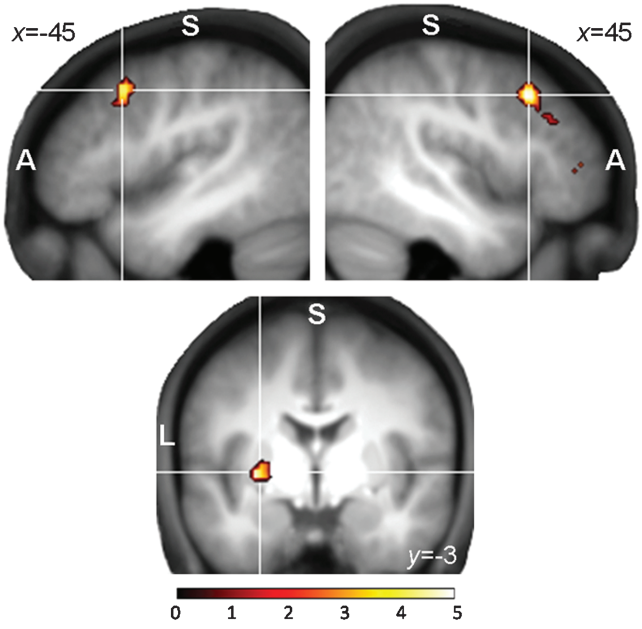

Figure 3. Sagittal (x = −45 and 45) and coronal (y = −3) sections showing brain activations reflecting the main effect of compatibility at time of action selection. Significant clusters were found in DLPFC, bilaterally, and left putamen. Images are presented at a whole-brain threshold of P(false discovery rate) < 0.05, k > 10. L = Left; A = Anterior; S = Superior. Color bar indicates t-statistic value.

Incompatibility of Action Selection Triggers Online Coding of Agency in AG

Previous studies reported AG activation increasing with the discrepancy between predicted and actual consequences of movement (Farrer et al. 2003, 2008). More specifically, the AG has been suggested to compare predicted and actual "effects" of an action, attributing the effect either to one's own actions (in the case of a match) or some other cause in the case of a mismatch (Farrer et al. 2008). Our result goes beyond this previous literature in 3 important ways. First, we show that AG also participates in a quite different form of mismatch, namely the mismatch between "prime" and "target" (see Wenke et al. 2010). Crucially, and unlike the classical mismatch between intention and action outcome (Farrer et al. 2003, 2008), the mismatch between prime and target in our design is confined to the moment of action selection itself. Thus, AG codes mismatches "online," during action selection, and not only during retrospective processing of action outcomes. Second, we demonstrated that this parietal coding is predictive of the "level" of experienced control, in a proportional fashion. Specifically, our participants experienced reduced sense of control and showed higher AG activation on prime–target incompatible trials compared with compatible trials. This difference occurred in the absence of any mismatch between the visible target, the motor action, and its external effect—ruling out the possibility that our AG activation reflects classical action-effect predictability. Third, since participants had no perceptual awareness of the preceding subliminal prime, the only process induced by the primes that can explain variation in control ratings is the fluency of action selection. We show that this internal action selection signal is capable of triggering prospective coding of agency in AG.

Importantly, and consistent with previous findings (see Farrer et al. 2008), AG activation did not vary with experienced control in the compatible (i.e., fluent) condition. This reinforces previous accounts of agency as a default experience (Frith et al. 2000). We generally experience our actions as a background of uninterrupted flow from intentions to effects (Haggard 2005). When intention and effect match, no detailed coding of control is required, and agency is simply assumed. Absence of modulation of AG activity in compatible trials thus confirms that AG codes only for "violations" of this default mode of action experience.

Functional Connectivity (PPI)

Finally, to investigate in more detail the relation between subjective sense of control and action selection, we additionally performed connectivity analyses (PPI) to assess how mismatch-related coding of subjective agency by AG might depend on regions that objectively coded for prime–target compatibility (i.e., DLPFC, orbitofrontal cortex, and left putamen) (for details, see Supplementary Information). PPI revealed that the dysfluency of action selection caused by prime–target mismatches triggered a change in the pattern of frontoparietal interactions. Specifically, incompatible trials induced a significant decrease in functional connectivity between left AG and left DLPFC, with greater activation in DLPFC being associated with lower activation in AG (local maximum at –42, 9, 45, T = 3.84, P < 0.001) (Fig. 4*b*). In compatible trials, in contrast, no covariation between these regions was observed.

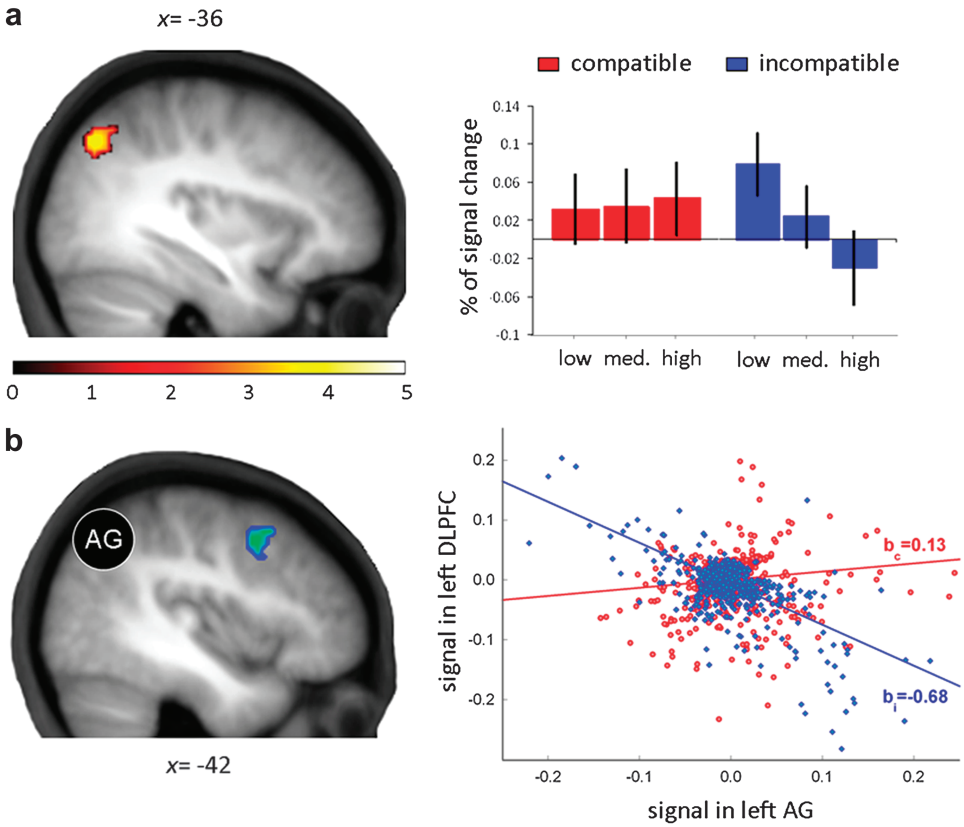

Figure 4. Parametric interaction of control and compatibility in the AG, and analyses of functional connectivity between AG and DLPFC. (*a*) Left AG is differentially modulated by participants' control ratings (low, medium, and high) depending on how fluent action selection is; scale shows *t*-value. (*b*) PPI of left AG and left DLPFC for a single subject: dysfluency of action selection led to significantly decreased connectivity between both regions. Measurements during the COMPATIBLE condition (prime–target "match"): red circles; measurements during the INCOMPATIBLE condition (prime–target "mismatch"): blue diamonds. Mean-corrected activity in left DLPFC (−42, 9, 45) is displayed as a function of mean-corrected activity in left AG (−36, −69, 45). Condition-specific regression slopes, b_c (compatible) and b_i (incompatible). The difference between regression slopes constitutes the PPI ($P < 0.001$, $t = 3.84$).

AG Prospectively Monitors Signals Relating to Action Selection by DLPFC

We suggest 2 alternative interpretations of the antagonistic relation between AG and DLPFC revealed by the PPI analyses:

On one interpretation, our DLPFC activation could reflect an intentional fluency akin to the well-established DLPFC contribution to willed action (e.g., Frith et al. 1991a, 1991b). Interestingly, previous studies of willed action also noticed the same frontoparietal correlation observed here, namely that increased activity in DLPFC was associated with decreased activity in the AG (Frith et al. 1991a). Our results are directly analogous: compatible primes might partly engage circuits for willed action, while incompatible primes might relatively decrease activity in this circuit (Wenke et al. 2010). Decreased DLPFC activity due to incompatible primes might result in a concomitant increase in AG activity and a subjective loss of control.

A second alternative interpretation may be related to the role of DLPFC in top–down cognitive control and selection of appropriate responses according to current task demands (Miller and Cohen 2001; Koechlin et al. 2003). In particular, a key control function of DLPFC is to resolve conflicts by allowing responses with weaker activation levels to gain priority over stronger ones under appropriate circumstances. In the present study, DLPFC activation in incompatible trials could reflect this "overriding of contention scheduling" (Shallice 1988). Strong DLPFC activation may be required to exert cognitive control in cases of incompatible priming (Lau and Passingham 2007). Strong DLPFC activation would therefore reduce mismatch-related activation in AG. Since AG activation is in turn negatively correlated with the subjective sense of control, such executive activation of DLPFC would therefore tend to produce a relative increase in sense of control. However, this conflict-based account of DLPFC-AG connectivity does not fit easily with the findings of our contrast analyses. There, we found that DLPFC was more strongly activated on compatible than incompatible trials. The conflict account assumes that DLPFC activation on incompatible trials is proportional to prime-induced conflict, but this seems implausible given the stronger DLPFC activation on compatible trials, where prime-induced conflict should be absent. For this reason, our connectivity results fit more convincingly with the view that compatible subliminal priming partly recruits brain mechanisms for willed action than the view that incompatible subliminal priming recruits brain mechanisms for cognitive control over conflicts.

Future work is required to test the exact function of DLPFC in this paradigm. Importantly, however, both interpretations promote the same general intuition, namely, that subjective sense of control over action effects is computed by the AG at the time of response selection, by monitoring signals relating to either selection of one action from the possible response space

(i.e., conflict resolution) or signals relating to intentional willed action. Both signals may involve, or be generated by, the DLPFC.

Discussion

In summary, our findings confirm that fluency of action selection influences the sense of control during subsequent operant action (Wenke et al. 2010). When participants made actions that matched a subliminally primed response tendency, they experienced greater control over a subsequent effect than following incompatible prime–target associations. That is, priming action selection and generation to increase the fluency of action produced a stronger sense of control. Importantly, priming did not influence the actual objective level of control that participants had over the colors presented after their actions: the contingency between action and color effect was similar for compatibly primed and incompatibly primed trials. So the prospective sense of control identified in our experiment is in fact an illusion of control, since it is not based on differences in the actual statistical relation between action and effect. In everyday life, however, prospective and retrospective contributions to sense of control generally agree: to take our original example, the successful manager feels in control when she makes decisions, and her sense of control is later confirmed when quarterly sales figures come in.

Our results highlight the neural basis of prospective sense of control for the first time. When incompatible primes produced mismatches between response tendency and the required action, activity in the AG coded for violations of this default mode of self-agency. Furthermore, this mismatch-related activity predicted the magnitude of subsequent sense of control. Importantly, altered experience of control and its underlying neural coding occurred in the absence of any mismatch between the overt action and its external consequences.

Previous studies have shown that decreasing the predictability of action effects strongly reduces the sense of control (Blakemore et al. 1998; Sato and Yasuda 2005; Farrer et al. 2008; Moore and Haggard 2008; Sato 2009), suggesting that mismatch between intention and effect is a key determinant of sense of agency. In contrast, in our design, color effects could never be predicted from primes alone, or even from actions alone. Therefore, the classical retrospective view, that agency derives from matching intended and actual consequences of action, cannot account for the different levels of control that our participants felt in compatible and incompatible trials. Instead, our data suggest that an important component of the experience of control derives from online monitoring of processes occurring before movement. In particular, AG codes for the dysfluency triggered by prime–target mismatch, and this prospective coding influences subsequent sense of control over action effects.

To the best of our knowledge, these findings provide the first direct evidence of a prospective contribution to judgments of agency. We further demonstrate that the AG tracks violations of the default agency mode by monitoring fluency of action selection processes in DLPFC. This monitoring process may provide the subject with prospective information about control over action effects. Accordingly, we believe this finding bridges the apparent gap between 2 accounts of AG function. The inferior parietal cortex not only monitors sensory feedback offline, to produce retrospective beliefs about agency (Farrer et al. 2003, 2008), but also provides real-time monitoring of developing action-generation processes (Sirigu et al. 2004; Desmurget et al. 2009), in advance of the action itself. This online monitoring function would provide the subject with a subjective marker of the normal successful flow of information along the intention-action chain. We show that an error occurring along this chain, signaled by dysfluency of action selection, produces decreased ratings of control.

Taken together, these findings suggest an important qualification of recent post hoc determinist views of action control. In its strongest form, this view suggests that human behavior is unconsciously determined by subtle changes in the stimulus environment (Ackerman et al. 2010). Individuals are not therefore aware of how their behavior is shaped and transformed, although they can retrospectively integrate general information about past actions and environmental cues to make inferences about their own behavior: "people ... are not intrinsically informed about the authorship of their own action" (Wegner 2002). In contrast, our results suggest that monitoring fluency signals generated during action selection could provide an important prospective agency cue. While our participants did not have any conscious experience of the subliminal primes, they did have a real-time "subjective experience" deriving from their own prime-influenced action generation. We further show that subjects may use this online signal to estimate control over their unfolding action and its subsequent outcome.

The experience of agency has been linked to "conscious free will." Our belief in free will indeed arises because we strongly feel that we control our own actions (Haggard 2008). As such, fluency signals generated during action selection might provide an internal marker of volition. These signals could prevent delusions of volition arising from excessive reliance on post hoc judgments of action-effect associations—as occurs in schizophrenic "delusions of control" (Voss et al. 2010). At the same time, excessive reliance on these prospective signals may produce the opposite delusion of omnipotence, in which the mere decision to act is incorrectly assumed to produce successful action outcomes. This latter illusion appears to be common in historical despots but is interestingly absent in depressed people (Alloy and Abramson 1979). Our results suggest that real-time monitoring of action selection is one important contribution to sense of agency. Normally, however, both prospective and retrospective information relevant to agency are available. A robust and reliable sense of agency may require a mixture of both prospective and retrospective components.

Conclusion

We showed that fluency of action selection processes prospectively informs sense of agency. Specifically, the subjective sense of control over action effects is computed by the AG in advance of the action itself, by monitoring signals relating to fluency of action selection by DLPFC. Importantly, this computation arose prior to any (retrospective) comparison between the action being planned and its intended effects. This does not mean that effects of an action are irrelevant to sense of agency. Rather, the sense of control over action effects is additionally informed by early real-time signals arising during action programming and before action itself. Monitoring of these signals in the AG might provide a reliable marker of

volition, thus preventing delusions of agency that can arise from dependence on post hoc judgments of action effect associations. Although the prospective sense of control we have described may be strictly illusory, just like "conscious free will" (Libet et al. 1983), it is psychologically important. Specifically, neural monitoring of internal action selection processes may combine with monitoring of external action effects to produce the feeling of being in control.

Supplementary Material

Supplementary material can be found at: http://www.cercor.oxfordjournals.org/

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Notes

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References

Ackerman JM, Nocera CC, Bargh JC. 2010. Incidental haptic sensations influence social judgments and decisions. Science. 328:1712–1715.

Alloy LB, Abramson LY. 1979. Judgment of contingency in depressed and nondepressed students: sadder but wiser? J Exp Psychol Gen. 108:441–485.

Blakemore SJ, Wolpert D, Frith C. 1998. Central cancellation of self produced tickle sensation. Nat Neurosci. 1:635–640.

Desmurget M, Reilly KT, Richard N, Szathmari A, Mottolese C, Sirigu A. 2009. Movement intention after parietal cortex stimulation in humans. Science. 324:811–813.

Diedrichsen J, Shadmehr R. 2005. Detecting and adjusting for artifacts in fMRI time series data. Neuroimage. 27:624–634.

Evans AC, Kamber M, Collins DL, MacDonald D. 1994. A MRI-based probabilistic atlas of neuroanatomy. In: Shorvon S, Fish D, Andermann F, Bydder GM, Stefan H, editors. Magnetic resonance scanning and epilepsy. New York: Springer. p. 263–274.

Farrer C, Franck N, Georgieff N, Frith CD, Decety J, Jeannerod M. 2003. Modulating the experience of agency: a positron emission tomography study. Neuroimage. 18:324–333.

Farrer C, Frey SH, Van Horn JD, Tunik E, Turk D, Inati S, Grafton ST. 2008. The angular gyrus computes action awareness representations. Cereb Cortex. 18:254–261.

Farrer C, Frith CD. 2002. Experiencing oneself vs another person as being the cause of an action: the neural correlates of the experience of agency. Neuroimage. 15:596–603.

Frith CD, Blakemore SJ, Wolpert DM. 2000. Abnormalities in the awareness and control of action. Philos Trans R Soc Lond B Biol Sci. 355:1771–1788.

Frith CD, Friston K, Liddle PF, Frackowiak RSJ. 1991a. Willed action and the prefrontal cortex in man: a study with PET. Proc R Soc Lond B Bio Sci. 244:241–246.

Frith CD, Friston K, Liddle PF, Frackowiak RSJ. 1991b. A PET study of word finding. Neuropsychologia. 29:1137–1148.

Genovese CR, Lazar NA, Nichols T. 2002. Thresholding of statistical maps in functional neuroimaging using the false discovery rate. Neuroimage. 15:870–878.

Haggard P. 2005. Conscious intention and motor cognition. Trends Cogn Sci. 9:290–295.

Haggard P. 2008. Human volition: towards a neuroscience of will. Nat Rev Neurosci. 9:934–946.

Haggard P, Clark S, Kalogeras J. 2002. Voluntary action and conscious awareness. Nat Neurosci. 5:382–385.

Haggard P, Tsakiris M. 2009. The experience of agency: feelings, judgements, and responsibility. Curr Dir Psychol Sci. 18:242–246.

Koechlin E, Ody C, Kouneiher F. 2003. The architecture of cognitive control in the human prefrontal cortex. Science. 302:1181–1184.

Lau HC, Passingham RE. 2007. Unconscious activation of the cognitive control system in the human prefrontal cortex. J Neurosci. 27:5805–5811.

Libet B, Gleason CA, Wright EW, Pearl DK. 1983. Time of conscious intention to act in relation to onset of cerebral activity (readiness-potential). The unconscious initiation of a freely voluntary act. Brain. 106:623–642.

Metcalfe J, Greene JG. 2007. Metacognition of agency. J Exp Psychol Gen. 136:184–199.

Miller EK, Cohen JD. 2001. An integrative theory of prefrontal cortex function. Annu Rev Neurosci. 24:167–202.

Moore J, Haggard P. 2008. Awareness of action: inference and prediction. Conscious Cogn. 17:136–144.

Nahab FB, Kundu P, Gallea C, Kakareka J, Pursley R, Pohida T, Miletta N, Friedman J, Hallett M. 2011. The neural processes underlying self-agency. Cereb Cortex. 21:48–55.

Sato A. 2009. Both motor prediction and conceptual congruency between preview and action–effect contribute to explicit judgement of agency. Cognition. 110:74–83.

Sato A, Yasuda A. 2005. Illusion of sense of self-agency: discrepancy between the predicted and actual consequences of actions modulates the sense of self-agency, but not the sense of self-ownership. Cognition. 94:241–255.

Shallice T. 1988. From neuropsychology to mental structure. Cambridge: Cambridge University Press.

Sirigu A, Daprati E, Ciancia S, Giraux P, Nighoghossian N, Posada A, Haggard P. 2004. Altered awareness of voluntary action after damage to the parietal cortex. Nat Neurosci. 7:80–84.

Vorberg D, Mattler U, Heinecke A, Schmidt T, Schwarzbach J. 2003. Different time courses for visual perception and action priming. Proc Natl Acad Sci U S A. 100:6275–6280.

Voss M, Moore J, Hauser M, Gallinat J, Heinz A, Haggard P. 2010. Altered awareness of action in schizophrenia: a specific deficit in predicting action consequences. Brain. 133:3104–3112.

Wegner DM. 2002. The illusion of conscious will. Cambridge (MA): MIT Press.

Wegner DM, Sparrow B, Winerman L. 2004. Vicarious agency: experiencing control over the movements of others. J Pers Soc Psychol. 86:838–848.

Wenke D, Fleming SM, Haggard P. 2010. Subliminal priming of actions influences sense of control over effects of action. Cognition. 115:26–38.