Prediction error and regularity detection underlie two dissociable mechanisms for computing the sense of agency

Wen Wen[1, 2, 3] and Patrick Haggard[1]

[1]Institute of Cognitive Neuroscience, University College London, Alexandra House, 17-19 Queen Square, London WC1N 3AZ, UK

[2]Department of Precision Engineering, University of Tokyo, 7-3-1 Hongo, Bunkyo-ku, Tokyo 113-8656, Japan

[3]Japan Society for the Promotion of Science, 5-3-1 Kojimachi, Chiyoda-ku, Tokyo 102-0083, Japan

Corresponding author:

Wen Wen (wen@robot.t.u-tokyo.ac.jp)

Co-author:

Patrick Haggard (p.haggard@ucl.ac.uk)

Abstract

The sense of agency refers to the subjective feeling of controlling one's own actions, and through them, events in the outside world. According to computational motor control models, the prediction errors from comparison between the predicted sensory feedback and actual sensory feedback determine whether people feel agency over the corresponding outcome event, or not. This mechanism requires a model of the relation between action and outcome. However, in a novel environment, where this model has not yet been learned, the sense of agency must emerge during exploratory behaviours. In the present study, we designed a novel control detection task, in which participants explored the extent to which they could control the movement of three dots with a computer mouse, and then identified the dot that they felt they could control. Pre-recorded motions were applied for two dots, and the participants' real-time motion only influenced one dot's motion (i.e. the target dot). We disturbed participants' control over the motion of the target dot in one of two ways. In one case, we applied a fixed angular bias transformation between participant's movements and dot movements. In another condition, we mixed the participant's current movement with replay of another movement, and used the resulting hybrid signal to drive visual dot position. The former intervention changes the match between motor action and visual outcome, but maintains a regular relation between the two. In contrast, the latter alters both matching and motor-visual correlation. Crucially, we carefully selected the strength of these two perturbations so that they caused the same magnitude of impairment of motor performance in a simple reaching task, suggesting that both interventions produced comparable prediction errors. However, we found the visuomotor transformation had much less effect on the ability to detect which dot was under one's own control than did the nonlinear disturbance. This suggests a specific role of a correlation-like mechanism that detects ongoing visual-motor regularity in the human sense of agency. These regularity-detection mechanisms would remain intact under the linear, but not the nonlinear transformation. Human sense of agency may depend on monitoring ongoing motor-visual regularities, as well as on detecting prediction errors.

Keywords: sense of agency, motor control, regularity, comparator, internal model

Introduction

People rapidly notice when environmental events depend on their actions. They then self-attribute these stimuli and feel sense of agency (Gallagher, 2000; Haggard & Chambon, 2012) over them. Thus, we readily perceive whether a sound of footsteps is caused by our own walking or not. Comparator models provide a framework examining this self-attribution process (Blakemore, Wolpert, & Frith, 1998, 2002; Frith, Blakemore, & Wolpert, 2000; Wolpert & Flanagan, 2001). According to this computational framework, agency is computed by comparing a prediction generated from an internal model, using an efference copy of motor commands, and actual sensory feedback (blue background in Figure 1). The sense of agency diminishes if the comparator produces a mismatch (i.e. a prediction error). For example, an incorrect internal model produces both poor motor control performance, and a large prediction error at the output of the comparator. In contrast, a well-adjusted internal model produces fluent motor control, together with predictable sensory inflow. This results in no prediction error at the output of the comparator, and, therefore, a "sense of agency", or feeling that the action and feedback are self-caused. Besides the framework of comparator, many other motor control theories, such as the ideomotor theory (Prinz, 1997), suggest that the anticipation of action outcomes is important for motor control and the sense of agency (Spengler, von Cramon, & Brass, 2009). In other words, knowing what and how to control is considered to be a major premise of sense of agency.

On the other hand, active inference and learning theory suggests that behaviour has exploratory and exploitative aspects (Friston et al., 2016). Exploratory behaviours performed in environments containing ambiguity of control may rely on a cognitive mechanism that detects environmental statistics. Once the statistical relations between one's exploratory actions and the events in the external world are detected, sense of agency may emerge. Once a sense of agency has been acquired through exploration, it can then be exploited in goal-directed behaviours, producing further evidence for self-attribution.

In this paper, we describe how extracting the natural statistics of motor and visual events during exploratory action involves a form of *regularity detection*. Importantly, regularity detection differs from model-based processes of motor control in that the former does not require a precise prediction of the outcome for each action. Developmental research offers some support for the idea of a regularity detection mechanism. Infants of 9-12 weeks infants' made more foot thrust movements when their ankle was looped to an overhead suspension bar (Rovee & Rovee, 1969), so that their movements produced visual effects. Infants at this age have only minimal motor skill, and lack the precise forward and inverse models required for aimed movement. Therefore, the reinforcement of their exploratory behaviour is probably due to the perception of a regular relation between events in the external world (i.e. motion of the suspension bar) and their own actions (i.e. foot thrust). The perception of self-generated regularity can also contribute to sense of agency in later development. For example, this may account for the widespread preference for actions that reliably produce outcomes, over actions that do not (Karsh, Eitam, Mark, & Higgins, 2016; Nafcha, Higgins, & Eitam, 2016).

In the present study, we investigate whether motor performance and sense of agency are inextricably linked, as comparator models suggest, or may dissociate. On the former view, an efficient internal model leads to both good motor performance and strong sense of agency, as a result of a common cause of reduced low prediction errors. On another view, different computations might underlie objective motor performance and subjective sense of agency, potentially producing dissociations. Here we investigate a possibility that sense of agency is partly based on detecting global regularities between one's actions and their outcomes through repeated sampling (pink background in Figure 1). This process would bypass the internal (forward and inverse) model (Kawato, 1999; Wolpert & Kawato, 1998), using buffered samples of action and sensory feedbacks to calculate a correlation between them. Importantly, this putative regularity mechanism would detect a sense of agency using the same kind of pattern-detection processes used in other cognitive and perceptual functions, and without any special or privileged link to the motor control system that decides and generates actions. When we perform a series of actions successfully, the comparator mechanism repeatedly signals no prediction error, and the regularity mechanism accumulates repeated samples in which action and outcome are strongly related. However, the two mechanisms are potentially dissociable. For example, across a series of actions, there might be a *consistent* prediction error, perhaps due to an unadapted internal model, yet there might be a regular relation between actions and outcomes. For example, action and sensory feedback in Figure 1 show a strong correlation but a consistent non-zero prediction error (appearing as a positive intercept in the scattergram in lower panel of Figure 1). In this case, the comparator mechanism would suggest no sense of agency should occur, while a regularity mechanism would suggest that normal sense of agency should be present. In addition, higher-level beliefs in one's own agency may also affect the processes in motor control and regularity detection, although this notion was not shown in Figure 1.

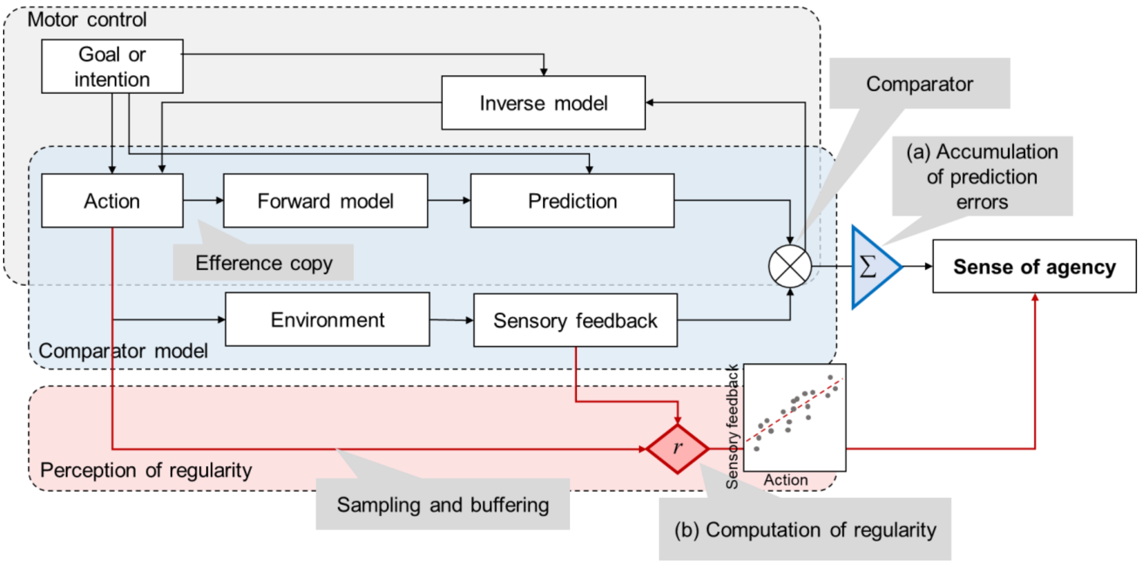

Figure 1. A model of two separate contributions to the sense of agency. The blue shaded area shows the classic comparator model of motor control. The red area shows a monitoring and buffering mechanism that allows computation of regularity between actions and outcomes. Both sources may potentially contribute to the sense of agency.

To test the dual-route hypothesis of sense of agency shown schematically in Figure 1, we induced two factors that disturb the sense of agency by selectively influencing the prediction-error mechanism and the regularity-monitoring mechanism respectively. First, we provided a constant disturbance by applying a consistent angular bias in the visual feedback caused by participants' actions. This leads to large prediction errors at the comparator, but leaves intact any regularity in the relation between action and feedback. Given sufficient experience, people readily adapt to such consistent disturbances by updating their internal model, and prediction error decreases rapidly (Kitazawa, Kimura, & Uka, 1997). However, in our task, we minimised such adaptation by randomly mixing trials with different angular biases (e.g. 30° and 90°). As a result, a non-zero prediction error persisted, even though the relation between action and visual feedback was highly regular. The second form of disturbance involved mixing 60% of someone else's motion with the participants' own instantaneous motion in order to generate the visual feedback (Wen, Brann, Di Costa, & Haggard, 2018; Wen & Haggard, 2018). The highly nonlinear disturbance introduces errors at the comparator, which vary from one moment to the next. Importantly, such nonlinear disturbance produces a highly irregular relation between action and visual feedback. Note that the nonlinear and linear disturbances were alternatives, and were never combined in a single trial. In other words, participants *either* experienced an angular transformation *or* a mixture of their motion and someone else's motion in separate conditions. Finally, we ensured that these two qualitatively-different disturbances had quantitatively similar effects on performance in our motor control task (see below). This meant we could investigate the extent to which each kind disturbance might influence the sense of agency, without confounding differences in motor performance. In addition, we also included a condition of 30° angular bias, and a condition of 90% other's motion, for references of good and poor control, respectively. Therefore, we measured both motor control performance and the sense of agency, using a reaching task and a control detection task, respectively, in each of the above four disturbance conditions (30° and 90° angular bias, 60% and 90% others' motion).

Methods

Participants

Twenty-four healthy volunteers were recruited from a participant database (mean age = 23.2, range = 18-30, *SD* = 3.2, 14 women). A power calculation was performed using an estimate of effect size for the difference in control detection between the conditions of 90° angular bias and 60% of other's motion, based on the data from the first 5 participants (Cohen's d = 0.70). This indicated that a sample size of 19 would be sufficient to provide a power of 0.8 (with $\alpha = .025$, rather than the conventional .05, reflecting the probability hit associated with making 2 sequential tests, first for initial power calculation, and again for subsequent hypothesis testing). However, we decided to choose a larger sample size of 24 to ensure a higher power. All participants were right-handed and reported normal or corrected-to-normal visual acuity. The study was approved by the local ethics committee (University College London). All participants provided written informed consent before participation and received a small reimbursement.

Task

The experimental task was conducted with a computer, a 17-inch LCD monitor (width 338 × height 270 mm, resolution 1280 × 1024 pixels at 60 Hz), a keyboard, and a computer mouse. There were two types of task: Control detection task and motor control task (Figure 2). In the control detection task (Figure 2A), participants pressed a space key to start each trial, and then saw three 10.5-mm (40 pixels) white dots on a black screen. The initial positions of the dots were randomly generated, ensuring a minimal distance of 52.8 mm (200 pixels) between dots and a maximal distance of 66 mm (250 pixels) from the centre of the screen. Once participants started to move the mouse, all the dots started to move. The onset, offset, and velocity of dot motion corresponded to participants' mouse movement, but the relation between the dots' trajectories and participants' mouse movement could vary (see S1 for a demonstration video of the control detection task). In two nonlinear disturbance conditions, some proportion of another participant's pre-recorded mouse movement was mixed with the participant's own movement in order to drive the visually-displayed dots (Wen et al., 2018; Wen & Haggard, 2018). Specifically, in a condition with 60% nonlinear disturbance, participants' mouse movement in x- and y-axis was mixed with a pre-recorded x- and y-axis pair on a 40/60 ratio at each frame when the screen is refreshed. Two values of nonlinear disturbance were used (60%, and 90%). In addition, we studied two linear disturbances, which involved a clockwise angular bias in the transformation between participant's mouse movements and the visually-displayed dots. Two values of linear disturbances were used (30°, and 90°). In each control detection trial, participants moved the mouse freely for 10 s, to find out which dot they were able to control. The motion of one dot was related to the mouse movement but distorted using the above two types of manipulation, while the other two dots always moved in trajectories pre-recorded from other participants. Ten seconds after the first onset of the mouse movement, the three dots stopped with a number (1, 2, or 3) near each of them, and a question "Which dot do you feel that you could control?" appeared on the top of the screen. Participants pressed a number key to respond. The two conditions of 30° angular bias and 90% of other's motion mainly served as a manipulation check: We predicted that they should produce good and poor motor performance respectively, and also high and low sense of agency.

The motor control task was designed to measure prediction errors in each experimental condition when people attempt to move the stimulus. In this task (Figure 2B), participants pressed a space key to start each trial, and then saw one dot that was initially presented at the centre of the screen. The onset, offset, and velocity of the motion of the dot corresponded to the mouse movement, but the trajectory was distorted by the nonlinear or linear disturbance. A 5.3-mm (20 pixels) red cross was randomly presented at one of four positions, which were 202.8 mm (768 pixels) horizontally or vertically away from the centre of the screen. Participants were told to move the dot to touch the red cross as soon as possible by moving the mouse. The red cross disappeared once it was touched by the dot, and appeared at a new position (one out of the rest three possible positions). Participants were instructed to repeatedly reach for the red cross as many times as possible in each trial. Each motor control trial lasted for 10 s from the onset of the first mouse movement. Less successful touches indicate larger prediction errors.

There were four experimental conditions each involving different disturbances. The disturbance conditions were: 90% nonlinear disturbance (& 0° angular bias), 60% nonlinear disturbance (& 0° angular bias), 90° angular bias (& 0% nonlinear disturbance), 30° angular bias (& 0% nonlinear disturbance). The nonlinear and linear disturbances were never combined. In the condition of 90% nonlinear disturbance, participants had extremely poor control over the stimuli, while in the condition of 30° angular bias, participants had good control over the stimuli. Importantly, participants had partial control over the stimuli in the two conditions of 60% nonlinear disturbance and 90° angular bias. These two disturbances were chosen on the basis of pilot data to achieve matched levels of motor control performance. Each disturbance was applied to both the control detection task, and to the reaching task, resulting in eight types of trial (4 types of disturbance × 2 types of task). Each type of trial was repeated for 10 times, resulted in a total of 80 trials. The trial order was randomized between participants.

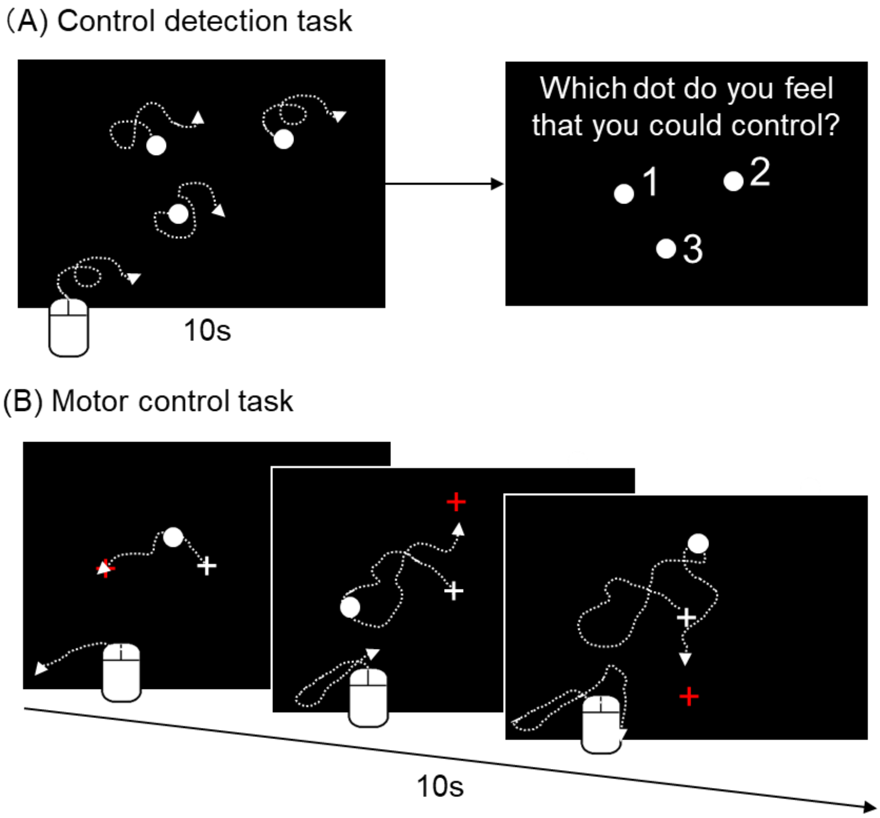

Figure 2. Timelines of a control detection trial (A) and a motor control trial (B). In the control detection task, participants moved the mouse freely to trigger the motion of three dots for 10 s. They explored which dot they were able to control. Two dots' motion was pre-recorded other's motion, and one target dot moved either corresponding to participants' motion with an angular transformation (30° or 90°), or in a hybrid direction mixed with participants' motion and pre-recorded other's motion (in a ratio of 40/60 or 10/90). In the motor control task, participants moved the dot to touch a red cross as soon as possible by moving the mouse for 10 s. The red cross disappeared once

it was touched by the dot, and appeared at a new position. The experimental conditions in the motor control task were identical to these in the control detection task. Dashed curves with arrows illustrate of dots' trajectories and mouse motion.

Procedure

Participants were tested individually in a quite testing room, seated on a chair positioned approximately 60 cm from a 17-inch LCD monitor. Having received an explanation regarding the experimental tasks, participants practiced for 8 trials, containing 1 trial of each condition of each task. The actual task contained 80 trials in a random order, and participants were allowed to take short breaks freely between trials if needed. The experiment lasted for approximately 30 min.

Experimental Design and Statistical Procedures

In summary, the independent variable was the type of disturbance of control over the target dot in each task. There were four conditions of the independent variable: 90% nonlinear disturbance, 60% nonlinear disturbance, 90° angular bias, 30° angular bias. The dependent variables were the detection accuracy in the control detection task, and the number of successful touches in the motor control task. In addition, we also recorded participants' mouse motion in each task for analyses. For each task, the dependent variables were analysed with repeated measures ANOVAs (one-factor, four conditions), and the differences between conditions were examined with Bonferroni-adjusted *t* tests. Lastly, a correlation analysis was conducted between the performance of the motor control and control detection tasks to quantify the dissociation of motor control and sense of agency.

Results

Figure 3 shows the control detection accuracy (red bars) and the motor control performance (blue bars) in our four conditions. First, as predicted, the linear and nonlinear disturbances indeed caused impairments in reaching performance ($F(3, 69) = 229.93$, $p < .001$, $\eta^2_p = .909$). Post hoc tests, Bonferroni-adjusted for four disturbance conditions, showed that motor performance in the condition with 30° linear disturbance was significantly better than the other conditions (Bonferroni-adjusted *p*s < .001), and motor performance in the condition of 90% nonlinear disturbance was significantly worse than the other conditions (Bonferroni-adjusted *p*s < .01). Most importantly, there was no significant difference between the conditions of 60% nonlinear and 90° linear disturbance in motor performance (Bonferroni-adjusted $p > .999$). In order to further compare the task difficulty between the two conditions in the reaching task, we also examined the variability in task performance. There was no significant difference in the individual standard deviation between these two conditions of 60% nonlinear and 90° linear disturbance (paired-*t* test, $t(23) = 0.255$, $p = .801$, Cohen's d = 0.052). In short, participants had similar levels of actual control over the dot in the conditions of 60% nonlinear and 90° linear disturbance.

Despite this almost identical motor performance in the 90° linear disturbance and the 60% nonlinear disturbance conditions, these conditions differed significantly in the sense of agency, as measured by successful detection of which dot was under one's own control. The main effect of condition on detecting the controlled dot was significant ($F(3, 69) = 61.62$, $p < .001$, $\eta^2_p = .728$). Post hoc tests showed that all between-condition differences were significant (Bonferroni-adjusted *p*s < .001), except the difference between 90% nonlinear and 60% nonlinear disturbances (Bonferroni-adjusted $p = .121$). As these two conditions showed the lowest rates for detecting one's own control, a floor effect cannot be excluded. More crucially for our hypotheses, the 60% nonlinear disturbance impaired sense of agency to a significantly greater extent than did 90° linear disturbance (Bonferroni-adjusted $p < .001$), even though these conditions had similar effects on the motor control performance. The results therefore clearly supported the hypothesis of a dissociation between objective motor performance and subjective sense of agency.

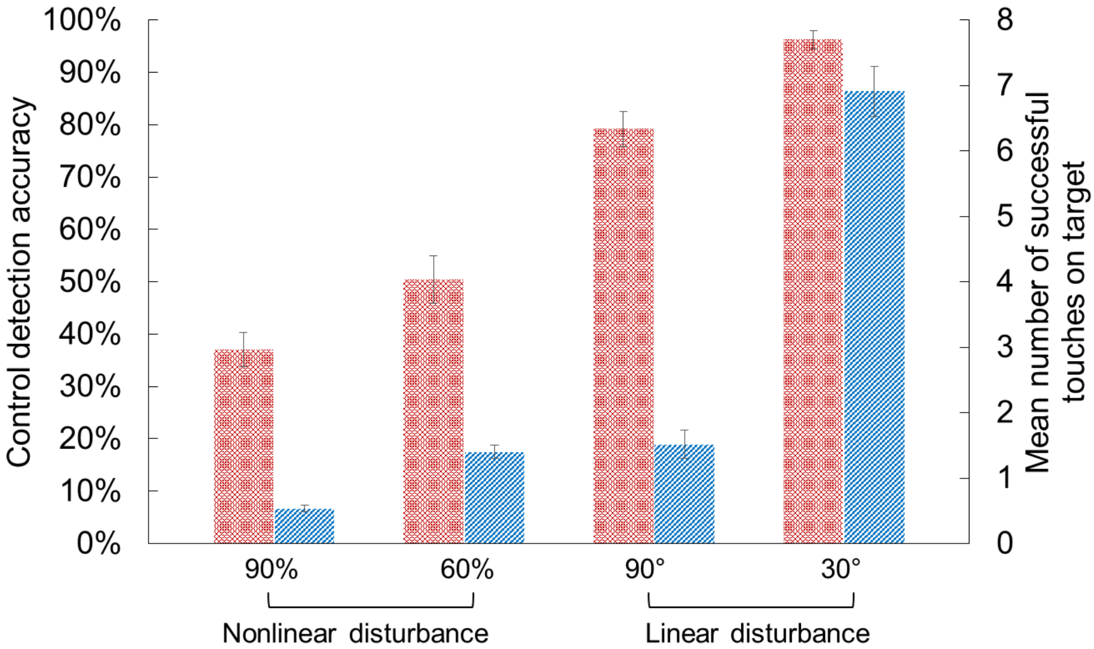

Figure 3. Differences between condition in sense of agency, as measured by control detection accuracy (red bars, left hand ordinate) and in motor control performance, as measured by mean number of successful touches on target (blue bars, right hand

ordinate) in control detection task and the motor control task, respectively. Error bars represent standard errors. In addition, supplementary material S2 shows the correlation between the performance of the motor control task and the performance in the control detection task in the two key conditions (i.e. 90° angular bias and 60% other's motion). There was no significant correlations between the performance in the two tasks, indicating that an individual participant's ability to detect control over an object was not related to how well they actually controlled the object.

Finally, we examined the detailed kinematics of movements made in the control detection task, and in the reaching task. If the kinematics in the two tasks differed strongly, then a dissociation between their corresponding dependent variables of sense of agency and motor performance would be unsurprising. Figure 4 depicts the trajectories of participants' mouse movements in all the trials of each condition of each task. A 2 × 4 (task × control condition) repeated-measures ANOVA on moving distance revealed a significant main effect of condition ($F(3, 69) = 19.62$, $p < .001$, $\eta^2_p = .460$) and a significant interaction between task and condition ($F(3, 69) = 14.77$, $p < .001$, $\eta^2_p = .391$), but no significant main effect of task ($F(1, 23) = 0.59$, $p = .452$, $\eta^2_p = .025$). Post hoc tests on the effect of control condition showed that participants moved less in 30° linear disturbance condition than in the other conditions (Bonferroni-adjusted *p*s < .05), and moved the most in the condition of 90% nonlinear disturbance (Bonferroni-adjusted *p*s < .01). There was no significant difference between the conditions of 90° linear and 60% nonlinear disturbance (Bonferroni-adjusted $p > .999$). The significant interaction resulted from less movement in the motor control task than the control detection task, specifically when people had very good control (i.e. with 30° linear disturbance; a Bonferroni-adjusted *p* level of 0.0125 was used; $t(23) = 2.98$, $p = .007$, Cohen's d = 0.61) but no significant difference between the two tasks in the other conditions (For 90% nonlinear disturbance: $t(23) = 1.30$, $p = .207$, Cohen's d = 0.27; for 60% nonlinear disturbance: $t(23) = 1.22$, $p = .235$, Cohen's d = 0.25; for 90° linear disturbance: $t(23) = 0.23$, $p = .820$, Cohen's d = 0.05). In general, people tended to move less when they had better control, but the amount of movement did not differ significantly between the reaching task and the control detection task. To summarise, the difference in control detection accuracy between the conditions of 90° linear and 60% nonlinear disturbances did not simply reflect differences in the way the participants moved in the two conditions.

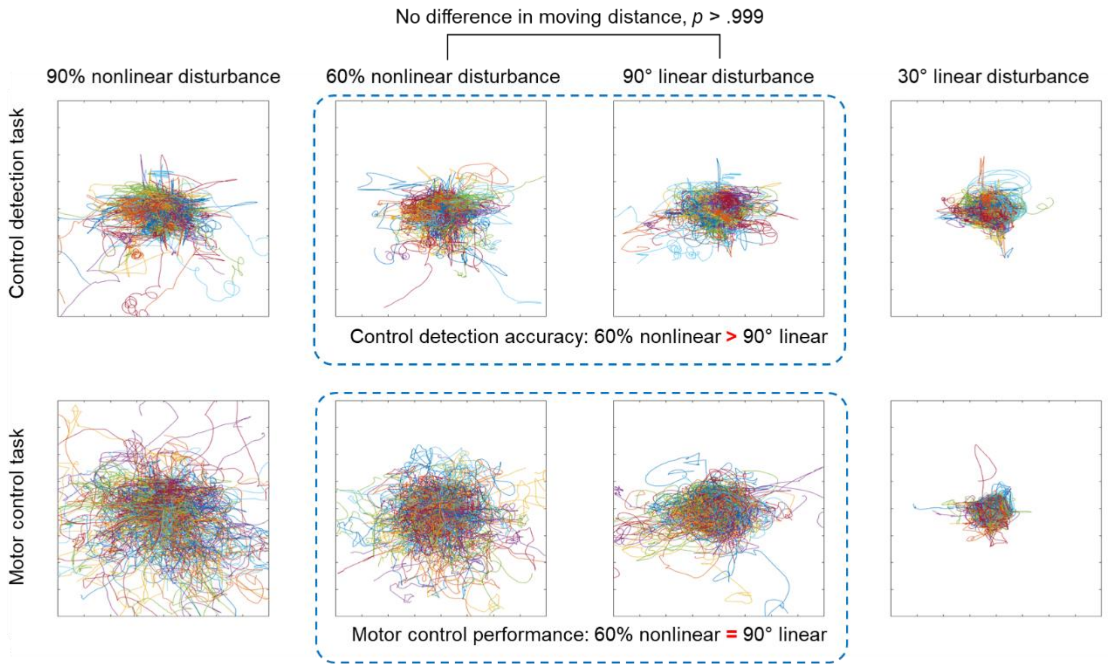

Figure 4. Participants' mouse movements in the four conditions of the two tasks.

Discussion

The present study focused on the different contributions of motor control models and of exploratory regularity-detection mechanisms to the overall sense of agency. The classic view suggests that the sense of agency depends on a comparator that combines sensory feedback with predicted feedback (De Vignemont & Fourneret, 2004; Haggard, 2017). This comparator mechanism is necessarily based on predictions from *individual* sensorimotor commands to corresponding *individual* sensory feedback events. When a continuous action episode involves several movements, the prediction errors are presumably accumulated, and an overall sense of agency is synthesized. Thus, a general sense of agency could emerge from accumulating experiences of several individual actions. However, when experience of several actions and their feedback is available, an additional mechanism can contribute to computing sense of agency, using a form of environmental statistics. In particular, one might detect the regular relation between ones' actions and observed events. Importantly, a regular action-outcome relation may be detected even when a comparator consistently produces a constant, large prediction error. We hypothesised that both regularity detection and model-comparator processes might contribute to sense of agency. To examine our hypothesis, we induced two types of disturbance designed to influence the comparator and regularity computation mechanisms respectively. A linear disturbance of angular bias greatly disturbed the comparator and consequently resulted in poor motor control, but left the computation of regularity intact. On the other hand, a nonlinear disturbance based on mixing visual feedback with someone else's motion interrupted both comparator and regularity computation. Importantly, the severity of these two very different types of disturbance was chosen to match their detrimental effects on motor control performance. Our results confirmed that these two qualitatively different disturbances had similar effects on motor performance. Specifically, participants' motor performance was essentially equal in the conditions of 90° angular bias and 60% other's motion. This absence of motor performance differences did not simply indicate ceiling/floor effects, since both these conditions were significantly better than the extremely poor control observed in the condition with 90% other's motion, and significantly worse than the very good control observed in the 30° angular bias condition. This showed that the participants had some degree of control over the dot, but nevertheless received substantial prediction errors in the two intermediate control conditions. In particular, the poor performance in the 90° linear transformation condition, showed that the participants' internal model was not adapted. They did not completely learn the new movement-visual feedback mapping, due to the randomised mixture of disturbances across trials, and they therefore generated large prediction errors when they moved the dot. However, because the regular relation between action and visual outcome was preserved in the condition of 90° linear disturbance, our measure of sense of agency, based on detection of which of several dots was under one's own control, was relatively unaffected. In particular, our sense of agency measure was significantly greater under a 90° linear disturbance than under a 60% nonlinear disturbance. In addition, participants' ability to control the dot in the goal-directed actions of our motor performance trials, was not correlated with their ability to detect which dot they controlled during exploratory actions (S2). These findings support our hypothesis that the computation of regularity is an important input for computing sense of agency, which dissociates from the classical system of an internal model plus comparator. Our results therefore support the two-route model of sense of agency, schematized in Figure 1.

Numerous studies have revealed the link between motor control and the sense of agency. Generally, better performance is associated with a stronger sense of agency, regardless of whether the good performance is a direct result of the participant's own action or not (Metcalfe, Eich, & Miele, 2013; Metcalfe & Greene, 2007; Wen, Yamashita, & Asama, 2015b, 2015a). However, our results firstly showed that the sense of agency could be preserved even when the comparator produces consistently large prediction errors, and when motor control performance is correspondingly poor. In the condition of 90° angular disturbance, the participants failed to learn a model of the linear transformation because they experienced several different levels of linear and nonlinear transformations in randomised order during the experiment, with only a brief exposure to the current transformation in any one trial. Previous research confirms that forward models cannot be learned under such conditions of mixed or randomised exposure (Shadmehr Reza & Brashers-Krug, 1997). Nevertheless, the relation between motor action and visual dot motion remained regular under our linear disturbance, so a regularity-detection mechanism could still contribute to sense of agency. Indeed, we found that sense of agency, as measured by control detection accuracy remained high.

Conversely, our 60% nonlinear disturbance would cause both a prediction error, and also a reduced estimate of regularity. The action-visual feedback relation is irregular in this condition, because the visual dot moves largely in response to another, pre-recorded movement, and not in any relation to the current movement direction. We found that the 60% nonlinear disturbance reduced reaching performance to the same extent as the 90° angular disturbance, suggesting similar prediction errors in these two conditions. However, control detection was significantly worse under the 60% nonlinear disturbance than under the 90° angular disturbance. This result implies that some factor that is absent for 60% nonlinear disturbance but present for the 90° angular disturbance contributes to human sense of agency. We suggest that this factor may involve computing the *ongoing regularity* of the relation between actions and outcomes, as opposed to merely computing instantaneous prediction error. Computation of regularity may continue throughout people's ongoing interactions with the external world, and is unaffected by linear disturbances. Importantly, the regularity of action-outcome relations requires several samples, and cannot be done for a single action. In other words, people could only perceive a regular relation between their actions and sensory feedback after they had sampled sufficient evidence. Many previous studies of agency dealt with individual, brief, discrete actions (Haggard, Clark, & Kalogeras, 2002). Our tasks involved 10 s of *continuous* movement and visual feedback, giving a greater opportunity to accumulate evidence, and to detecting possible regularities in the action-visual feedback relation.

The relative contributions of the motor control mechanism and the perception of regularity mechanism may vary depending on the type of action and the participant's intention. For example, when performing a single goal-directed movement, the comparator mechanism may dominate the sense of agency. Indeed, this is the situation classically considered in many motor control paradigms (Bays & Wolpert, 2007; Shergill, Bays, Frith, & Daniel M., 2003). In our control detection task, people moved continuously, without a specific goal to reach any particular target. Rather, the goal was to detect which of the dots moved in a manner closest to their own movement. In such situations of ongoing visual-motor contingency, the sense of agency might depend more on computations of regularity. In addition, in the control detection task, if people are able to identify the dot over which the regularity was the highest even when the regularity perception has not reached the threshold of sense of agency, the detection accuracy of control may be, in theory, distinct from the sense of agency. However, in the control detection task, we explicitly asked participants the question: “Which dot do you feel that you could control?” We assume that, if their score is above chance, then they must have some experience which is related to the fact of controlling that particular dot.

Interestingly, although the 90° linear disturbance should not have affected the regularity, we found that it did significantly decrease control detection accuracy, relative to 30° linear disturbance. Regularity detection clearly cannot therefore be the only mechanism contributing to sense of agency. However, a larger angular disturbance will produce a greater prediction error than a smaller angular disturbance, at least prior to learning. This indicates that both signals from a comparator and the computation of regularity were important for the sense of agency. We have not tested conditions that combined both the linear and nonlinear disturbances, so it remains unclear whether and how the two mechanisms contributing to agency might interact. Future work is required to test this issue.

The mechanism of regularity detection may be particularly important when exploring a novel environment. Exploratory behaviours in novel environments may generate large prediction errors because no model of the action-outcome relation yet exists, so any predictions are imprecise and inaccurate. However, regularity detection allows people to detect the relation between their actions and the events and to update their belief about what objects in the environment are under their own control. The sense of agency arising from regularity detection can thereafter trigger the sensorimotor recalibration and updating of an internal model. Developmental research on the reinforcement of infant exploratory behaviour showed that such regularity detection mechanisms are present in early infancy (Rovee & Rovee, 1969; Siqueland & DeLucia, 1969), and probably ground the later development of goal-directed motor control. Further, neurorobotics approaches emphasise the importance of exploratory movements (Barto, Mirolli, & Baldassarre, 2013; Oudeyer & Kaplan, 2007; Parr & Friston, 2017; Schmidhuber, 2010). Once the ambiguity regarding whether an object is under one's own control or not is resolved, exploratory behaviour can give way to pragmatic reward-seeking behaviour in which the ability to control an object is exploited, by using model-based control to produce exactly those movements most likely to trigger a reward, or achieve a goal (Friston et al., 2016). Our findings of greater excursions of motor kinematics, during conditions in which the sensory consequences of action were unpredictable (i.e. uncontrollable), are exactly consistent with this account; namely, the need to discover through exploration which aspects in the external world are under one's own control, and which are not.

In conclusion, the present study highlighted the contribution of perception of regularity to the sense of agency, over and above the well-established comparator model. Previous studies generally considered sense of agency with respect to discrete actions, often conceptualised as individual motor commands. Our study shows that sense of agency with respect to *continuous* motor episodes additionally depends on sampling and memory mechanisms, and on computation of motor-visual regularity across a prolonged history of actions. Further work is required to explore other possible dissociations between the prediction-error and regularity-detection aspects of sense of agency. For example, a combination of volitional control and prediction error may be necessary for notions of responsibility, while regularity-detection might be insufficient (Haggard, 2019). We speculate that disordered sense of agency, notably in psychosis, could result from either impairment of motor prediction-error mechanisms, or from impairment of regularity detection. Identifying which mechanism is impaired, either in clinical subtypes, or in individual patients, could inspire future computationally-motivated rehabilitation approaches.

Acknowledgement

This work was supported by the European Research Council Advanced Grant HUMVOL (Grant 323943). W. W. was additionally supported by a fellowship from JSPS (RPD) and JSPS KAKENHI Grant Number 17J40078. We also thank two anonymous reviewers for their insightful and helpful comments

References

Barto, A., Mirolli, M., & Baldassarre, G. (2013). Novelty or Surprise ? *Frontiers in Psychology*, *4*, article 907. https://doi.org/10.3389/fpsyg.2013.00907

Bays, P. M., & Wolpert, D. M. (2007). Computational principles of sensorimotor control that minimize uncertainty and variability. *The Journal of Physiology*, *578*(2), 387–396. https://doi.org/10.1113/jphysiol.2006.120121

Blakemore, S.-J., Wolpert, D. M., & Frith, C. D. (1998). Central cancellation of self-produced tickle sensation. *Nature Neuroscience*, *1*(7), 635–640. https://doi.org/doi:10.1038/2870

Blakemore, S.-J., Wolpert, D. M., & Frith, C. D. (2002). Abnormalities in the awareness of action. *Trends in Cognitive Sciences*, *6*(6), 237–242. https://doi.org/10.1016/S1364-6613(02)01907-1

De Vignemont, F., & Fourneret, P. (2004). The sense of agency: A philosophical and empirical review of the “who” system. *Consciousness and Cognition*, *13*(1), 1–19. https://doi.org/10.1016/S1053-8100(03)00022-9

Friston, K., FitzGerald, T., Rigoli, F., Schwartenbeck, P., O’Doherty, J., & Pezzulo, G. (2016). Active inference and learning. *Neuroscience and Biobehavioral Reviews*, *68*, 862–879. https://doi.org/10.1016/j.neubiorev.2016.06.022

Frith, C. D., Blakemore, S.-J., & Wolpert, D. M. (2000). Abnormalities in the awareness and control of action. *Philosophical Transactions of the Royal Society of London Series B – Biological Sciences*, *355*, 1771–1788. https://doi.org/10.1016/S1364-6613(02)01907-1

Gallagher, S. (2000). Philosophical conceptions of the self: Implications for cognitive science. *Trends in Cognitive Sciences*, *4*(1), 14–21. https://doi.org/10.1016/S1364-6613(99)01417-5

Haggard, P. (2017). Sense of agency in the human brain. *Nature Reviews Neuroscience*, *18*(4), 197–208. https://doi.org/10.1038/nrn.2017.14

Haggard, P. (2019). The neurocognitive bases of human volition. *Annual Review of Psychology*, *70*(1), annurev-psych-010418-103348. https://doi.org/10.1146/annurev-psych-010418-103348

Haggard, P., & Chambon, V. (2012). Sense of agency. *Current Biology*, *22*(10), R390–R392. https://doi.org/10.1016/j.cub.2012.02.040

Haggard, P., Clark, S., & Kalogeras, J. (2002). Voluntary action and conscious awareness. *Nature Neuroscience*, *5*(4), 382–385. https://doi.org/10.1038/nn827

Karsh, N., Eitam, B., Mark, I., & Higgins, E. T. (2016). Bootstrapping agency: How control-relevant information affects motivation. *Journal of Experimental Psychology: General*, *145*(10), 1333–1350. https://doi.org/10.1037/xge0000212

Kawato, M. (1999). Internal models for motor control and trajectory planning. *Current Opinion in Neurobiology*, *9*(6), 718–727. https://doi.org/10.1016/S0959-4388(99)00028-8

Kitazawa, S., Kimura, T., & Uka, T. (1997). Prism adaptation of reaching movements: specificity for the velocity of reaching. *Journal of Neuroscience*, *17*(4), 1481–1492. https://doi.org/citeulike-article-id:437225

Metcalfe, J., Eich, T. S., & Miele, D. B. (2013). Metacognition of agency: Proximal action and distal outcome. *Experimental Brain Research*, *229*(3), 485–496. https://doi.org/10.1007/s00221-012-3371-6

Metcalfe, J., & Greene, M. J. (2007). Metacognition of agency. *Journal of Experimental Psychology. General*, *136*(2), 184–199. https://doi.org/10.1037/0096-3445.136.2.184

Nafcha, O., Higgins, E. T., & Eitam, B. (2016). Control feedback as the motivational force behind habitual behavior. In *Motivation: Theory, neurobiology and applications*.

Oudeyer, P., & Kaplan, F. (2007). What is intrinsic motivation ? A typology of computational approaches. *Frontiers in Neurorobotics*, *1*, article 6. https://doi.org/10.3389/neuro.12.006.2007

Parr, T., & Friston, K. J. (2017). Uncertainty , epistemics and active inference. *Journal of the Royal Society Interface*, *14*(36), 20170376. https://doi.org/10.1016/j.neuron.2005.04.026

Prinz, W. (1997). Perception and Action Planning. *European Journal of Cognitive Psychology*, *9*(2), 129–154.

Rovee, C. K., & Rovee, D. T. (1969). Conjugate reinforcement of infant exploratory behavior. *Journal of Experimental Child Psychology*, *8*(1), 33–39.

Schmidhuber, J. (2010). Formal theory of creativity, fun, and intrinsic motivation (1990–2010). *IEEE Transactions on Autonomous Mental Development*, *2*(3), 230–247. https://doi.org/10.1109/TAMD.2010.2056368

Shadmehr Reza, & Brashers-Krug, T. (1997). Functional stages in the formation of human long-term motor memory. *Journal of Neuroscience*, *17*(1), 409–419. https://doi.org/citeulike-article-id:407791

Shergill, S. S., Bays, P. M., Frith, C. D., & Daniel M. (2003). Two eyes for an eye: The neuroscience of force escalation. *Science, 301*(5630), 187–187. https://doi.org/10.1126/science.1085327

Siqueland, E. R., & DeLucia, C. a. (1969). Visual reinforcement of nonnutritive sucking in human infants. *Science*, *165*(3898), 1144–1146. https://doi.org/10.1126/science.165.3898.1144

Spengler, S., von Cramon, D. Y., & Brass, M. (2009). Was it me or was it you? How the sense of agency originates from ideomotor learning revealed by fMRI. *NeuroImage*, *46*(1), 290–298. https://doi.org/10.1016/j.neuroimage.2009.01.047

Wen, W., Brann, E., Di Costa, S., & Haggard, P. (2018). Enhanced perceptual processing of self-generated motion: Evidence from steady-state visual evoked potentials. *NeuroImage*, *175*, 438–448. https://doi.org/10.1016/j.neuroimage.2018.04.019

Wen, W., & Haggard, P. (2018). Control changes the way we look at the world. *Journal of Cognitive Neuroscience*, *30*(4), 603–619. https://doi.org/10.1162/jocn_a_01226

Wen, W., Yamashita, A., & Asama, H. (2015a). The influence of goals on sense of control. *Consciousness and Cognition*, *37*, 83–90. https://doi.org/doi:10.1016/j.concog.2015.08.012

Wen, W., Yamashita, A., & Asama, H. (2015b). The sense of agency during continuous action: Performance is more important than action-feedback association. *PLoS ONE*, *10*(4), e0125226. https://doi.org/10.1371/journal.pone.0125226

Wolpert, D. M., & Flanagan, J. R. (2001). Motor prediction. *Current Biology*, *11*(18), R729–R732. https://doi.org/10.1016/S0960-9822(01)00432-8

Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural Networks*, *11*(7–8), 1317–1329. https://doi.org/10.1016/S0893-6080(98)00066-5

Supplementary Material

S1. A demonstration video of the control detection task showing the motion of the stimuli. Notice that this video was not recorded from the actual experiment.

S2. Correlation analysis between motor performance and control detection performance. Motor performance was not correlated with control detection performance. The performance of the motor control task was not significantly correlated with the performance in the control detection task in both the condition of 90° angular bias and 60% other's motion (For the condition of 90° angular bias, $R^2 = .006$, $F(1, 23) = 0.13$, $p = .723$; For the condition of 60% other's motion, $R^2 = .047$, $F(1, 23) = 1.08$, $p = .311$). In other words, an individual participant's ability to detect control over an object was not related to how well they actually controlled the object. This result suggests that the processes for motor control and for exploring which object one could control are largely non-overlapping. This is especially true in the condition of 90° angular bias in which the sense of agency could strongly rely on regularity detection instead of computation of prediction errors.

S3. Dataset. The dataset file is organised in Excel format and includes five worksheet. The first worksheet lists participants' age and gender. The second worksheet contains the trial-by-trial response data in the two experimental tasks from all the participants. The third worksheet summarises the detection accuracy in the control detection task. The fourth worksheet summarises the results of successful touches on target in the reaching task. The fifth worksheet contains the average moving distance in each condition for each participant.