

How action selection influences the sense of agency: An ERP study



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ABSTRACT

Sense of agency (SoA) refers to the feeling that we are in control of our actions and, through them, of events in the outside world. One influential view claims that the SoA depends on retrospectively matching the expected and actual outcomes of action. However, recent studies have revealed an additional, prospective component to SoA, driven by action selection processes. We used event-related potentials (ERPs) to clarify the neural mechanisms underlying prospective agency. Subliminal priming was used to manipulate the fluency of selecting a left or right hand action in response to a supraliminal target. These actions were followed by one of several coloured circles, after a variable delay. Participants then rated their degree of control over this visual outcome. Incompatible priming impaired action selection, and reduced sense of agency over action outcomes, relative to compatible priming. More negative ERPs immediately after the action, linked to post-decisional action monitoring, were associated with reduced agency ratings over action outcomes. Additionally, feedback-related negativity evoked by the outcome was also associated with reduced agency ratings. These ERP components may reflect brain processes underlying prospective and retrospective components of sense of agency respectively.

Introduction

The sense of agency (SoA) refers to the feeling that we are in control of our actions and, through them, of events in the outside world (Haggard and Tsakiris, 2009). Typically, SoA figures mostly in the background of our mental lives (Gallagher, 2012; Legrand, 2007), but we become acutely aware of our experience of agency when the smooth flow from intention to action to outcome is disrupted (Haggard and Chambon, 2012). Many studies have focused on the link between actions and outcomes. The dominant view suggests that SoA relies on a comparison between expected and observed action outcomes (Blakemore et al., 2002; Hughes et al., 2013; Wegner and Wheatley, 1999). When there is a mismatch between expected and observed outcomes, our SoA is reduced. According to this view, SoA depends primarily on a match between predictive and retrospective information.

More recently, we have investigated an additional, *prospective* component of the SoA, involving the mechanisms of generating the action. Because action generation processes necessarily occur prior to action, and are, crucially, unrelated to outcomes, this component does not depend on retrospective information, or on the processing of outcomes (see Chambon et al., 2014 for a review). More specifically, the

mechanisms underlying selection between alternative actions contribute significantly to SoA. Dysfluency, or difficulty, in action selection, triggered by subliminal or supraliminal stimuli associated with a conflicting response, leads to a reduction in the SoA over action outcomes (Chambon and Haggard, 2012; Chambon et al., 2013; Sidarus et al., 2013; Sidarus and Haggard, 2016; Wenke et al., 2010).

The neural correlates of this prospective component of SoA (henceforth, *prospective SoA* for short) have been studied with fMRI (Chambon et al., 2013), using subliminal priming to manipulate action selection. As this experiment was the starting point for the present work, we describe it in some detail. Participants responded to a left or right pointing arrow with a corresponding left or right hand action. After a variable delay, a coloured circle would appear. At the end of the trial, participants were asked to judge how much control they felt over that coloured circle. Importantly, and unbeknownst to the subject, a prime arrow was subliminally presented before the visible target arrow (Vorberg et al., 2003). If the prime arrow was compatible with the target, i.e. pointed in the same direction, action selection was facilitated, leading to shorter reaction times (RTs). When the prime was incompatible with the target, i.e. pointed in the opposite direction, action selection was impaired, as evidenced by slower RTs and more

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errors. These incompatible priming trials were associated with lower agency ratings, relative to compatible priming. fMRI results showed that activity in the angular gyrus (AG) was related to a loss of agency in incompatible priming trials, such that trials with greater AG activity were associated with lower agency ratings. Notably, this activation pattern was modelled during the action selection period, between prime onset and action, thus before the outcome was known, and long before agency ratings were given.

The poor temporal resolution of fMRI does not permit a more detailed investigation of the temporal dynamics of prospective signals to SoA. In contrast to fMRI, the higher temporal resolution of EEG may help differentiate prospective processes linked to action monitoring, from later retrospective processes linked to outcome monitoring. Here we used event-related potentials (ERP), and the aforementioned subliminal priming task (Chambon et al., 2013), to investigate the contribution of three distinct stages of processing to SoA, locked to the target, the action, and the outcome. We next briefly consider the role of each, based on previous literature.

Action monitoring

ERP studies of action priming have shown that incompatible prime-target combinations are associated with an N2 component, 200–350 ms after target onset, which is absent or greatly reduced for compatible priming (Hughes et al., 2009; Jiang et al., 2013; Verleger and Jaskowski, 2008; Wang et al., 2013). A similar component was previously identified using the Eriksen flanker task, when distractors are incompatible with a central target (e.g. HSHH; Kopp et al., 1996). The N2 component is thought to reflect pre-response conflict detection and resolution (Donkers and van Boxtel, 2004; Yeung et al., 2004). N2 amplitude is linked to both the degree of conflict in a given task, and of cognitive control recruited to resolve conflict (Larson et al., 2014). We therefore predicted that the N2 to the target stimulus would be larger following incompatible, relative to compatible, priming. Moreover, as N2 amplitude is thought to reflect the degree of conflict, it might serve as an early index of action selection dysfluency, and in turn be associated with prospective SoA. Thus, we predicted that larger N2 amplitude would be related with a reduction in SoA.

A recent transcranial magnetic stimulation (TMS) study showed that disrupting the inferior parietal lobe (to target the AG), both before and immediately after the action, abolished action priming effects on SoA (Chambon et al., 2015). This suggests that action monitoring even after action execution is related to the effects of action selection fluency on SoA. Crucially, this post-decisional action monitoring occurs before, and independently of, outcome monitoring. Therefore, it can provide a prospective signal to SoA.

The error-related negativity (ERN) is a well-known component in response-locked ERPs, elicited within 100 ms of erroneous responses, with a fronto-central scalp distribution, and thought to index post-decisional conflict monitoring (for reviews, see Larson et al., 2014; Yeung and Summerfield, 2012). Even in correct trials, the correct-related negativity (CRN) has been argued to reflect similar processes. Studies on metacognition have shown that these response-related negativities (C/ERN) scaled with confidence judgements, with most negative potentials for high confidence of an error, average when uncertain, to least negative for high confidence in being correct (Boldt and Yeung, 2015; Scheffers and Coles, 2000). A larger CRN has also been associated with greater objective uncertainty or difficulty in perceptual discrimination tasks (Endrass et al., 2012; Pailing and Segalowitz, 2004). Because post-decisional monitoring allows the integration of initial conflict signals with information about conflict resolution processes, the CRN may serve to signal a continued need for cognitive control (Grützmann et al., 2014). Therefore, as a post-response index of selection dysfluency, we hypothesised that the CRN might be associated with prospective SoA, with a larger CRN being associated with a reduction in SoA.

Outcome monitoring

Previous ERP studies on SoA have shown that voluntary actions lead to an attenuation of outcome processing, relative to comparable externally-triggered events (Gentsch and Schütz-Bosbach, 2011; Kühn et al., 2011; Timm et al., 2013). Sensory attenuation of outcomes has been proposed as a marker of agency also in behavioural studies (Blakemore et al., 1998; Shergill et al., 2005). However, sensory attenuation depends on outcomes being highly predictable, close in time to the action (see Hughes et al., 2013 for a review), and high in salience (Reznik et al., 2015). Therefore, under conditions of uncertainty about the outcome, such as during the learning of new action-outcome associations, sensory attenuation may be less relevant to outcome monitoring.

Another well-known outcome monitoring component is the feedback-related negativity (FRN), a fronto-central component seen around 250–300 ms after outcome feedback. This is generally larger following negative or unexpected feedback (for reviews, see San Martín, 2012; Ullsperger et al., 2014). The reinforcement learning account (Holroyd and Coles, 2002; Holroyd et al., 2008) suggests that the FRN reflects dopaminergic prediction-error signals, with worse than expected outcomes resulting in a larger FRN. The expectancy-deviation account (Oliveira et al., 2007) proposes that the FRN is associated with ACC-mediated monitoring and learning of action-outcome associations more generally. Mismatches between expected and observed outcomes would result in greater ACC activation, and larger FRN, serving to signal a need for cognitive control, and updating of internal models of action-outcome contingencies. Moreover, previous studies comparing FRN between gains and losses have shown greater FRN sensitivity associated with outcomes perceived as contingent, relative to non-contingent, on action (Yeung et al., 2005); and with greater perceived responsibility over outcomes (Li et al., 2010; Li et al., 2011).

However, the terminology for this component has been disputed. Novel or surprising events can elicit an N2 component, with a similar latency and scalp distribution, which could be confounded with, or reflect similar mechanisms to, the FRN (Folstein and Van Petten, 2008; Wessel et al., 2012). On another view, this component would be best described as a positive-going potential for positive outcomes, termed feedback-correct related positivity (fCRP; Holroyd et al., 2008; Oliveira et al., 2007). In fact, a recent study on agency attribution showed that a smaller fCRP (or more negative potentials) were associated with outcomes that were externally- vs. self-attributed (Bednark and Franz, 2014). Irrespective of naming conventions, these findings generally agree that less negative (or more positive) potentials, similar to the FRN, are typically associated with correct, expected, or rewarding outcomes, and thus could be a putative correlate of greater SoA. To place our findings within the context of an outcome/performance monitoring framework (e.g. San Martín, 2012; Ullsperger et al., 2014), we will use the FRN label to refer to this hypothesised substrate of the retrospective component of SoA.

Present study

The present study aimed to investigate putative neural correlates of SoA. Each trial involved subliminal action primes, supraliminal target stimuli, manual responses to those targets, a delayed visual outcome, and an explicit judgement of agency (Chambon et al., 2013). We measured candidate ERPs to different events in this sequence, to investigate potential neural correlates of prospective and retrospective components contributing to SoA (see Fig. 1). A putative neural correlate of prospective SoA should occur prior to any action outcome, thus be related to action monitoring, and should correlate with agency ratings. Finally, we included both free choice and instructed trials, to investigate whether the endogenous vs. exogenous origins of action contribute similarly to SoA.

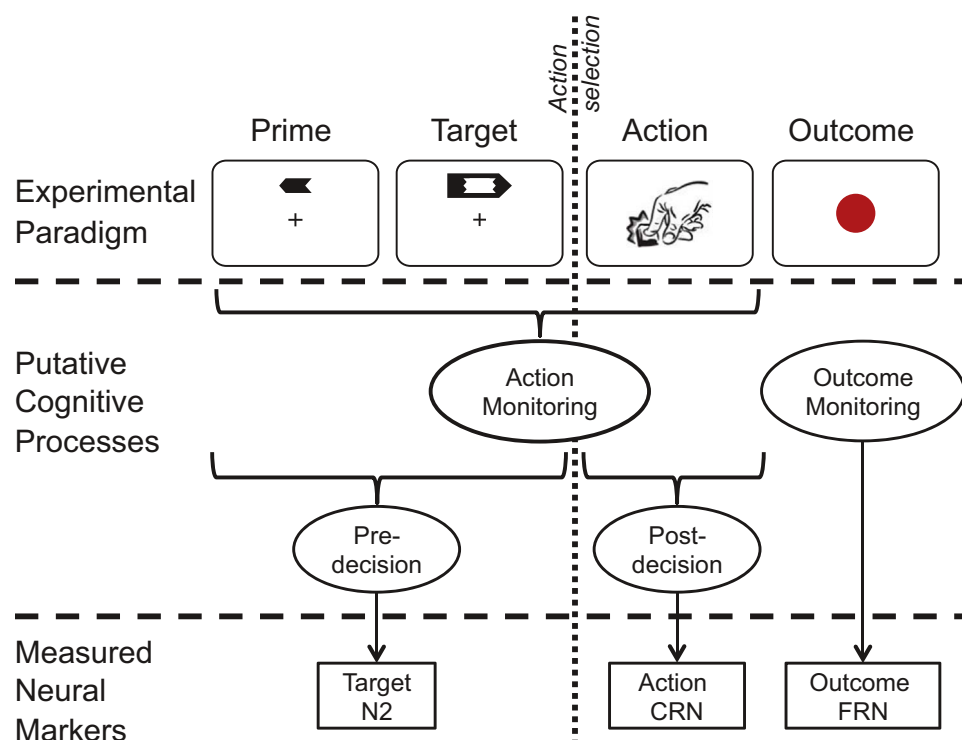


Fig. 1. Schematic outline of the experimental paradigm with the putative cognitive processes involved at different stages of voluntary action. These processes are thought to be respectively indexed by the neural markers measured here. The ERP components thought to index action monitoring processes, i.e. Target-locked N2 and Action-locked correct related negativity (CRN), are hypothesised to relate to the prospective component of SoA. The Outcome-locked feedback-related negativity (FRN) is thought to index outcome monitoring, and hence is hypothesised to reflect the retrospective component of SoA.

Materials and methods

Participants

Thirty-five participants were recruited via a UCL online database, to obtain a desired sample size of 24, based on an *a priori* power calculation (given Cohen's $d_z=0.65$ for within-subjects comparison of compatibility effect on agency ratings Chambon et al. (2013), power=0.8, alpha=0.05). All were right-handed, with normal or corrected-to-normal vision, did not suffer from colour blindness, and had no history of psychiatric or neurological disorders. Participants received payment of £7.50/hour. Written informed consent was obtained from all participants. The study had ethical approval from the UCL Research Ethics Committee. Seven participants were excluded due to high artefact rejection rates (above 30% of the data). Three participants were excluded as they were uncooperative, or did not adequately follow instructions (e.g. repeatedly falling asleep during study; reported pre-deciding their response prior to each trial; reported in debriefing that they based their agency ratings on colour preference rather than on the relation to their own action). One further participant was excluded because they may have consciously perceived the primes (post-test $d^2=0.65$, over 2 SD's above the group mean $d^2=0.02$, $SD=0.21$). Twenty-four participants remained (12 females, mean age=24.38, $SD=4.90$).

Apparatus and materials

The experiment was programmed using Psychophysics Toolbox v3 (Brainard, 1997; Kleiner et al., 2007; Pelli, 1997). Stimuli were presented on a mid-grey background, on a 17" CRT monitor (75 Hz refresh rate) positioned at approximately 60 cm distance from participants. Prime and mask stimuli consisted of left- or right-pointing arrows, presented in dark grey. Primes subtended visual angles of $0.8^\circ \times 1.86^\circ$, and masks $1.09^\circ \times 3.47^\circ$. Prime and mask could appear

randomly 1.38° above or below fixation to enhance the masking effect (Vorberg et al., 2003). Each action was followed by a visual stimulus in one of 8 colours (see later) subtending 3.8° .

Design and procedure

Agency task. In the main task, participants had to respond to a target arrow with left or right hand action, which would trigger the appearance of a visual outcome – a coloured circle (see Fig. 2 below for an outline of the paradigm). At the end of a trial, they were asked to rate how much control they felt they had over the visual outcome they had just seen.

In forced choice trials, a directional arrow (pointing randomly to the left or right) instructed participants to perform the corresponding left or right hand action. In free choice trials, a bi-directional arrow indicated that participants could choose themselves whether to make a left or right hand action. Participants were instructed to try and make their choices as spontaneously as possible, and avoid deciding in advance of a trial, but at the same time, to try to choose each hand about 50% of the time. To ensure similar number of trials across actions, feedback was given at the end of each block on the percentage of left and right hand choices. Forced and free choice trials were randomised, and equiprobable.

Primes and actions could either be compatible or incompatible. In forced choice trials, prime direction could be the same as the target direction, and thus would also be compatible with the action, or primes might point in the opposite direction as the target arrow, and be incompatible with the action. Prime-action compatibility was determined online for free choice trials. When participants chose the action suggested by the prime, i.e. a left action following a left prime, trials were classed as compatible. Trials were classed as incompatible when participants chose the opposite action to the prime (i.e. a right action).

Crucially, the outcome colours were not directly related to the

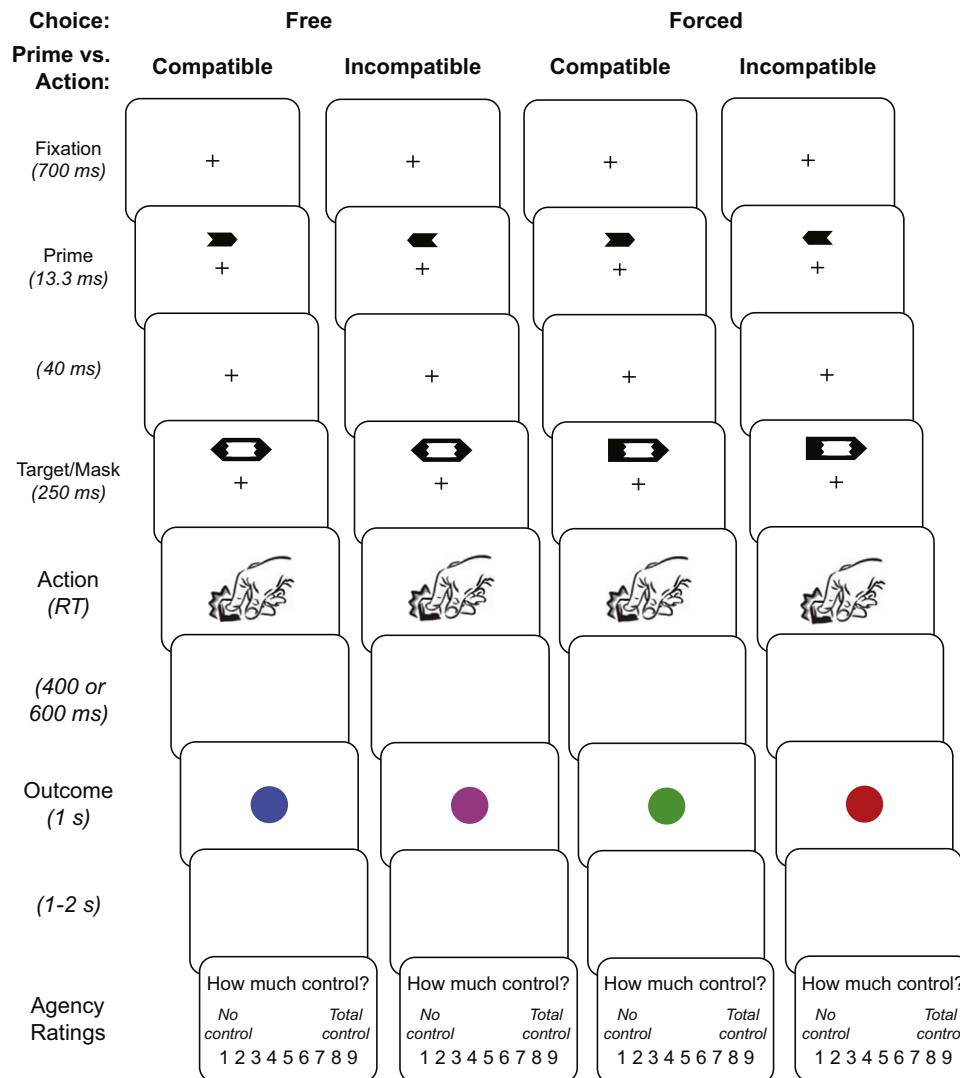


Fig. 2. Experimental paradigm. Left or right subliminal prime arrows were briefly flashed before a target arrow, containing a metacontrast mask. Participants responded to the target by either following the instruction of directional arrows, or choosing which action to perform in response to the bi-directional (free choice) arrow. Primes and actions could be compatible (left prime – left action) or incompatible (left prime – right action). Actions triggered the onset of a visual outcome, after a variable delay. At the end of the trial, participants gave agency ratings.

primes alone, or to the actions alone. Rather, the outcome colour was based on the *combination* of prime and target, or prime and action, so that compatible and incompatible trials were associated with different colours. Further, different colours were used for free and forced choices. Hence, within a block, 4 colours were associated with each choice condition. Of these, two colours were associated with each action, one for each level of prime-action compatibility (cf. [Wenke et al., 2010](#)). Moreover, to ensure that the frequency of each coloured outcome was equal despite differences in error rates for compatible and incompatible priming, error trials were replaced at the end of a block. Finally, to exclude any idiosyncratic preference effects, the colours were latin square rotated across 8 blocks of trials, so that each colour appeared once in each choice×action×compatibility condition. An extra block of trials with a random assignment of colours to conditions was completed at the end of the 8 blocks. This block was included to detect any anomalous use of the rating scale, but was not otherwise analysed.

The interval between action and outcome was randomly either 400 or 600 ms. The minimum interval of 400 ms between action and outcome helped to reduce the influence of action-related components on the outcome-locked ERP ([Hughes and Waszak, 2011](#)). Action-outcome interval was jittered because variation in temporal contiguity was predicted to lead to varying sense of agency, and thus to reduce

stereotyped agency judgements ([Haggard et al., 2002](#); [Wenke et al., 2010](#)). Interval duration was orthogonal to the factors of interest in the present study (choice, action and prime-action compatibility).

A trial started with a central fixation cross presented for 700 ms. Primes were shown for 13.3 ms and, after a 40 ms delay, the target/mask stimulus was displayed for 250 ms. Previous studies have shown that these parameters allow for robust priming effects, without conscious perception of primes ([Vorberg et al., 2003](#)). Participants were instructed to respond as quickly as possible to the target arrow by pressing a corresponding left or right arrow key, or to choose which action to make when bi-directional targets were shown. If they pressed the wrong key (in forced choice trials), or were too slow (> 1.2 s), a black cross appeared, indicating an error. Otherwise, after a variable delay a coloured circle would appear, for 1 s. Participants were instructed to pay attention to the relation between their action and the coloured circle that followed. To prevent EEG artefacts, participants were instructed not to blink until after the coloured circle disappeared.

After a variable delay between 1 and 2 s, the agency rating scale was presented until participants made a response. Participants were asked to judge how much control they felt over the coloured circle, on a Likert-type scale ranging from 1 to 9 (1=very little control, 9=very

strong control). They were asked to judge how strongly they felt that the action they had just made was related to the colour that followed. They were further asked to use the whole range of the scale, to indicate differences between cases in which they felt more control over the colour (using higher ratings) compared to when they felt less in control (using lower ratings). [See [Supplementary materials](#) for histograms of agency ratings across participants.] Inter-trial intervals varied randomly between 1 and 1.5 s.

The study started with a training block of 48 trials. If participants felt confident about the task and agency ratings, they proceeded to main experiment. The main experiment consisted of 8 blocks of 64 trials. Participants could take small breaks between the blocks. After the main experiment, participants were debriefed on the presence of primes and completed a prime awareness test.

Prime awareness test. To assess whether primes remained subliminal for all participants, after the main experiment participants were debriefed about the presence of primes and completed a prime awareness test. This task resembled the main experiment, except without any colours following the action, or agency ratings. Participants were instructed to press the left- or right-arrow key according to the direction of the prime arrow, ignoring the supraliminal target arrow. To avoid possible response biases induced by directional targets (Vermeiren and Cleeremans, 2012), only the bi-directional arrow target was used. Additionally, a delay was introduced after mask presentation in which participants could not respond (Wenke et al., 2010). This served to prevent conscious reports from being biased by unconscious motor activations triggered by primes (Vorberg et al., 2003). This delay varied randomly between 600 and 800 ms, with an auditory tone (600 Hz, 150 ms duration) signalling that participants could respond. This test consisted of 3 blocks of 60 trials.

EEG recording and analysis

EEG was acquired with a 64 channel BioSemi Active-Two system (Biosemi Inc, Amsterdam, Netherlands) and sampled at 512 Hz. The CMS (common mode sense) and DRL (driven right leg) electrodes were used as reference and ground electrodes. Additional electrodes were placed on the left and right mastoid. Vertical and horizontal EOGs were recorded from electrodes placed above and below the right eye and on the outer canthi of the left and right eyes.

EEG data analysis was performed with Fieldtrip (Oostenveld et al., 2011) and custom-built Matlab scripts (MATLAB 8.1, The MathWorks Inc., Natick, MA, 2013). All channels were 0.1–30 Hz band-pass filtered, and re-referenced to average mastoids. An automatic artefact rejection procedure was employed. To identify epochs with eye-blink artefacts, EOG channels were bandpass filtered from 1–15 Hz (Butterworth filter, 4th order) and any epochs with activity exceeding $\pm 60 \mu\text{V}$ were rejected. Additionally, any epochs where EEG activity exceeded $\pm 60 \mu\text{V}$ were excluded. Due to recording difficulties with some subjects, and given that these electrodes were not of interest, the following channels were excluded from analysis: T7, T8, TP7, TP8, P9 and P10. In four participants, 1 channel had to be interpolated due to abnormal noise (P7, AF3, F5 and P2 for each participant respectively). Error trials, in which participants pressed the wrong key after a forced choice target ($M=3.26\%$ $SD=2.66$), or exceeded the response window (> 1.2 s; $M=1.54\%$ $SD=1.33$) were excluded.

Target-locked ERPs. Target-locked epochs were selected from 200 ms pre-stimulus to 600 ms after. Baseline correction was applied with a 100 ms interval prior to prime onset (–155 to –55 ms). Separate ERPs were calculated for each choice and priming condition. Based on previous studies (Larson et al., 2014) and observation of grand ERPs and scalp topography, the Target N2 component was analysed as the

average amplitude at Cz, between 250 and 325 ms.

Action-locked ERPs. Action-locked epochs were selected from 600 ms before the action to 400 ms after, with a 100 ms baseline before action. Based on previous studies on the Error and Correct Related Negativity (ERN/CRN; e.g. Boldt and Yeung, 2015; Scheffers and Coles, 2000), CRN was measured as the average amplitude at FCz from 0 to 100 ms after the action. Although some differences between conditions can be seen in the action-locked ERPs more than 100 ms post-action in Fig. 4c, these were not analysed since they did not correspond to our *a priori* ERP components of interest. The ERP plots are nonetheless presented for completeness.

Outcome-locked ERPs. Outcome-locked epochs were selected from 200 ms before stimulus to 600 ms after, with a 100 ms pre-stimulus baseline. Feedback Related Negativity (FRN) was measured as the average amplitude from 250 to 300 ms at FCz, based on observation of the data and previous research (Yeung et al., 2005).

Trials with available artefact-free epochs locked to all three events (target, action, and outcome) were identified, and matched to the behavioural data. This resulted in an average N trials=92, min=45, across choice \times priming conditions. ERP components were analysed with hierarchical linear regression models (also known as linear mixed-effects models). This approach, unlike classical ANOVA models, performs well with unbalanced data (Baayen et al., 2008; Bagiella et al., 2000; Tibon and Levy, 2015). Additionally, it allowed us to investigate the relation between agency ratings and ERP components, by modeling single-trial level data with continuous predictors. Analyses were conducted using the *lme4* package (Bates et al., 2014) in R (R Core Team, 2015). Parameter estimates (b) and their associated t -tests (t , p), calculated using the Satterthwaite approximation for degrees of freedom (Kuznetsova et al., 2015), are presented to show the magnitude of the effects, with bootstrapped 95% confidence intervals. Plots of model predictions were obtained from 10,000 simulations from the posterior distribution of plausible parameter values under uniform priors (Gelman and Su, 2015).

For display purposes only, but not for statistical analysis, agency ratings were median split to demonstrate the relation between neural processes indexed by ERP components and SoA. For each subject, and for each choice and priming condition, median agency rating values were obtained, and trials were classed as low or high agency ratings with respect to the median.

Results

Agency task

Mean RTs were submitted to a repeated measures analysis of variance (ANOVA), with the factors choice (free vs. forced) and priming condition (compatible vs. incompatible). This revealed a significant main effect of choice ($F_{(1,23)}=5.92$, $p=0.023$, $\eta_p^2=0.21$), such that free choice trials led to slower RTs than forced choice (free: $M=432.11$, $SD=147.69$; forced: $M=420.65$, $SD=124.11$). There was also a significant main effect of prime-action compatibility ($F_{(1,23)}=74.36$, $p < 0.001$, $\eta_p^2=0.76$), as predicted, with slower RTs for prime incompatible actions than prime compatible actions (compatible: $M=414.95$, $SD=34.12$; incompatible: $M=440.52$, $SD=31.82$; see Fig. 3a). The interaction was not significant ($F_{(1,23)}=1.98$, $p=0.17$, $\eta_p^2=0.079$).

In free choice trials, prime compatible choices were made on 59% ($SD=0.06$) of trials, revealing a choice bias. A one-sample t -test revealed this was significantly different from chance level of 50%

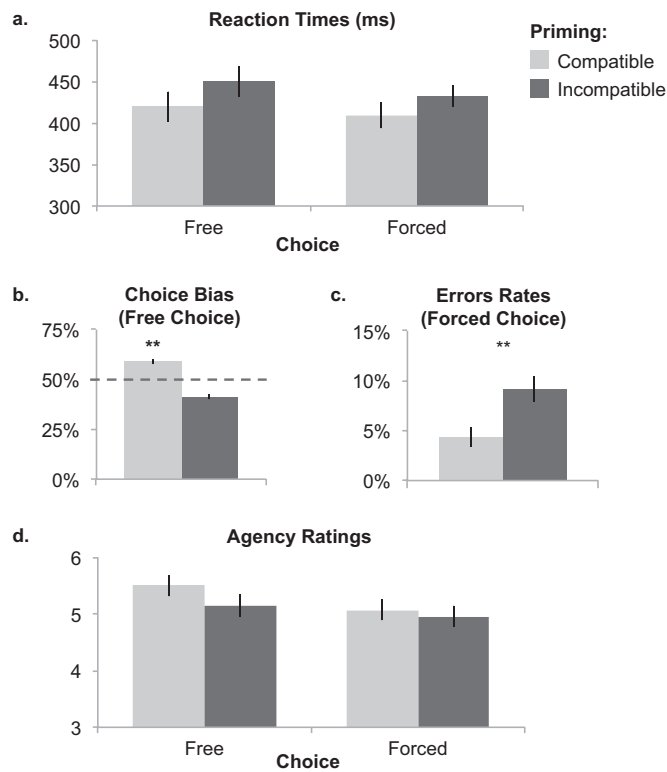


Fig. 3. Behavioural results. **a.** Mean reaction times across choice and priming conditions. **b.** Percentage of prime-compatible and prime-incompatible actions on free choice trials, showing the choice bias induced by primes. **c.** Mean error rates across priming conditions in forced choice trials. **d.** Mean agency ratings across choice and priming conditions. Error bars represent standard error of the mean. ** - $p < 0.001$.

($t_{(23)}=7.12$, $p < 0.001$, $d_z=2.97$; see Fig. 3b). For forced choice trials, error rates for prime compatible and incompatible actions were submitted to a paired-samples t -test. This showed that participants made significantly more errors when primes were incompatible with the target, compared to compatible ($M = 9.10\%$, $SD=6.26$ and $M=4.28\%$, $SD=4.71$, respectively; $t_{(23)}=-5.55$, $p < 0.001$, $d_z=-2.31$; see Fig. 3c).

Agency ratings were submitted to a $2 \times 2 \times 2$ repeated measures ANOVA, with factors of choice (free vs. forced), prime-action compatibility (compatible vs. incompatible) and action-outcome interval (400 vs. 600 ms). Results showed a significant main effect of choice ($F_{(1,23)}=4.45$, $p=0.046$, $\eta_p^2=0.16$), with higher ratings in free, compared to forced, choice trials (free: $M=5.26$, $SD=0.44$; forced: $M=5.01$, $SD=0.40$, see Fig. 3d). A significant main effect of prime-action compatibility was also found ($F_{(1,23)}=10.42$, $p=0.004$, $\eta_p^2=0.31$), with compatible priming leading to higher agency ratings than incompatible priming ($M=5.30$, $SD=0.41$ and $M=5.05$, $SD=0.46$ respectively). The interaction between choice and priming was not significant ($F_{(1,23)}=2.96$, $p=0.099$, $\eta_p^2=0.11$). Finally, there was no effect of action-outcome interval, nor any interaction with the other factors ($F_s < 1$). Action-outcome interval did influence agency ratings in previous studies (Chambon et al., 2014), but those studies used more intervals and a wider range than the present study. Importantly, action-outcome interval was not a key factor of interest here, and did not interact with the other factors. Therefore, it will not be discussed further.

ERPs

ERP analyses focused on three neural processes that might inform SoA, at three different time points in the trial. Processes related to action monitoring were assessed at pre- and post-response stages, by

analysing the target-locked N2 (Target N2) and the action-locked CRN (Action CRN) components, respectively. Finally, the outcome-locked FRN (Outcome FRN) was assessed as an index of outcome processing.

Action monitoring

Pre-response – Target N2. Using hierarchical linear regression, N2 amplitude was predicted from choice and priming condition (coded as 1/-1 for free/forced choice and as 1/-1 for compatible/incompatible priming), and choice by priming interaction, as fixed effects. Participants were modelled as random intercepts and random slope effects. RTs and their interactions with other factors were entered as fixed covariates, after first log-transforming the RT data, to render the distribution more normal, and standardizing it within participants.

The model predicting the Target N2 revealed a significant main effect of priming condition ($b=0.34$, $t_{(34)}=2.41$, $p=0.022$, 95% CI=[0.081, 0.61]), a significant negative relation with RTs ($b=-1.98$, $t_{(8325)}=-17.04$, $p < 0.001$, 95% CI=[-2.20, -1.75]), and a significant interaction between priming and RTs ($b=-0.25$, $t_{(8449)}=-2.13$, $p=0.033$, 95% CI=[-0.45, -0.015]). No significant effect of choice, nor any other interactions were found (see Table S1 in Supplementary materials, for full results). These results showed that greater N2 amplitudes (more negative potentials) occurred for incompatible priming trials, relative to compatible priming (see Fig. 4a). Additionally, greater N2 amplitudes were associated with slower RTs. To probe the interaction between priming condition and RTs, point estimates and standard errors were obtained from model predictions at ± 1 SDs of the RTs, and one sample t -tests were performed, using a conservative $N-1$ degrees of freedom (Snijders and Bosker, 1999). The priming \times RTs interaction (see Fig. S1) showed that the compatibility effect on Target N2 amplitude (greater N2 for incompatible) was largest for fast RTs (-1 SD RT: $b=1.17$, $t_{(23)}=3.17$, $p=0.004$), still robust at average RTs (mean RT: $b=0.67$, $t_{(23)}=2.41$, $p=0.024$), but no longer statistically significant for slow RTs ($+1$ SD RT: $b=0.18$, $t_{(23)}=0.49$, $p=0.63$). These results are broadly consistent with an association between the Target N2 and conflict monitoring and resolution processes.

Post-response – Action CRN. The same analysis model was also applied to the mean Action CRN amplitude. The Action CRN model revealed a significant effect of priming ($b=-0.27$, $t_{(24)}=-2.12$, $p=0.044$, 95% CI=[-0.52, -0.008]), a significant relation with RTs ($b=-0.54$, $t_{(8485)}=-5.55$, $p < 0.001$, 95% CI=[-0.73, -0.33]), and a significant priming by RTs interaction ($b=0.37$, $t_{(8667)}=3.85$, $p < 0.001$, 95% CI=[0.19, 0.56]). No effects of choice, nor any other interactions were found (see Table S2).

Larger CRN amplitude (more negative potentials) was associated with compatible, relative to incompatible, priming (see Fig. 4c). Additionally, larger CRN was associated with slower RTs. Model predictions and point estimates were again used to assess the priming by RTs interaction (see Fig. S2). First, the relation between Action CRN and RTs was assessed separately for each priming condition. For compatible priming, CRN amplitude was not significantly different between fast (-1 SD) and slow ($+1$ SD) RT trials ($b=-0.33$, $t_{(23)}=-1.27$, $p=0.22$). However, for incompatible priming, there was a significant negative relation between RTs and CRN amplitude, such that slower RTs were associated with larger CRN than faster RTs ($+1$ vs -1 SD RT: $b=-1.82$, $t_{(23)}=-6.30$, $p < 0.001$). This revealed that the interaction between priming and RTs was driven by a modulation of CRN amplitude across RTs in incompatible priming trials, but not in compatible trials. Second, CRN amplitude was compared across priming conditions. This showed that the compatibility effect – smaller CRN for incompatible versus compatible trials – was largest for fast

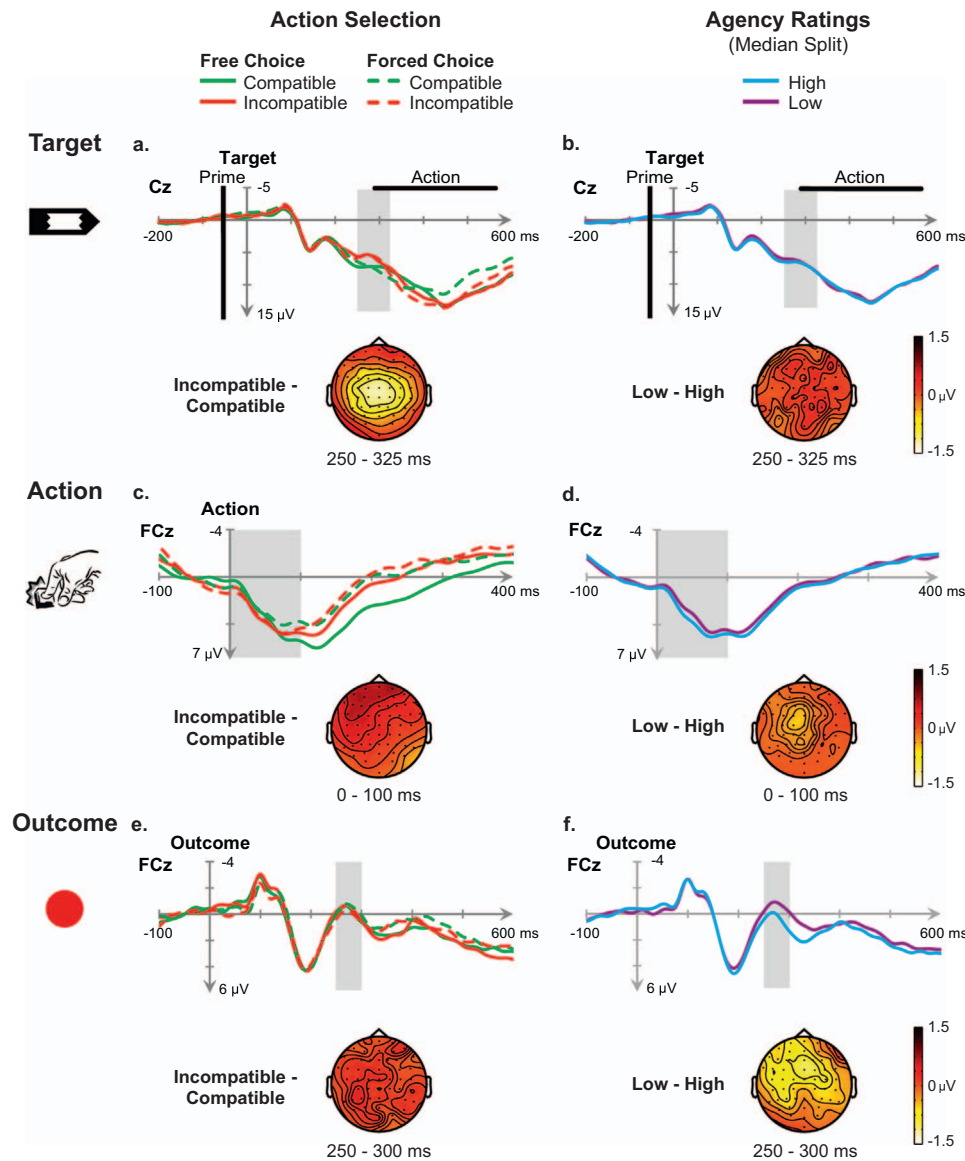


Fig. 4. ERPs for target, action and outcome events. Left column: differences between action selection conditions (choice×priming). Right column: correlation with agency ratings, shown as median split for visualisation purposes only. Time-windows selected a priori for analysis (see text) are highlighted in grey. Topographic plots show differences between incompatible-compatible priming (left column), and low-high ratings subtraction on the right). For target-locked ERPs, the black vertical line before the target shows the onset of the prime, and the horizontal bar indicates average RT, \pm 1 SD.

RTs (-1 SD RT: $b=-1.29$, $t_{(23)}=-3.97$, $p=0.001$) and reduced for average RTs (mean RT: $b=-0.54$, $t_{(23)}=-2.12$, $p=0.045$). For slow RTs ($+1$ SD), the compatibility effect was no longer significant ($b=0.20$, $t_{(23)}=0.64$, $p=0.53$), but reversed at very slow RTs ($+2$ SD RT: $b=0.95$, $t_{(23)}=2.07$, $p=0.050$). Together, these results are consistent with an association between Action CRN and post-response conflict monitoring. They further point to the possibility that the CRN could be suppressed in incompatible priming trials in which conflict is well resolved, resulting in fast or average RTs.

To test a possible trade-off between pre- and post-response conflict monitoring, indexed by the Target N2 and Action CRN respectively, mean Target N2 amplitude (standardised within-subjects) was added as a fixed covariate to the previous Action CRN model. Indeed, results showed a significant negative relation between Target N2 and Action CRN ($b=-0.94$, $t_{(8775)}=-10.02$, $p < 0.001$, 95% CI=[-1.14 , -0.74], see Table S3). Larger Target N2 (more negative potential) was associated with a smaller Action CRN (more positive potential). Notably, the Target N2 seemed to explain some of the variance previously accounted for by the main effect of priming, as priming now became only a

marginal predictor of Action CRN ($b=-0.24$, $t_{(24)}=1.91$, $p=0.069$, 95% CI=[-0.52 , 0.023]), whereas RTs became a stronger predictor ($b=-0.71$, $t_{(8495)}=-7.27$, $p < 0.001$, 95% CI=[-0.89 , -0.53]). The priming by RTs interaction remained significant ($b=0.35$, $t_{(8663)}=-3.62$, $p < 0.001$, 95% CI=[0.15 , 0.53]). These results support a distinction between pre- and post-response conflict monitoring, as the latter may integrate initial conflict signals with actual conflict resolution.

Outcome monitoring

To test the hypothesis that manipulating action selection fluency may affect SoA by altering outcome processing, we modelled Outcome FRN by choice and priming condition, and their interaction, as both fixed and participant random effects. Results showed no significant effects of choice ($b=-0.015$, $t_{(23)}=-0.085$, $p=0.93$, 95% CI=[-0.36 , 0.31]), priming ($b=-0.094$, $t_{(42)}=-0.75$, $p=0.93$, 95% CI=[-0.33 , 0.15]), or choice×priming interaction ($b=0.13$, $t_{(29)}=1.00$, $p=0.33$, 95% CI=[-0.12 , 0.39]; see Table S4). Therefore, we found no evidence that Outcome FRN was affected by our manipulations of action

selection (see Fig. 4e).

Additionally, we tested a possible relation between Action CRN and Outcome FRN, by adding Action CRN to the previous Outcome FRN model. The new model revealed no significant effect of Action CRN ($b=-0.087$, $t_{(8778)}=-0.76$, $p=0.45$, 95% CI=[-0.32, 0.15]; see Table S5). Since null effects cannot be clearly interpreted within frequentist statistics, Bayesian hypothesis testing (Wagenmakers, 2007) was used to further probe this relation. By comparing the Bayesian Information Criterion (BIC) between a model *with* a predictor (alternative hypothesis) and a model *without* that predictor (null hypothesis), a Bayes factor can be approximated in order to weigh the evidence *for* or *against* the null hypothesis, i.e. that the predictor is *not* related to the dependent variable. Comparing the BIC for the previous, null model with the new, alternative model yielded a Bayes factor of 70.52, indicating strong evidence *for* the null hypothesis of no association between Action CRN and Outcome FRN.

Predicting agency ratings

Finally, we modelled agency ratings to investigate the neural correlates of the subjective experience of agency. As above, the experimental factors of choice and priming were entered as fixed and participant random effects. Target N2, Action CRN and Outcome FRN, as well as RTs (log-transformed), were entered as fixed covariates (standardised within-subjects). Importantly, including the RTs as a predictor in the model ensures that other effects, such as priming effects, are estimated after taking into account the possible contribution of RTs.

Considering the experimental factors, results were consistent with the previous analysis: there was a significant effect of priming ($b=0.10$, $t_{(23)}=2.45$, $p=0.022$, 95% CI=[0.027, 0.20]), a marginal effect of choice ($b=0.15$, $t_{(23)}=2.06$, $p=0.051$, 95% CI=[0.001, 0.30]), and no significant choice×priming interaction ($b=0.023$, $t_{(23)}=0.56$, $p=0.58$, 95% CI=[-0.061, 0.11]; see Fig. 5 and Table S6). The reduced effect of choice on agency ratings seen here, relative to the ANOVA analysis above, is due to the EEG artefact rejection procedures. Only trials with ERP data in all 3 time windows could be used for the ERP analysis, whereas all correct trials were used for behavioural data analysis.

The model further showed a significant negative relation between agency ratings and RTs ($b=-0.15$, $t_{(8726)}=-5.94$, $p < 0.001$, 95% CI=[-0.20, -0.097]), such that slower RTs were associated with lower agency ratings. This shows that RT monitoring may partly contribute to SoA. Notwithstanding that, results show that the effect of priming on SoA could not be fully explained by differences in RTs across priming conditions.

Turning to the putative neural correlates of agency, it had been hypothesised that Target N2, as a pre-response index of conflict monitoring, might be related to agency ratings. Larger Target N2 amplitudes (more negative potentials) would imply stronger response conflict and hence be associated with lower agency ratings. However, the model revealed no significant effect of Target N2 ($b=-0.023$, $t_{(8754)}=-0.92$, $p=0.36$, 95% CI=[-0.070, 0.020]; see Fig. 4b). Comparing the previous model, which included the Target N2 as a predictor, to a model without the Target N2 predictor (null hypothesis), resulted in a Bayes factor of 61.46, indicating strong evidence *for* the null hypothesis of no relation between Target N2 and agency ratings. The degree of conflict experienced, or of cognitive control recruited, during initial action selection was not directly related to SoA.

Alternatively, as an index of post-response action monitoring, it was hypothesised that Action CRN could be related to SoA. Indeed, Action CRN was found to have a significant positive relation to agency ratings ($b=0.079$, $t_{(8760)}=3.22$, $p=0.001$, 95% CI=[0.026, 0.13]). Larger Action CRN amplitudes (more negative potentials) were associated with lower agency ratings (see Fig. 4d), consistent with a role of Action CRN in post-response conflict monitoring, with unresolved conflict leading to greater Action CRN, and thus a reduction in SoA.

Finally, looking at neural correlates of outcome processing, we

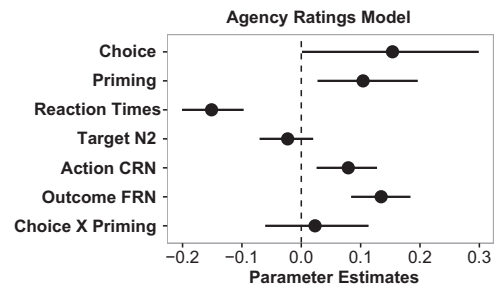


Fig. 5. Parameter estimates for the model predicting agency ratings, with 95% bootstrapped confidence intervals.

found a significant positive relation between Outcome FRN and agency ratings ($b=0.13$, $t_{(8760)}=5.52$, $p < 0.001$, 95% CI=[0.084, 0.18]). Larger Outcome FRN amplitudes (more negative potentials) were associated with lower agency ratings (see Fig. 4f). The Outcome FRN may indicate a violation of outcome expectations, or more negative responses to the outcomes, thus leading to a reduction in SoA.

Supplementary analyses were conducted to test the robustness of the observed effects.¹ First, we checked that the observed association between Action CRN and agency ratings did not result from possible confounds introduced by baselining the Action-locked ERP in the active period before the action. For this, we computed Action-locked ERPs that used the same neutral baseline as that used for the Target-locked ERPs (see Supplementary analysis A). Results confirmed that the Action CRN remained a significant predictor of agency ratings ($b=0.06$, $t_{(8735)}=2.58$, $p=0.010$, 95% CI=[0.01, 0.11]; see Table S7).

Second, we assessed whether our results might change across trials during the course of each block, as participants learn action-outcome associations. We might hypothesise that: a) agency ratings could increase across the block; b) this change could, in turn, alter the relation between ERPs and agency ratings; or c) the relation between ERPs and agency ratings might itself change across the trials. In particular, as the Outcome FRN is sensitive to unexpected or unpredicted outcomes, this signal might become less relevant to SoA as action-outcome contingencies are learned. Predictions about changes in the contribution of action-related ERPs (Target N2 and Action CRN) to agency during learning remain less clear. Yet, one might hypothesise a trade-off between relying on outcome monitoring in an initial learning phase, and later relying on action monitoring, as outcomes are well learned.

To test these hypotheses, we extended the agency model described above (with the original Action CRN, with a pre-action baseline), by adding trial as linear and quadratic predictors. Additionally, hypothesis ii) was tested by including interactions between a linear effect of trial and the 3 ERP components (details in Supplementary analysis B, and Table S8). Results showed that indeed agency ratings increased as participants learned action-outcome associations, with large linear and quadratic effects of trial (linear: $b=5.72$, $t_{(8370)}=30.18$, $p < 0.001$, 95% CI=[5.32, 6.09]; quadratic: $b=-1.75$, $t_{(8367)}=-9.24$, $p < 0.001$, 95% CI=[-2.11, -1.39]). Importantly, both Action CRN and Outcome FRN remained significant predictors of agency ratings (Action CRN: $b=0.07$, $t_{(8373)}=2.77$, $p=0.006$, 95% CI=[0.02, 0.12]; Outcome FRN: $b=0.13$, $t_{(8373)}=5.50$, $p < 0.001$, 95% CI=[0.08, 0.17]). Therefore, the effects of trial number on agency ratings did not account for the relations between these ERPs components and agency ratings. Moreover, the linear effect of trial did not interact with the Target N2, nor with the Action CRN components (Trial×Target N2: $b=-0.06$, $t_{(8367)}=-0.31$, $p=0.76$, 95% CI=[-0.45, 0.38]; Trial×Action CRN: $b=-0.06$, $t_{(8366)}=-0.31$, $p=0.76$, 95% CI=[-0.42, 0.33]). Thus, action monitoring had a stable effect on agency ratings, independent of

¹ We are thankful to an anonymous reviewer for directing us towards these extra analyses.

instrumental learning and outcome monitoring. Interestingly, the linear effect of trial did interact with Outcome FRN ($b = -0.58$, $t_{(8371)} = -3.07$, $p = 0.002$, 95% CI = $[-0.96, -0.22]$). As predicted, this interaction showed that the effect of Outcome FRN on agency ratings gradually reduced across the trials (see Fig. S4). Hence, it was especially in the beginning of the block that larger Outcome FRN amplitudes were associated with a greater reduction in agency.

Discussion

The present study aimed to clarify the neural correlates of SoA, and specifically the neural basis of prospective cues to SoA based on action selection. Behaviourally, we found that incompatible action priming led to slower RTs than compatible priming, in both free and forced choice trials. Free choices were biased towards prime-compatible choices, while incompatible priming led to more errors than compatible priming in forced choice trials. These results are consistent with previous subliminal priming studies including free choice trials (Kiesel et al., 2006; O'Connor and Neill, 2011; Schlaghecken and Eimer, 2004). More importantly, the disruption to action selection induced by incompatible priming led to a reduction in agency ratings over action outcomes, relative to compatible priming (Chambon and Haggard, 2012; Chambon et al., 2013, 2015; Sidarus et al., 2013; Wenke et al., 2010). Additionally, free choice trials led to a stronger SoA than forced choice trials (cf. Wenke et al., 2010), but response conflict had a similar effect on SoA for both choice conditions, in line with previous studies (Sidarus and Haggard, 2016; Wenke et al., 2010). At a neural level, we identified ERP components associated with SoA at the time of the action, and also at the time of the outcome. Based on previous work, these components could be identified with action monitoring and outcome monitoring, respectively (recall Fig. 1).

Action monitoring

Previous studies into the neural correlates of prospective cues to SoA (Chambon et al., 2013, 2015) had not been able to disentangle the role of pre- and post-decisional action monitoring stages to SoA. The high temporal resolution of EEG allowed us to investigate this question. Broadly, components that occur early, and are related to target processing, reflect pre-decisional monitoring, while components that occur later, namely at the time of the action, reflect post-decisional monitoring processes.

As predicted, we found evidence of pre-response conflict monitoring, with a larger Target N2 associated with incompatible priming trials (Hughes et al., 2009; Jiang et al., 2013; Verleger and Jaskowski, 2008; Wang et al., 2013). Moreover, we found that larger Target N2 amplitude was related to slower RTs, in line with previous studies (Beste et al., 2008; Yeung et al., 2004; Yeung and Nieuwenhuis, 2009). We also found an interaction between RTs and the effect of priming on Target N2 amplitude. The compatibility effect on Target N2 (more negative amplitude for incompatible trials) was greater for fast responses than for slow responses. A previous subliminal priming study, that split RTs into deciles, found that the delaying effects of incompatible, relative to compatible, priming were reduced for slower RTs (Atas and Cleeremans, 2015). Similar effects have been reported for tasks involving conscious response conflict (Burle et al., 2014; Ridderinkhof, 2002a, 2002b; Ridderinkhof et al., 2004). Trials with slower RTs may already reflect enhanced cognitive control, resulting in reduced response interference from incompatible primes. The observed correlation between larger Target N2 and slower RTs for both compatible and incompatible trials supports this view, as well as the suggestion that Target N2 reflects the recruitment of cognitive control. Intriguingly, the Target N2 was comparable in incompatible priming trials for both free and forced choices. To our knowledge this has not been previously investigated, but seems consistent with the observed choice bias introduced by the primes. This suggests a specific cost, or

effort, is involved in 'freely' choosing a prime-incompatible action. Finally, we did not find any relationship between Target N2 amplitude and agency ratings. This suggests that the effects of action priming on agency were not *directly* related to the *pre-decisional* monitoring of early conflict signals arising during action selection.

We found a clear neural correlate of the SoA at the *post-decisional* monitoring stage. Larger Action CRN was associated with lower agency ratings. This finding is consistent with studies showing that a larger Action CRN was related to a reduction in subjective confidence (Boldt and Yeung, 2015; Scheffers and Coles, 2000), as well as with increases in objective task difficulty (Endrass et al., 2012; Pailing and Segalowitz, 2004). These results are thus consistent with a view of the Action CRN as reflecting to post-response conflict monitoring (Grützmann et al., 2014; Larson et al., 2014; Yeung et al., 2004), and/or uncertainty about the correct response (Pailing and Segalowitz, 2004; Scheffers and Coles, 2000). They further suggest that prospective signals contributing to the SoA and to confidence judgements draw on information from post-decisional processes, which integrate early and late action selection signals, rather than rely only on pre-decisional processes.

The effects of action priming on the Action CRN require further consideration. Overall, we found that compatible priming was associated with a larger Action CRN than incompatible priming. At first glance, this would seem to go against a conflict monitoring account, since one might predict that incompatible priming trials would be associated with higher conflict, than compatible priming, and hence should have a larger Action CRN. Yet, the literature does not support this prediction: to our knowledge, no previous studies using subliminal priming have looked at compatibility effects on CRN. A few studies using the flanker task have analysed conflict effects on action-locked ERPs for correct trials, but their results are inconsistent. In line with our findings, one study found an overall larger Action CRN for compatible, relative to incompatible, flanker trials (Grützmann et al., 2014). However, while others have shown non-significant effects in the same direction (Cohen and Donner, 2013; Scheffers and Coles, 2000), another study has reported the opposite effect (larger Action CRN for incompatible flankers; Bartholow et al., 2005).

We additionally found that a larger Action CRN was associated with slower RTs, consistent with a conflict monitoring account. Importantly, there was a significant interaction between priming and RTs, qualifying the two main effects. In fact, it was specifically in incompatible priming trials that Action CRN and RTs were related, whereas for compatible priming trials Action CRN was stable across fast and slow RTs. We might speculate that fast RTs following incompatible primes would reflect a trial in which the prime was less processed, leading to a reduced, or absent, response conflict. However, this account would predict no difference in Action CRN between compatible and incompatible trials for fast RTs. In fact, the current results show that incompatible priming was associated with smaller Action CRN than compatible priming for fast and average RTs. To account for this, we might instead speculate that incompatible priming trials with fast RTs could reflect trials with faster and/or more efficient recruitment of cognitive control processes to overcome response conflict. Hence, fast incompatible trials might show a suppression of Action CRN as efficient cognitive control would be deployed before the action, whereas such control would not be necessary in compatible priming trials. While this proposal remains highly speculative, it would point to a complementarity, or trade-off, between pre- and post-response conflict monitoring (cf. Grützmann et al., 2014; Larson et al., 2014). Interestingly, our results showed that a larger Target N2 was associated with a smaller Action CRN, consistent with a previous study (Grützmann et al., 2014) that showed this relation both at the within- and the between-subject level.

Together, these findings support the view that post-response action monitoring integrates initial conflict signals with actual conflict resolution. Both the pre-response N2 and post-response negativities (Action CRN/ERN) have been linked to the anterior cingulate cortex (ACC),

and are suggested to reflect two successive recruitment events of a single conflict monitoring circuit (van Veen and Carter, 2002; Yeung et al., 2004). If conflict is adequately detected and resolved before the response, there may be no need for further conflict-related processing after the response. However, if conflict is not fully processed before the response, post-response conflict signals could be important to help prevent future errors (Grützmann et al., 2014).

Our findings suggest that prospective SoA may be linked to a post-decisional integration of signals both early and late in the action-generation process (see Fig. 1). A putative role of the prospective component of SoA may be as an experiential marker, or an epistemic feeling (Proust, 2008), of the unfolding voluntary action. If an error is made, corrective action may help to avoid unintended outcomes. Even when the correct action is made, a subjective experience of difficulty, or dysfluency, in action selection may be informative in guiding behavioural adaptation, even if triggered by subliminal primes (Desender et al., 2014). This feeling that “something went wrong” (Pacherie, 2008) might thus weaken the link between the action and ensuing outcome, leading to a reduced SoA over the outcome. One might hypothesise that when learning new action-outcome contingencies, it may be adaptive to *learn* following fluent, high-confidence actions, but *not learn* following dysfluent, low-confidence, actions.

Alternatively, conflicts can serve as aversive signals (Botvinick, 2007). Conflict induces negative evaluations of subsequent neutral stimuli (Fritz and Dreisbach, 2013), and triggers behavioural adjustments in subsequent trials (Dreisbach and Fischer, 2011, 2012). In fact, post-response negativities (CRN/ERN) have been linked to negative affect (Hajcak et al., 2004; Simon-Thomas and Knight, 2005), and to the motivational significance of errors (Aarts et al., 2013; Grützmann et al., 2014; Hajcak and Foti, 2008). From this perspective, our finding of reduced SoA over outcomes following response conflict could be interpreted as the negative valence of conflict “leaking” into outcome evaluation.

Outcome monitoring

After outcome onset, we found that larger (more negative) Outcome FRN amplitudes were associated with lower agency ratings. Moreover, this relation was particularly evident at the start of a block, and gradually reduced as action-outcome associations were learned. These results are consistent with a recent study showing that more negative potentials in a similar time window were associated with more external attribution of agency over action outcomes (Bednark and Franz, 2014). Previous studies comparing responses to gains and losses have also shown that the FRN is sensitive to the controllability of action outcomes (Li et al., 2010, 2011; Yeung et al., 2005).

Previous EEG studies on agency have found sensory attenuation to self-triggered and predicted/expected outcomes in early (N1) processing (Gentsch et al., 2012; Gentsch and Schütz-Bosbach, 2011); as well as smaller P3a for self-attributed, relative to externally-attributed, outcomes (Kühn et al., 2011). Such studies have typically invoked alternative agents, or violated well-learned action-outcome associations to trigger changes in SoA. Additionally, using subliminal action priming with fully predictable outcomes, a study has found a sensory attenuation of outcomes that followed compatibly primed, relative to incompatibly primed, actions (Stenner et al., 2014). Notably, sensory attenuation depends on the ability to adequately predict a sensory event (see Hughes et al., 2013 for a review), therefore such measures were not particularly suited to our design.

In our study, outcomes were always relatively unpredictable, as there were many possible outcomes (8), and action-outcome contingencies had to be learned anew in each block. Within a block, participants could learn that left and right hand actions were associated with 4 colours each, 2 for free and 2 for forced choice trials. The compatibility relation between prime and action disambiguated the remaining 2 colours, but this information was not available since the

primes were subliminal. Participants were asked to learn these relatively complex action-outcome contingencies. Rather than depend on variations in the control over triggering outcomes, we assumed that participants’ SoA would vary across trials based on monitoring outcome identity (i.e. colour) and comparing that to their current knowledge of action-outcome contingencies. In line with these predictions, we found that agency ratings gradually increased across the block. Finally, **Supplementary analyses** did not show any evidence of sensory attenuation associated with the priming manipulation, nor any association between N1 amplitude and agency ratings (see Fig. 4f, and **Supplementary analysis C**). Furthermore, whilst sensory attenuation should increase as action-outcome contingencies are learned, we found that Outcome FRN amplitude was most predictive of agency ratings at the start of the block.

Several accounts would predict a larger FRN following unpredicted or surprising outcomes (Holroyd and Coles, 2002; Oliveira et al., 2007; Wessel et al., 2012). Our FRN results could reflect larger Outcome FRN being evoked in trials with outcome prediction errors, which were in turn related to lower agency ratings. As action-outcome associations were changed between blocks, prediction-errors and expectancy violations would be maximal at the start of a block. Consistently, we found that the contribution of Outcome FRN to agency ratings gradually reduced throughout the block (see Fig. S4, in **Supplementary analysis B**). Our results further showed no effects of priming or choice on Outcome FRN. This suggests that priming did not affect agency by directly altering outcome processing, namely by disrupting outcome predictions.

The FRN has been widely linked to negative outcomes (San Martín, 2012), such as monetary losses (Gehring and Willoughby, 2002), or no reward relative to reward (e.g. Holroyd et al., 2009). Therefore, the present Outcome FRN findings could also reflect varying affective evaluations of the outcome. As mentioned before, response conflict can be considered aversive, and influence affective responses to ensuing events (Fritz and Dreisbach, 2013). Disruptions in action selection, induced by incompatible priming, could have led to more negative affective responses to action outcomes, leading to larger Outcome FRN and lower SoA.

Importantly, the relation between Outcome FRN and SoA was independent of a possible link between Action CRN and conflict-induced negative affect. In modelling of agency ratings, we found no relation between these two ERPs, suggesting that the Outcome FRN did not *directly* reflect an affective response linked to the preceding action. Furthermore, Action CRN and Outcome FRN were significant predictors of agency ratings, suggesting that they explained different portions of the variance. Outcome monitoring, as indexed by the Outcome FRN, may be partly influenced by action monitoring signals, but it also integrates information about the observed outcome, and whether it matches internal models of action-outcome contingencies. Our study supports the proposal that prospective, action selection-based, and retrospective, outcome-based, cues can make independent contributions to the SoA (Sidarus et al., 2013), at least when outcomes are not highly predictable (Stenner et al., 2014; Stenner et al., 2015).

Common performance monitoring framework

Converging evidence shows that response-related negativities, i.e. Action CRN/ERN, and the Outcome FRN have common neural mechanisms, linked to the ACC (Botvinick, 2007; Frank et al., 2005; Holroyd and Coles, 2002; Larson et al., 2014; San Martín, 2012). The ACC is thought to be involved in goal-directed action, driving action-outcome learning and adaptive behaviour (Botvinick, 2007; Holroyd and Yeung, 2012). Monitoring actions and outcomes for response conflict, errors, and negative or unexpected outcomes, the ACC can signal a need for cognitive control. Structures such as the dorsolateral pre-frontal cortex can in turn adjust current behavioural strategies or internal models of action-outcome associations.

Notwithstanding this commonality, action and outcome monitoring use different information, available at different times. Action monitoring relies on internal, prospective signals about action selection and execution, whereas outcome monitoring depends on external, retrospective feedback processing in sensory areas. Here we saw that the SoA was independently related to both Action CRN and Outcome FRN, consistent with the idea that they integrate different information. Interestingly, a study has reported a disruption in ERN but intact FRN in patients with schizophrenia (Horan et al., 2012), supporting a dissociation between these two monitoring processes, and potentially their role in SoA. Other studies have similarly suggested that schizophrenia patients have impaired monitoring of internal, action-related signals, and are instead over-reliant on external, outcome monitoring (Metcalfe et al., 2012; Voss et al., 2010). Furthermore, the ERN is sensitive to whether errors are internally or externally generated, e.g. a response button malfunction (Gentsch et al., 2009; Padrao et al., 2016; Steinhäuser and Kiesel, 2011). Internally-generated errors led to a large ERN, whereas externally-generated errors were associated with later ERP components, arguably FRN-like (Gentsch et al., 2009).

Interestingly, with the exception of studies on error monitoring, the ACC and ACC-mediated performance monitoring have rarely been linked to SoA. The agency literature has typically employed considerably different tasks from the one used here, focusing especially on the *attributional* aspect of agency, i.e. “who did it” (Chambon et al., 2014). For example, participants may be asked to judge whether outcomes were caused by oneself or another agent. This research has linked sensorimotor control and outcome monitoring to the parietal cortex, though other frontal and premotor areas have been implicated (David et al., 2008; Farrer et al., 2008; Fink et al., 1999; Miele et al., 2011).

In contrast, our study focused on the *instrumental* aspect of agency, involving monitoring and using more abstract action-outcome associations. As the ACC is involved in goal-directed actions and performance monitoring more generally, it is especially relevant to this aspect of SoA, rather than to agency attribution. The SoA is complex and multifaceted, involving the integration of multiple signals, from internal sensorimotor signals, to external feedback, to higher-level beliefs and inferences (Gallagher, 2012; Synofzik et al., 2013). We speculate that regions previously associated with SoA may integrate signals from the ACC with other inputs relevant to determining agency. The AG is a likely candidate for this integration as it has been linked to a subjective loss of agency associated with dysfluent action selection (Chambon et al., 2013), as well as with unexpected outcomes (Farrer et al., 2003, 2008; Farrer and Frith, 2002; Nahab et al., 2011). The AG may subserve an online monitoring system that tracks the whole intentional action chain, from intentions, to actions, to outcomes, and signals a loss of agency.

Conclusions

We found that an unconscious influence on action selection processes, from subliminal priming, can affect the conscious experience of agency over action outcomes. ERP results showed that action monitoring signals influence SoA prospectively, since the neural correlates of SoA emerge at the time of the action, long before the outcome is known. The association seen here between Action CRN and agency ratings mirrors associations found between Action CRN/ERN and confidence ratings (Boldt and Yeung, 2015; Scheffers and Coles, 2000). This suggests that the signals related to action selection which influence SoA could be better described as relating to *confidence* in selecting or having selected the appropriate response, and not only to *selection fluency* as has been previously described (Chambon et al., 2014; Wenke et al., 2010). Our results therefore link prospective sense of agency to the processes of action monitoring and cognitive control. These results invite speculations about possible functions of SoA within human cognition generally. In particular, the SoA may provide an important experiential marker, both for alerting to the need for corrective action, and for guiding learning.

Conflict of interest

None declared.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.neuroimage.2017.02.015.

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