



Priming of actions increases sense of control over unexpected outcomes [☆]



Nura Sidarus ^{*}, Valérian Chambon, Patrick Haggard

Institute of Cognitive Neuroscience, University College London, 17 Queen Square, London WC1N 3AR, UK

ARTICLE INFO

Article history:

Received 5 May 2013

Keywords:

Agency
Action selection
Action priming
Outcome expectation

ABSTRACT

Sense of agency (SoA) refers to the feeling that we are in control of our own actions and, through them, events in the outside world. SoA depends partly on retrospectively matching outcomes to expectations, and partly on prospective processes occurring prior to action, notably action selection.

To assess the relative contribution of these processes, we factorially varied subliminal priming of action selection and expectation of action outcomes. Both factors affected SoA, and there was also a significant interaction. Compatible action primes increased SoA more strongly for unexpected than expected outcomes. Outcome expectation had strong effects on SoA following incompatible action priming, but only weak effects following compatible action priming. Prospective and retrospective SoA may have distinct and complementary functions.

© 2013 The Authors. Published by Elsevier Inc. All rights reserved.

1. Introduction

The sense of agency (SoA) refers to the feeling of controlling one's actions and, through them, events in the outside world (Haggard & Tsakiris, 2009). The SoA has both a statistical, objective aspect and a phenomenological, subjective aspect. First, instrumental action implies a link between action and its sensory consequences (Thorndike, 1898). The SoA is indeed sensitive to the statistical contingency between action and outcome (Moore & Haggard, 2008; Moore, Lagnado, Deal, & Haggard, 2009; Sato, 2009). However, it is generally agreed that there is a phenomenal experience of agency, in addition to the statistical computation of contingency. The phenomenology known as SoA comprises the experience of being the author of one's actions, and thus feeling that one is responsible for their outcomes. SoA is an essential feature of normal human mental life and of human society. In particular, it underpins the societal concept of responsibility for action (Spence, 2009), and the legal system. Moreover, many psychiatric disorders, including schizophrenia and OCD, involve an altered SoA.

The SoA can, in fact, be erroneous even in healthy people. Wegner and Wheatley (1999) demonstrated that under certain conditions people can self-attribute actions performed by others. Based on this evidence, they suggested that SoA results from a retrospective process of inferring agency from the match between “prior thoughts” and an observed outcome (Wegner, 2004; Wegner & Wheatley, 1999). This allows the subject to attribute agency over a specific outcome either to oneself or to another agent. However, outcomes can only be attributed once they are known. Additionally, this account cannot explain the component of agency that exists independent of attribution. For example, one can feel more or less in control of a bicycle, even if it is always clear that it is oneself and not someone else riding the bicycle. That is, this theory provides an account of attribution, rather than an account of instrumentality.

[☆] This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.

^{*} Corresponding author. Fax: +44 207 916 8517.

E-mail address: n.sidarus.11@ucl.ac.uk (N. Sidarus).

Computational models of sensori-motor control (e.g. [Wolpert, Ghahramani, & Jordan, 1995](#)) have provided a formal basis for an alternative view of SoA. The model suggests that an efference copy of motor commands is used to predict sensory reafferences, or action outcomes. These are then compared to actual sensory descriptions of outcomes. The discrepancy between these two signals is associated with a respective decline in perceived control ([Blakemore, Wolpert, & Frith, 2002](#)). These sensori-motor predictions can become more precise as the contingency between sensory events and specific actions is learned, resulting in a more accurate experience of control. SoA is stronger for outcomes that are highly contingent on an executed action ([Moore & Haggard, 2008](#); [Moore, Lagnado, et al., 2009](#); [Sato, 2009](#)), as well as for highly predictable outcomes ([Moore & Haggard, 2008](#); [Moore, Lagnado, et al., 2009](#)).

The work reviewed above might suggest that SoA is simply a matter of monitoring outcomes to confirm that actions were successful. However, people may feel low levels of agency despite achieving the intended outcome. For example, [Metcalf and Greene \(2007\)](#) showed that participants could accurately report a low level of control even when performance in a task was high. Thus, other signals may contribute to SoA, in addition to action outcomes. Recent frameworks highlight the integrative nature of SoA, stressing the variety of cues to agency ([Gallagher, 2012](#); [Haggard & Tsakiris, 2009](#); [Moore & Fletcher, 2012](#); [Synofzik, Vosgerau, & Newen, 2008](#); [Wegner & Sparrow, 2004](#)). Nevertheless, it remains quite unclear how these different signals would be integrated computationally.

One candidate signal that may influence SoA appears to be generated already at the action selection stage ([Chambon & Haggard, 2012](#); [Chambon, Wenke, Fleming, Prinz, & Haggard, 2013](#); [Fukui & Gomi, 2012](#); [Wenke, Fleming, & Haggard, 2010](#)). [Wenke et al. \(2010\)](#) first showed that the fluency, or ease, of selecting between action alternatives can affect the subjective experience of agency. In this study, participants made a left or right key-press in response to a target arrow. The key-press triggered the appearance of a coloured circle. Critically, subliminal presentation of a prime arrow prior to the conscious target resulted in a facilitation of action selection for identical, i.e. compatible, prime and target directions, while opposite, i.e. incompatible, directions disrupted action selection ([Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003](#)). Results showed that participants felt more control over colours that followed compatibly-primed actions, than for colours that followed incompatibly-primed actions.

Importantly, the effect of action selection fluency on control ratings cannot be explained by monitoring reaction times ([Chambon & Haggard, 2012](#)). Previous studies have shown that increasing the interval between masked priming and the instruction stimulus reverses the polarity of the priming effect on reaction times (NCE; [Eimer & Schlaghecken, 1998, 2003](#); [Lingnau & Vorberg, 2005](#)). For short asynchronies (less than 70 ms) the typical “positive compatibility effect” (PCE) of priming is seen, with reduced RTs and errors for compatible, compared to incompatible, priming conditions. However, for longer delays, a “negative compatibility effect” (NCE) emerges: compatibility between prime and target now leads to increases in RTs and errors, compared to incompatible priming. [Chambon and Haggard \(2012\)](#) used this method to dissociate the role of prime–target compatibility and reaction time monitoring in the effects of selection fluency on SoA. They found that judgements of control were always higher for compatible than incompatible primes, even when an NCE timing was used so that compatible primes impaired motor performance relative to incompatible primes. This suggests that priming effects on SoA were indeed independent of motor execution, consistent with their arising at a premotor stage.

A recent neuroimaging study has further highlighted the interrelation between prospective and retrospective cues. In an fMRI adaptation of the [Wenke et al. \(2010\)](#) paradigm, it was found that activity in the angular gyrus (AG) increased in incompatible priming trials, compared to compatible trials, at the time of action selection ([Chambon et al., 2013](#)). Additionally, AG activity was negatively correlated with control ratings, i.e. more activity in AG was associated with a lower sense of control. In fact, previous studies have suggested that the AG and the inferior parietal cortex more broadly play a key role in the neural computations of SoA. For example, several studies have shown AG activation when action outcomes are not as expected ([Farrer & Frith, 2002](#); [Farrer et al., 2003, 2008](#); [Nahab et al., 2011](#); [Sperduti, Delaveau, Fossati, & Nadel, 2011](#)). Therefore, it seems the AG is involved in prospective agency, as well as outcome-based agency. This region could potentially integrate both prospective and retrospective cues to agency ([Chambon et al., 2013](#)).

The common activation of AG for prospective and outcome-based agency raises the question of how a single SoA can be computed from these various different cues. One view suggests that SoA is computed by integrating various cues in a Bayesian optimal way ([Moore & Fletcher, 2012](#)). Relatively few studies of agency judgement have investigated this possibility. However, indirect measures of SoA based on intentional binding, i.e., the perceived temporal attraction between action and outcome, have been used to do so. [Wolpe, Haggard, Siebner, and Rowe \(2013\)](#) provided direct evidence for such cue integration, suggesting that the temporal percept of an instrumental action is based on a weighted average of action signals and outcome signals. They found that increasing uncertainty about the outcome tone, by decreasing its signal-to-noise ratio, reduced the perceived temporal contraction between the tone onset and the action that caused it.

[Moore and Haggard \(2008\)](#) devised a method for comparing predictive and retrospective outcome-based processes in intentional binding by comparing the perceived time of actions which either were or were not followed by tones, across blocks where the probability of a tone given an action was either low or high. When outcome probability was low, action binding was found only on trials where the tone actually occurred, suggesting a retrospective, outcome-based mechanism. Conversely, when outcome probability was high, prior knowledge of the action–outcome association led to a predictive form of intentional binding, even on rare trials where outcomes were omitted. Interestingly, when both retrospective outcome-based and prior-prediction based information were available, binding was no greater than when each mechanism was available alone. This suggests that the two mechanisms may be combined by a weighting function, with the most reliable or most salient making the dominant contribution to SoA.

Previous studies on prospective SoA used 100% contingency between action and outcome. As a result, the relation between prospective and retrospective, outcome-based agency was not systematically assessed. Therefore, the present study aimed to explore the joint contributions of action selection fluency and contingent outcomes to SoA. We used situations with an intermediate contingency of 67% between two possible actions and four outcomes, i.e. two possible outcomes per action. This design allowed us to compare SoA for trials in which outcomes were expected or unexpected. By orthogonally manipulating prime–target compatibility, we could assess the interaction between prospective, selection-based and retrospective, outcome-based cues in the sense of agency.

2. Method

2.1. Design

The study was approved by the UCL Research Ethics Committee. Thirty participants (11 female, 3 left-handed) gave written informed consent to participate in the study and received payment of £7/h. Details of the paradigm and apparatus can be found elsewhere (Chambon & Haggard, 2012). Briefly, the participants were seated approximately 60 cm from a computer screen (resolution = 800 × 600 × 32, refresh rate = 60 Hz). The experiment was programmed and stimulations were delivered using Presentation (Neurobehavioral Systems, Albany, California). Primes consisted of grey left- or right-pointing arrows, followed by isoluminant metacontrast masks constructed by superimposing left- and right-oriented primes. Prime and mask stimuli could appear randomly above or below fixation to enhance the masking effect (Vorberg et al., 2003).

Participants were instructed to respond to left- or right-ward arrow targets by pressing a left or right key, respectively, which elicited the appearance of a coloured circle. At the end of a trial, participants judged how much control they felt over the colour of the circle, on a scale ranging from 1 to 8 (1 = no control, 8 = total control). Critically, targets also served as metacontrast masks for subliminal primes consisting of left or right pointing arrows (see Fig. 1). Outcome stimuli consisted of one of 4 coloured circles that appeared on the screen 100, 300 or 500 ms after a key-press. Jittering the action–outcome interval prevents a ceiling effect in control ratings derived from high temporal predictability (Haggard, Clark, & Kalogeras, 2002; Wenke et al., 2010). This manipulation was orthogonal to the factors of interest in the present study (prime–target compatibility and outcome predictability), and thus was not analysed.

Trials with subliminal prime and target arrows pointing in the same direction were classed as compatibly primed action trials. Incompatible priming involved prime and target arrows pointing in opposite directions (see Fig. 1 for an outline of the paradigm). The prime duration (17 ms) and interval between prime and mask/target (34 ms) were chosen on the basis of previous studies demonstrating that no conscious perception of prime direction is possible at these exposures (Chambon & Haggard, 2012; Chambon et al., 2013).

In each block, two colours were assigned to each hand, one for compatible and the other for incompatible priming trials. Therefore, outcome colour depended on both prime–target compatibility and action. Moreover, to manipulate outcome expectation, hand-to-colour mappings were reversed on a third of trials. For example, a colour that appeared on 67% of trials

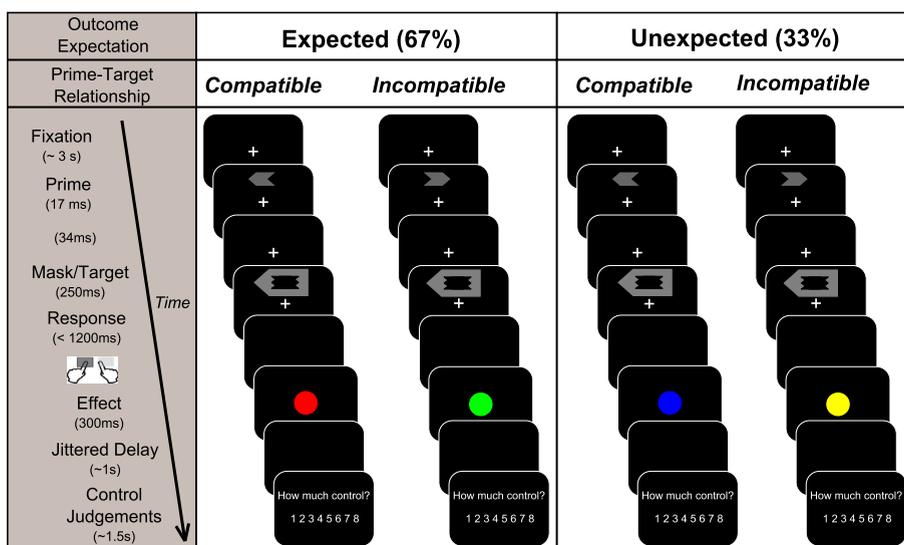


Fig. 1. Paradigm outline. This figure displays an example of the four conditions for left hand trials. On compatible priming trials, prime and target arrow pointed in the same direction, whilst on incompatible trials they pointed in opposite directions. On 67% of trials, left hand actions were followed by red or green coloured circles – the expected outcomes. This action–outcome mapping was reversed on 33% of trials, where left hand actions were followed by blue or yellow circles. These outcomes were unexpected, since these colours were those associated with right hand actions on 67% of trials. (For interpretation of the references to colors in this figure legend, the reader is referred to the web version of this paper.)

after a right-hand action was considered an expected outcome. On 33% of trials, that colour appeared after a left-hand action, thus becoming an unexpected outcome. In order to maintain any implicit associations between selection fluency and colours, the mapping between colours and compatibility conditions was retained. Additionally, error trials were repeated at the end of a block to ensure that errors did not unbalance the exposure to the different colours. Participants completed 4 blocks of 36 trials. This was preceded by one training block which used a different set of 4 outcome colours not seen in the experimental blocks. Thus, the colours shown on each trial depended on the combination of the target and the prime, and were used to create a 2×2 factorial arrangement of prime compatibility and outcome expectation: an example is shown in Table 1 below.

2.2. Analysis

Mean reaction times (RTs) and error rates were submitted to a 2×2 within subjects ANOVA, with factors action priming (compatible vs. incompatible) and outcome expectation (expected vs. unexpected). Control ratings were analysed with a $2 \times 2 \times 3$ within subjects ANOVA with factors action priming (compatible vs. incompatible), outcome expectation (expected vs. unexpected) and action–outcome interval (100, 300 or 500 ms). A Greenhouse–Geisser correction was used for tests involving the action–outcome interval factor, which violated the sphericity assumption of ANOVA. Post hoc simple effects *t*-tests were conducted on mean control ratings. Analysis of covariance was also performed on individual participants' raw data, to remove the possible impact of trial-to-trial variability in reaction time on control ratings. For this, a multiple regression model was fitted to each subject's data, using reaction times as a covariate. Prime compatibility and outcome expectation, and the interaction between them were all included in the regression model as dummy variables. Regression coefficients from the individual participants were then submitted to one-sample *t*-tests at the group level.

3. Results

3.1. Priming efficiency

An ANOVA on RTs revealed a main effect of action priming ($F_{(1,29)} = 36.44, p < .001$). Compatible action priming led to significantly faster RTs than incompatible priming (incompatible–compatible = 31.13 ms; see Fig. 2(a) below). There was no effect of outcome expectation on RTs ($F_{(1,29)} = 0.39, p = .54$), nor interaction between the two factors ($F_{(1,29)} = 0.54, p = .47$). Error rates showed a similar pattern, with compatible priming leading to significantly fewer errors than incompatible priming (see Fig. 2(b); $F_{(1,29)} = 10.91, p = .003$). There was no effect of outcome expectation on error rates ($F_{(1,29)} = 1.59, p = .22$), nor interaction between the two factors ($F_{(1,29)} = 0.30, p = .59$). These results confirm that our priming paradigm was effective at modulating action selection processes.

3.2. Control ratings

ANOVA on mean control ratings revealed that control ratings were higher following compatible action priming, compared to incompatible priming ($F_{(1,29)} = 4.25, p = .048$). Additionally, control ratings for expected outcomes were significantly

Table 1
Example schematic of colour mappings within a block.

Prime	Target	Outcome	Action priming	Outcome expectation
67% of trials				
←	←	●	Compatible	Expected
→	←	●	Incompatible	Expected
→	→	●	Compatible	Expected
←	→	●	Incompatible	Expected
33% of trials				
←	←	●	Compatible	Unexpected
→	←	●	Incompatible	Unexpected
→	→	●	Compatible	Unexpected
←	→	●	Incompatible	Unexpected

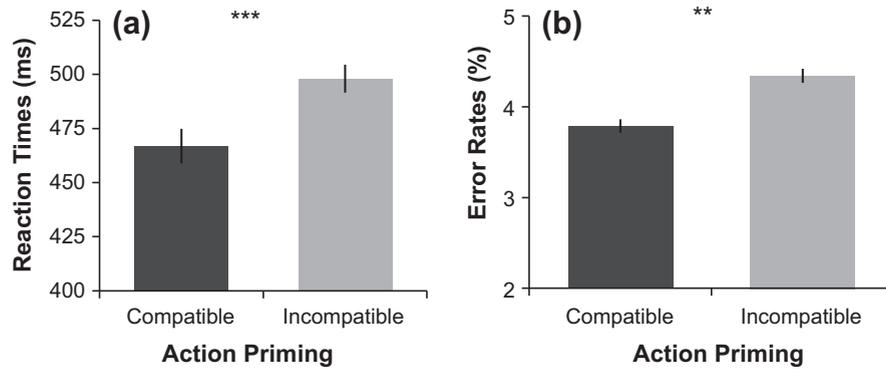


Fig. 2. Effect of action priming on reaction times and error rates. Panel (a) shows that reaction times were significantly faster for compatible than for incompatible action priming. Additionally, panel (b) shows that there were less errors when actions were compatibly primed, compared to when they were incompatibly primed. ** $p < .01$, *** $p < .001$.

higher than for unexpected outcomes ($F_{(1,29)} = 10.13, p = .003$). Numerically, the main effects of action priming (compatible–incompatible: $M = 0.37, SD = 0.98$ and outcome expectation (expected–unexpected: $M = 0.48, SD = 0.83$) were quite similar in mean magnitude.

The interaction between action priming and outcome expectation was also significant ($F_{(1,29)} = 5.956, p = .021$). This interaction can be observed in Fig. 3 below. Simple effects t -tests showed that the expectation of outcomes elicited did not affect control ratings for compatibly primed actions ($t_{(1, 29)} = 1.22, p = .231$). However, on incompatibly primed trials, participants gave significantly higher control ratings following expected outcomes than following unexpected outcomes ($t_{(1, 29)} = 2.97, p = .006$). Simple-effects t -tests were also performed between different levels of the priming compatibility factor, holding the outcome expectation constant. When outcomes were expected, compatible or incompatible action priming were associated with similar ratings ($t_{(1, 29)} = 0.47, p = .64$). When outcomes were unexpected, compatibly primed actions yielded higher control ratings than incompatibly primed actions ($t_{(1, 29)} = 3.725, p = .001$).

Control ratings were also modulated by action–outcome interval ($F_{(2,58)} = 137.73, p = .003$). Here, shorter intervals led to higher ratings than longer intervals (100 ms: $M = 5.48, SD = 1.06$; 300 ms: $M = 4.20, SD = 1.09$; 500 ms: $M = 3.37, SD = 1.07$; all pairwise comparisons: $p < .001$). Importantly, action–outcome interval did not interact with prime–target compatibility ($F_{(2,58)} = 1.47, p = .24$), nor with outcome expectation ($F_{(2,58)} = 1.53, p = .23$). Finally, the three-way interaction just failed to reach statistical significance ($F_{(2,58)} = 2.80, p = .073$).

In additional analyses, we used ANCOVA to investigate any possible relation between reaction time and control rating at the level of individual participants. For each participant, we predicted the control rating on each trial from the reaction time, whether the outcome for that trial was expected or unexpected, and whether the prime for that trial was compatible or incompatible with the target. The resulting coefficients were averaged and tested across individuals. There was no consistent relationship between reaction times and control ratings (average β across participants = 0.16, $t_{(1, 29)} = -0.54, p = .54$). Even after adjusting for any putative linear relationship between RTs and control ratings at the individual participant level, the effects found in the main ANOVA on control ratings still remained significant when the corresponding dummy variables were tested across individuals (expectation: average β across participants = 0.87, $t_{(1, 29)} = 4.32, p < .001$; compatibility: average $\beta = 0.75, t_{(1, 29)} = 3.53, p = .001$; interaction: average $\beta = -0.64, t_{(1, 29)} = -2.55, p = .016$).

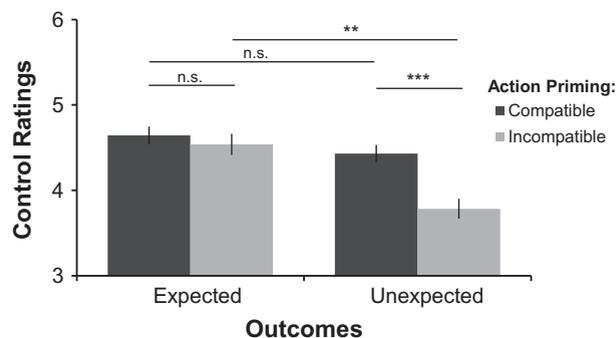


Fig. 3. Interaction between action priming and outcome expectation on control ratings. The figure shows that for expected outcomes, there was no significant effect of action priming. However, unexpected outcomes following compatibly primed actions had significantly higher ratings than unexpected outcomes following incompatibly primed actions. Additionally, expected outcomes led to significantly higher control ratings than unexpected outcomes following incompatibly primed actions, but not after compatibly primed actions. ** $p < .01$, *** $p < .001$.

4. Discussion

The present study replicated findings that outcome expectation modulates the sense of agency (Moore, Lagnado, et al., 2009; Moore, Wegner, & Haggard, 2009; Sato, 2009). We used a probabilistic assignment of colour outcomes to the left and right hands, to allow participants to learn about the possible outcomes of each (left, or right) action, and form predictive action–outcome associations. The main effect of outcome expectation on control ratings showed that participants reported higher levels of control when outcomes were expected, or consistent with predictions, compared to when they were not.

We also varied the interval between action and outcome. Consistent with previous studies (Chambon & Haggard, 2012; Chambon et al., 2013; Haggard et al., 2002; Wenke et al., 2010), the interval between action and outcome was an important retrospective cue to the sense of agency: participants experienced more control for shorter than for longer outcome delays. This, however, was not a variable of interest for the present study: we varied the delay only to ensure that participants experienced a wider range of levels of control during the experiment. The effect of delay did not significantly interact with our variables of interest; therefore, we will not discuss the role of this cue further.

Importantly, this study adds evidence to the growing literature on the contribution of prospective cues, specifically action selection fluency, to the experience of agency (Chambon & Haggard, 2012; Chambon et al., 2013; Wenke et al., 2010). Results showed that action selection fluency, induced by compatible action priming, led to higher control ratings than dysfluent action selection, induced by incompatible priming. The effects of action priming on control ratings could not readily be explained by factors related to motor execution, such as reaction time monitoring (cf. Chambon & Haggard, 2012; Chambon et al., 2013). An analysis of covariance failed to show any relationship between reaction times and control ratings, or a modulation of the effects of interest.

More surprisingly, we found that selection fluency interacted with outcome expectation. When actions were followed by expected outcomes, similar control ratings were found following compatibly and incompatibly primed actions. In contrast, when actions had unexpected outcomes, there was a strong effect of action selection fluency, with compatibly primed actions leading to a stronger sense of control than incompatibly primed actions. We argued above that fluent action selection contributes prospectively to sense of agency. Here we show that this contribution is stronger when predicted and actual outcomes do not match than when they do.

Many current accounts of agency emphasise the retrospective matching of actual action outcomes with predicted outcomes (Blakemore et al., 2002; Farrer et al., 2008; Frith, 2005). While this process makes reference to a prediction, the process itself is retrospective, since it can only be carried out after the outcome is known. Our study confirms that a prospective contribution to SoA also plays an important role. The contribution corresponding to our subliminal priming manipulation must be prospective, because it is based on facilitating or hindering the selection and programming of the appropriate action, prior to its actual execution. Strictly speaking, this prospective component of sense of control is illusory, because it does not correspond to any actual contingency between action and outcome. Indeed, the statistical relation between actions and outcomes were equivalent in compatibly and incompatibly primed trials.

We previously suggested that action selection may serve as a proxy for true agency (Chambon & Haggard, 2012). In many normal circumstances, the difficulties of action control are primarily in selecting what to do: the actual execution of action can be routinised and delegated to lower levels of the action system that do not require central cognitive resources. Action selection fluency may then be a useful *proxy* for sense of control: if one quickly grasps what to do and decides to do it, one can assume that everything flows smoothly from then on. However, this view cannot explain why selection fluency makes its largest contribution when the assumption of normal control turns out to be wrong, as in the case of an unexpected outcome.

Understanding the interaction effect between prospective and retrospective cues that we found may be easier if we consider possible alternative patterns of results in which this interaction would be absent. First, assuming we had found merely additive effects of action priming and outcome expectation, we might suggest that these two factors affected different processing stages in the computation of SoA. For example, prospective and retrospective mechanisms might be entirely independent. Second, suppose we had found that action selection fluency only influenced sense of agency when outcomes were expected. This might suggest that action selection fluency is mistakenly used as a proxy for “successful” goal-directed action (Chambon & Haggard, 2012).

However, our actual results clearly showed that action selection contributes to sense of control, but does so most when outcomes are not as expected. The direction of the interaction suggests that prospective and retrospective cues are reciprocal: prospective cues boost SoA when retrospective cues suggest lack of agency. The default assumption of being in control may be retained unless “sufficient” evidence is gathered against it. An unexpected outcome would challenge the default assumption of being in control. But in fact, Yu and Dayan’s (2005) concept of expected uncertainty offers a plausible explanation for why instrumental agency could be compatible with unexpected outcomes. In the present study the contingency between action and outcomes was not 100%, but only 67%. A degree of uncertainty regarding the outcome is therefore expected. Thus, the participant could predict the *likely* outcome but, at the same time, could predict the occasional occurrence of other outcomes. An unexpected outcome is thus ambiguous: do previous rules no longer apply, or is this merely an isolated spurious event? When a given cue fails to provide clear information about one’s agency, other cues may become more important. An individual unexpected outcome does not therefore disprove agency. We show that, under these circumstances, internal action selection signals that are normally associated with the experience of agency produce a positive SoA.

Alternatively, SoA may be based on a weighted average of several agency cues (Moore & Fletcher, 2012). In such models, each cue is normally weighted in proportion to its reliability (Ernst & Banks, 2002). These models cannot directly explain our results. First, the statistical reliability of our primes was zero, since primes did not predict outcomes. Only the combined prime and target information, i.e. the prime–target compatibility factor could predict outcomes. However, predictions based on prime–target compatibility would be different from those made based on the target and executed action alone.

The reliability of the statistical relation between metacognitive signals of fluency and successful action outcomes may be learned over lifetime experience. Therefore, people may use action selection fluency as a proxy for control, even when it is not a reliable indicator of actual agency *within* a particular experimental context. Previous experience outside the laboratory may justify using selection fluency as a reliable proxy for agency. Participants' use of prospective cues *in the experiment* may reflect this prior learning. Classically, optimal cue integration models view cue reliability as a property of a *distribution* of events. This should be distinguished from any single cue *value* (Ernst & Bühlhoff, 2004). In our design, compatibility and incompatibility could be seen as values of a prospective cue, while expected and unexpected could be seen as values of a retrospective cue. The reliability of each cue is given by its probability schedule, which in our experiment remained fixed throughout. Optimal cue integration models would clearly predict that a highly reliable action–outcome relation, such as 90% expected/10% unexpected, would increase the contribution of retrospective cues, compared to less reliable action–outcome relations, such as 60% expected/40% unexpected. This remains to be tested in future experiments. However, weighting models cannot readily explain how the weight of prospective and retrospective cues changes on a trial-by-trial basis, depending on the *values* of each individual cue, as opposed to the reliability of their overall distribution.

Our results can also be considered within the more general Bayesian framework that unexpected outcomes carry more information than expected outcomes – because unexpected outcomes involve a prediction error (Friston, 2009). On the prospective side, compatible and incompatible primes were equally uninformative about outcomes. On the retrospective side, the informational value of an expected outcome is clearly lower than that of an unexpected outcome. Yet, we found that the uninformative prospective mechanism makes its greatest contribution to SoA precisely when the retrospective mechanism carried the most information, i.e., in situations with unexpected outcomes.

In brief, our results suggest that SoA is not simply based on maximising information about the relation between action and outcome. Participants reported least control when selection of the action had been problematic due to an incompatible prime *and* action outcome was unexpected. The combination of dysfluency and action–outcome mismatch may have particularly disrupted the ‘buzz’ of agency (Synofzik et al., 2008). Neuroimaging studies showed that the angular gyrus receives information about both dysfluency (Chambon et al., 2013) and unexpected outcomes (Farrer et al., 2008). We speculate that this combination may be particularly important for instrumental learning. Reduced SoA could perhaps be a phenomenal marker of an instruction signal whose normal meaning outside the laboratory would be “don't do that again”. In addition, dysfluent action selection could serve to indicate that one should pay close attention to external signals regarding action outcomes, in order to adjust behaviour (Haggard & Chambon, 2012).

Another example of multiple signals for agency comes from neuropsychological studies of anarchic hand. Marcel (2003) suggests that anarchic hand patients have a sense of “authorship” over the action, but not over the intention that initiates the action. Similarly, Pacherie (2007) argues that these patients experience the anarchic hand's actions as their own, but do not experience their will as triggering the action. Both descriptions emphasise the dissociation between an experience of intention and an experience of body movement. Our findings point to a similar dissociation between prospective signals related to action selection, and signals related to action outcome. Our results suggest one can have some feeling of agency relating to the former, despite a reduced agency from the latter. If human SoA indeed involves a combination of several such signals at multiple levels, the brain must be doing more than simply tracking objective statistical contingency between action and outcome in order to produce SoA. This may explain why illusions and delusions of agency are so frequently reported (Alloy & Abramson, 1979). In future work, we hope to explore why a multi-level, combined SoA might be more valuable to the agent than an objectively correct description of action–outcome relations.

Our study has a number of limitations and difficulties. First, we did not directly test prime visibility, so we cannot show that our participants never saw the primes. However, the priming parameters and apparatus were the same as in a previous study showing no conscious perception of the primes (Chambon & Haggard, 2012). Additionally, these parameters were highly conservative, as a previous independent study using direct visibility testing found participants could not report the direction of prime arrows for prime–mask onset asynchronies up to 70 ms, even after more than 3000 trials (Vorberg et al., 2003). Therefore, we can be reasonably confident that our priming was subliminal.

A second issue with our study is the apparent lack of an effect of selection fluency on control ratings for expected outcomes. Previous studies (Chambon et al., 2013; Haggard & Chambon, 2012; Wenke et al., 2010) found this effect using 100% contingency between action and outcomes. The 67% contingency outcomes in this study should most closely mirror this condition. While we did find a numerical difference in the same direction, this failed to reach significance. The statistical relation between action and outcome appears to determine how prospective selection-related mechanisms contribute to agency, but the basis of this relation remains unclear. For the moment, we make the tentative suggestion that action selection may be used as a supportive proxy for outcome contingency when contingency is high, but may be used as an alternative for agency when outcome contingency is low, and unexpected outcomes are therefore frequent.

5. Conclusions

Our study is the first to show that the prospective metacognitive feeling associated with action selection fluency is present when action–outcome relationships are not fully predictable. Moreover, results showed that action selection fluency interacts with prediction–outcome matching. Notably, promoting fluent action selection with subliminal priming led to stronger sense of control than dysfluent action selection, especially for outcomes that were unexpected, and did not match predictions.

Bayesian modelling of cue integration in the sense of agency may prove helpful to clarify the mechanisms underlying the complex integration of agency-related information. However, our results imply a paradox: prospective signals unrelated to actual action–outcome relations contributed most to SoA precisely when the occurrence of an unexpected outcome potentially offered the most actual information about action–outcome relations. This result is difficult to interpret within Bayesian frameworks (Moore & Fletcher, 2012). Human SoA may be statistically suboptimal in this sense and, in fact, SoA is known to have other peculiarities, such as a self-serving bias. More detailed computational models would be required to explain how prospective and retrospective information may be integrated. This might also hint at new treatments for psychiatric disorders, like schizophrenia. A recent study has suggested that the SoA in schizophrenia involves overreliance on retrospective signals (Voss et al., 2010). Improved understanding of prospective SoA mechanisms could have future therapeutic value.

Acknowledgments

N.S. was supported by UCL Impact Scholarship and the Belgian Science Policy Office project “Mechanisms of conscious and unconscious learning” (IAP P7/33). V.C. was supported by a Post-doctoral Study Grant of the Fyssen Foundation, and a Post-doctoral Fellowship of the Région Île-de-France (Paris). P.H. was supported by an ESRC Professorial Fellowship, an ESRC/ESF ECRP Research Project, an ERC Advanced Grant (HUMVOL) and by EU FP7 Project VERE, Work Package 1.

References

- Alloy, L. B., & Abramson, L. Y. (1979). Judgment of contingency in depressed and nondepressed students: Sadder but wiser? *Journal of Experimental Psychology. General*, *108*(4), 441–485.
- Blakemore, S. J., Wolpert, D. M., & Frith, C. D. (2002). Abnormalities in the awareness of action. *Trends in Cognitive Sciences*, *6*(6), 237–242.
- Chambon, V., & Haggard, P. (2012). Sense of control depends on fluency of action selection, not motor performance. *Cognition*. <http://dx.doi.org/10.1016/j.cognition.2012.07.011>.
- Chambon, V., Wenke, D., Fleming, S. M., Prinz, W., & Haggard, P. (2013). An online neural substrate for sense of agency. *Cerebral Cortex*, *23*(5), 1031–1037. <http://dx.doi.org/10.1093/cercor/bhs059>.
- Eimer, M., & Schlaghecken, F. (1998). Effects of masked stimuli on motor activation: Behavioral and electrophysiological evidence. *Journal of Experimental Psychology. Human Perception and Performance*, *24*(6), 1737–1747.
- Eimer, M., & Schlaghecken, F. (2003). Response facilitation and inhibition in subliminal priming. *Biological Psychology*, *64*(1–2), 7–26.
- Ernst, M. O., & Banks, M. S. (2002). Humans integrate visual and haptic information in a statistically optimal fashion. *Nature*, *415*(6870), 429–433. <http://dx.doi.org/10.1038/415429a>.
- Ernst, M. O., & Bühlhoff, H. H. (2004). Merging the senses into a robust percept. *Trends in Cognitive Sciences*, *8*(4), 162–169. <http://dx.doi.org/10.1016/j.tics.2004.02.002>.
- Farrer, C., Franck, N., Georgieff, N., Frith, C. D., Decety, J., & Jeannerod, M. (2003). Modulating the experience of agency: A positron emission tomography study. *NeuroImage*, *18*(2), 324–333.
- Farrer, C., Frey, S. H., Van Horn, J. D., Tunik, E., Turk, D., Inati, S., et al (2008). The angular gyrus computes action awareness representations. *Cerebral Cortex*, *18*(2), 254–261. <http://dx.doi.org/10.1093/cercor/bhm050>.
- Farrer, C., & Frith, C. D. (2002). Experiencing oneself vs another person as being the cause of an action: The neural correlates of the experience of agency. *NeuroImage*, *15*(3), 596–603. <http://dx.doi.org/10.1006/nimg.2001.1009>.
- Friston, K. (2009). The free-energy principle: A rough guide to the brain? *Trends in Cognitive Sciences*, *13*(7), 293–301. <http://dx.doi.org/10.1016/j.tics.2009.04.005>.
- Frith, C. (2005). The self in action: Lessons from delusions of control. *Consciousness and Cognition*, *14*(4), 752–770. <http://dx.doi.org/10.1016/j.concog.2005.04.002>.
- Fukui, T., & Gomi, H. (2012). Action evaluation is modulated dominantly by internal sensorimotor information and partly by noncausal external cue. *PLoS ONE*, *7*(5), e34985. <http://dx.doi.org/10.1371/journal.pone.0034985>.
- Gallagher, S. (2012). Multiple aspects in the sense of agency. *New Ideas in Psychology*, *30*(1), 15–31. <http://dx.doi.org/10.1016/j.newideapsych.2010.03.003>.
- Haggard, P., & Chambon, V. (2012). Sense of agency. *Current Biology: CB*, *22*(10), R390–392. <http://dx.doi.org/10.1016/j.cub.2012.02.040>.
- Haggard, P., Clark, S., & Kalogerias, J. (2002). Voluntary action and conscious awareness. *Nature Neuroscience*, *5*(4), 382–385. <http://dx.doi.org/10.1038/nn827>.
- Haggard, P., & Tsakiris, M. (2009). The experience of agency. *Current Directions in Psychological Science*, *18*(4), 242–246. <http://dx.doi.org/10.1111/j.1467-8721.2009.01644.x>.
- Lingnau, A., & Vorberg, D. (2005). The time course of response inhibition in masked priming. *Perception & Psychophysics*, *67*(3), 545–557.
- Marcel, A. J. (2003). The sense of agency: Awareness and ownership of action. In *Agency and self-awareness: Issues in philosophy and psychology*. Oxford: Clarendon Press.
- Metcalfe, J., & Greene, M. J. (2007). Metacognition of agency. *Journal of Experimental Psychology. General*, *136*(2), 184–199. <http://dx.doi.org/10.1037/0096-3445.136.2.184>.
- Moore, J. W., & Fletcher, P. C. (2012). Sense of agency in health and disease: A review of cue integration approaches. *Consciousness and Cognition*, *21*(1), 59–68. <http://dx.doi.org/10.1016/j.concog.2011.08.010>.
- Moore, J. W., & Haggard, P. (2008). Awareness of action: Inference and prediction. *Consciousness and Cognition*, *17*(1), 136–144. <http://dx.doi.org/10.1016/j.concog.2006.12.004>.
- Moore, J. W., Lagnado, D., Deal, D. C., & Haggard, P. (2009). Feelings of control: Contingency determines experience of action. *Cognition*, *110*(2), 279–283. <http://dx.doi.org/10.1016/j.cognition.2008.11.006>.
- Moore, J. W., Wegner, D. M., & Haggard, P. (2009). Modulating the sense of agency with external cues. *Consciousness and Cognition*, *18*(4), 1056–1064. <http://dx.doi.org/10.1016/j.concog.2009.05.004>.

- Nahab, F. B., Kundu, P., Gallea, C., Kakareka, J., Pursley, R., Pohida, T., et al. (2011). The neural processes underlying self-agency. *Cerebral Cortex (New York, NY: 1991)*, 21(1), 48–55. <http://dx.doi.org/10.1093/cercor/bhq059>.
- Pacherie, E. (2007). The anarchic hand syndrome and utilization behavior: A window onto agentive self-awareness. *Functional Neurology*, 22(4), 211–217.
- Sato, A. (2009). Both motor prediction and conceptual congruency between preview and action-effect contribute to explicit judgment of agency. *Cognition*, 110(1), 74–83. <http://dx.doi.org/10.1016/j.cognition.2008.10.011>.
- Spence, S. (2009). *The actor's brain: Exploring the cognitive neuroscience of free will* (1st ed.). OUP Oxford.
- Sperduti, M., Delaveau, P., Fossati, P., & Nadel, J. (2011). Different brain structures related to self- and external-agency attribution: A brief review and meta-analysis. *Brain Structure & Function*, 216(2), 151–157. <http://dx.doi.org/10.1007/s00429-010-0298-1>.
- Synofzik, M., Vosgerau, G., & Newen, A. (2008). Beyond the comparator model: A multifactorial two-step account of agency. *Consciousness and Cognition*, 17(1), 219–239. <http://dx.doi.org/10.1016/j.concog.2007.03.010>.
- Vorberg, D., Mattler, U., Heinecke, A., Schmidt, T., & Schwarzbach, J. (2003). Different time courses for visual perception and action priming. *Proceedings of the National Academy of Sciences*, 100(10), 6275–6280. <http://dx.doi.org/10.1073/pnas.0931489100>.
- Thorndike, E. L. (1898). Animal intelligence: An experimental study of the associative processes in animals. *The Psychological Review: Monograph Supplements*, 2(4), i–109. <http://dx.doi.org/10.1037/h0092987>.
- Voss, M., Moore, J. W., Hauser, M., Gallinat, J., Heinz, A., & Haggard, P. (2010). Altered awareness of action in schizophrenia: A specific deficit in predicting action consequences. *Brain: A Journal of Neurology*, 133(10), 3104–3112. <http://dx.doi.org/10.1093/brain/awq152>.
- Wegner, D. M. (2004). Précis of the illusion of conscious will. *The Behavioral and Brain Sciences*, 27(5), 649–659. discussion 659–692.
- Wegner, D. M., & Sparrow, B. (2004). Authorship processing. In M. S. Gazzaniga (Ed.), *The cognitive neurosciences* (3rd ed., pp. 1201–1209). Cambridge, MA: MIT Press.
- Wegner, D. M., & Wheatley, T. (1999). Apparent mental causation. Sources of the experience of will. *The American Psychologist*, 54(7), 480–492.
- Wenke, D., Fleming, S. M., & Haggard, P. (2010). Subliminal priming of actions influences sense of control over effects of action. *Cognition*, 115(1), 26–38. <http://dx.doi.org/10.1016/j.cognition.2009.10.016>.
- Wolpe, N., Haggard, P., Siebner, H. R., & Rowe, J. B. (2013). Cue integration and the perception of action in intentional binding. *Experimental Brain Research. Experimentelle Hirnforschung. Experimentation Cerebrale*. <http://dx.doi.org/10.1007/s00221-013-3419-2>.
- Wolpert, D. M., Ghahramani, Z., & Jordan, M. I. (1995). An internal model for sensorimotor integration. *Science (New York, NY)*, 269(5232), 1880–1882.
- Yu, A. J., & Dayan, P. (2005). Uncertainty, neuromodulation, and attention. *Neuron*, 46(4), 681–692. <http://dx.doi.org/10.1016/j.neuron.2005.04.026>.