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Michael Pereira, Rafal Skiba, Yann Cojan, Patrik Vuilleumier, Indrit Bègue. Preserved metacognition for undetected visuomotor deviations. Journal of Neuroscience, 2023, 43 (35), pp.6176-6184. 10.1523/JNEUROSCI.0133-23.2023. hal-04199348

HAL Id: hal-04199348 https://cnrs.hal.science/hal-04199348

Submitted on 7 Sep 2023

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Preserved metacognition for undetected visuomotor deviations

Abreviated title: Preserved metacognition for undetected deviations

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- 18 Email: indrit.begue@unige.ch
- 20 Number of pages: 52

Number of Figures: 3

22 Number of Tables: 2

Number of words for abstract: 150

Number of words for introduction: 567

Number of words for discussion: 1652

The authors declare no conflict of interest

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26

Acknowledgements: This study was conducted on the imaging platform at the Brain and Behavior

- 30 Lab (BBL), at the University of Geneva, Switzerland and benefited from support of the BBL technical staff. Special thanks to Christophe Mermoud for programming of the experimental
- 32 protocol. We thank Nathan Faivre for constructive comments on the manuscript.

34 Abstract

Humans can successfully correct deviations of movements without conscious detection of such deviations, suggesting limited awareness of movement details. We ask whether such limited awareness impairs confidence (metacognition). We recorded functional magnetic resonance imaging data while 31 human female and male participants detected cursor deviations during a visuomotor reaching task and rated their confidence retrospectively. We show that participants monitor a summary statistic of the unfolding visual feedback (the peak cursor error) to detect visuomotor deviations and adjust their confidence ratings, even when they report being unaware of a deviation. Crucially, confidence ratings were as metacognitively efficient for aware and unaware deviations. At the neural level, activity in the ventral striatum tracks high confidence, whereas a broad network encodes cursor error but not confidence. These findings challenge the notion of limited conscious action monitoring and uncover how humans monitor their movements as they unfold, even when unaware of ongoing deviations.

48 Statement of relevance

We are unaware of the small corrections we apply to our movements as long as our goals are achieved. Here, although we replicate the finding that participants deny perceiving small deviations that they correct, we show that their confidence reliably reflects the presence or absence of a deviation. This observation shows that they can metacognitively monitor the presence of a deviation, even when they deny perceiving it. We also describe the hemodynamic correlates of confidence ratings. Our study questions the extent to which humans are unaware of the details of their movements and describes a plausible mechanism for metacognition in a visuomotor task, along with its neural correlates and has important implications for the construction of the sense of self.

58 Introduction

Whether reaching for popcorn while viewing a movie or biking while enjoying the scenery, humans rely on reciprocal intricate connections between vision and motor processing to perform efficient behavior. Such visuomotor loops seem to occur mostly in the absence of awareness. Indeed, seminal work from (Fourneret & Jeannerod, 1998) showed that participants are unaware of their true hand position under imposed visuomotor deviations, although they appropriately correct their movement trajectories. Humans also neglect small spatial incongruences in feedback about their own movements (Farrer et al., 2008) and can reach targets that they cannot consciously report (Binsted et al., 2007) or that are displaced without being noticed (Goodale et al., 1986). These findings support the notion that participants show limited *awareness* of the details of an ongoing movement, as long as their goal is achieved (Blakemore et al., 2002; Custers & Aarts, 2010; Gaveau et al., 2014; Tsay et al., 2020).

Rather than awareness of movement details, other studies tested whether humans can monitor the accuracy of decisions based on movement details (Sinanaj et al., 2015; Arbuzova et al., 2020; Charles et al., 2020; Locke et al., 2020). This ability to monitor (and control) one's internal processes is referred to as *metacognition* (Flavell, 1979; Koriat, 2006). A standard measure of metacognition in humans is to ask them to make a decision (about a stimulus or an action) and subsequently rate their confidence in this decision (Rahnev et al., 2020). Together, these two lines of research suggest that, although humans have limited *awareness* of their movement details, they can *metacognitively monitor* decisions about these movements' details. As the discrimination tasks used previously (Arbuzova et al., 2020; Charles et al., 2020; Locke et al., 2020) were not specifically designed to contrast trials with and without awareness, it remains unknown whether awareness is necessary for metacognitive monitoring during motor control.

Indeed, during perceptual decision-making, participants are better at using perceptual information to scale their confidence about the presence of a stimulus than about the absence of a stimulus, showing that metacognitive *efficiency* is impaired when perceptual information is insufficient to reach awareness (Kanai et al., 2010; Meuwese et al., 2014; Mazor et al., 2020). It remains unresolved whether awareness has a similar effect on metacognitive efficiency in visuomotor decisions. In a previous study on metacognition of movement with a visuomotor *detection task*, participants reported being aware of only some of the experimental deviations in the visual

feedback of their movements. Individual differences in metacognitive efficiency were associated with variability in brain gray matter volume in prefrontal cortex, insular, and visual areas (Sinanaj et al., 2015). However, the degree to which metacognitive efficiency is related to awareness of visuomotor deviation and to specific movement parameters, as well as their functional neural underpinning, were not examined in our first study.

Here, we sought to explain how confidence is computed in the presence or absence of reported awareness – measured using introspective subjective reports (Mudrik & Deouell, 2022) – of a visuomotor deviation and unveil brain regions mediating this process using functional magnetic resonance imaging (fMRI) data. We could thus determine how visual information about participants' movements was integrated into their confidence ratings, while dissociating trials for which they reported being aware of the deviation from those for which they reported not being aware of it. Finally, we identified brain regions whose activity correlated with confidence, detection response, and monitoring of performance during a visuomotor task.

104 Method

Participants

We recruited 32 healthy right-handed participants based on convenience sampling. One participant did not complete the experimental task, therefore, the final sample included 31 participants of either sex (age: 26 years ± 4.7). Participants gave written informed consent prior to the experiment and received 20 Swiss francs per hour as compensation. They had normal or corrected-to-normal vision and reported no neurological or psychiatric disorder. The study was approved by the Ethics Committee of the University of Geneva and University Hospitals of Geneva (CER:11-214/NAC 11-077). All participants read and signed an informed consent form, and were screened for contraindications to MRI with a standard safety questionnaire.

Experimental procedure

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We asked participants to perform a visuomotor reaching task (Fourneret & Jeannerod, 1998; Farrer et al., 2008). After a short preparation period (white triangle became red, duration 1-2 seconds, jittered) participants had to reach a centrally-located target on the screen with a cursor moving at constant speed in a direction controlled by the joystick (Figure 1A). The experimental manipulation (79% of the trials) consisted in introducing deviations in the mapping between the joystick and the cursor direction: the cursor direction was deviated by a certain deviation angle, positive for right (clockwise) deviations and negative for left (anticlockwise) deviations. These deviations were gradually applied (0.3 s ramp), starting after participants reached a fixed distance from the starting point corresponding to 13% of the vertical distance between the initial cursor error and the final target. Participants were informed that these externally originating deviations would not occur all the time, however, when they occurred, participants had to correct for these deviations using the joystick in order to reach the target. After reaching the target, participants reported whether they noticed any externally originating deviations of their trajectory ("yes" detection responses) or whether they did not ("no" responses), and subsequently rated their confidence in their own judgment on a scale ranging from 1 = not certain to 5 = completely certain (Figure 1A). Participants did not receive feedback about the accuracy of either detection, or confidence judgments. We encouraged participants to use the whole confidence scale. Participants selected "yes" or "no" responses as well as confidence ratings through joystick handle movements on the right and left, respectively, then pressing a button on the joystick.

We asked participants to perform a training run outside the scanner, consisting of 30 non-deviated trajectories to familiarize them with the joystick and experimental environment. For each experimental session, we ran an adaptive staircase procedure that made the task more difficult after two consecutive correct responses by decreasing the next deviation by 2.64°, but made it easier after an incorrect response by increasing the next deviation by 1°. After the training session, participants entered the scanner and performed a 'threshold' session of 80 trials in order to stabilize the staircase procedure. After the threshold

session, participants completed two experimental runs. A structural T1 image was acquired between these two runs. Overall, there were 208 trials (21% without experimental deviations). Each trial lasted 11.5 s and was followed by a blank screen with a jittered duration (3 to 6 s).

Behavioral analyses

We defined a trial with an experimental deviation that was reported as such by participants as a hit and as a 142 miss in case it was not reported. A trial was a correct rejection when there was no deviation and participants 144 correctly reported no deviation and a false alarm if participants reported a deviation. We grouped hits and false alarms into "yes" responses and misses and correct rejections into "no" responses. We computed the 146 sensitivity d' and criterion c using signal detection theory. Cursor and joystick positions were defined every 10 ms. Cursor error was defined as the horizontal distance between the cursor position and the midline 148 between the starting point (triangle at a lower central position on the screen) and the target (top central position). For each trial, we defined peak cursor error as the peak value of this cursor error over time. Onset 150 error (onset err.) was defined as the cursor error at the onset of the deviation. We also defined the average position (avg. pos.) as the absolute value of the average position of the cursor with respect to the sagittal line 152 (the latter can be negative) as well as the average cursor error (avg. err.) as the average of the distance between the cursor and midline (always positive). A trial with a large deviation to the right followed by a large 154 deviation to the left would thus have an average position close to zero but a high average cursor error.

To build two-dimensional histograms of the cursor trajectories (Figure 1B), we mirrored trajectories when the deviation was towards the right (only for hits and misses). We then computed two-dimensional histograms of the position of the cursor in all trials of a signal detection theory category (hit, miss, correct rejection and false alarms) and normalized the resulting histograms by the number of trials in that category. Finally, we averaged across participants. Since the cursor at time k (c_k in the complex plane) can be defined knowing cursor position at time k-1 and the angle of the joystick handle at time k (α_k)

162 $c_k = c_{k-1} + \rho \exp(j(\alpha_k + \delta))$

with $c_0 = 0 + j^*0$, ρ a small real constant defining the speed and δ the angle of the experimental deviation, we could reconstruct the trajectories of the cursor, had there not been any deviation and construct histograms as described above for Figure 1B:

166 $\widehat{c}_k = \widehat{c}_{k-1} + \rho \exp(j(\alpha_k))$

For statistics, we defined Binomial link mixed-effects models to analyze detection responses and cumulative link mixed-effects models for confidence ratings using the ordinal package (Christensen, 2019) in R. Inclusion of random effects was guided by regression model selection based on Bayesian information criterion and led to the inclusion of all factors and interactions as random effects. Since most models are

multivariate, we ensured that variance inflation factors that measure how much the variance of one coefficient is increased because of collinearity were under 3, indicated weak collinearity that does not warrant any correction (Belsey et al., 1980). All statistical tests were two-tailed. For Figure 1E and 1F, we performed similar analyses but including a factor either for cursor or for joystick position. As these factors are defined every 10 ms time point, we fitted one mixed-effect model per time point and corrected p-values for multiple comparisons using the false-discovery rate. To assess the amount of information in the visual feedback (e.g. the visual trajectory displayed as subjects performed the visuomotor reaching task), we performed receiving operator characteristics analyses computing the true- and false-positive rate for a range of criterion values, from 0 to its maximum by steps of 0.01. We then searched for the criterion leading to the same false-positive (false-alarm) rate as found in the data and compared the corresponding true-positive rate (hit rate) to the one observed in the data.

For Figure 2D, we binned the peak cursor error into five quantiles computed independently for each participant but for all signal detection theory categories together. For Figure 2E, we plotted model predictions of the cumulative link model's fixed effects for each signal detection theory category and increasing values of peak cursor error. To estimate metacognitive efficiency, or to what extent the information available to the detection decision was used to scale their confidence, we used the M-ratio between meta-d' (Maniscalco & Lau, 2014) and d' estimated in a response-specific version of the HMeta-d' toolbox (Fleming, 2017). These meta-d' and d' allow to compute the M-Ratio: a ratio between meta-d' and d', which quantifies metacognitive efficiency, or how well information from first-order performance informs the metacognitive process. We used the default parameters of three chains of 10'000 samples with 1000 burn in samples for the MCMC procedures with no thinning. Visual inspection of MCMC and Rhat values well under 1.1 indicated good convergence. Of note, as the d' does not vary according to the response, differences in the M-Ratio are solely driven by differences in the meta-d'.

fMRI data collection, preprocessing and analyses

We acquired functional MRI images with a 3T whole-body scanner (Trio TIM, Siemens, Germany) with a 12-channel head-coil. Functional images were acquired with a susceptibility weighted EPI sequence with the following parameters: TR/TE = 2100/30 ms, flip angle = 80 degrees, PAT factor = 2, 64 × 64 voxel, 3.2 × 3.2 mm, 36 slices, 3.2 mm slice thickness, 20% slice gap. We acquired structural images using a T1-weighted 3D sequence using the following parameters: MPRAGE, TR/TI/TE = 1900/900/2.32 ms, flip angle = 9°, voxel dimensions: 0.9 mm isotropic, 256 × 256 × 192 voxels. We presented task stimuli on a back-projection screen inside the scanner bore using an LCD projector (CP-SX1350, Hitachi, Japan). We recorded responses via buttons placed on the joystick used for the visuomotor reaching task (HH-JOY-4, Current Designs Inc., USA

We used the SPM8 software (http://www.fil.ion.ucl.ac.uk/spm/) for statistical analyses of functional data with 208 a standard pipeline. We first corrected for head movements between scans by an affine registration and realignment to the mean of all images. The anatomical image was spatially normalized on the T1 template. 210 The functional images were also normalized to the EPI template, which were thereby transformed into standard stereotaxic space and resampled with a 3×3×3mm voxel size. The normalized images were 212 spatially smoothed using an 8 mm full-width at half-maximum (FWHM) Gaussian kernel. We used the general linear model (GLM) framework implemented in SPM to analyze our data. We modeled the convolved 214 standard hemodynamic response function with a delta (or "stick") function at the onset of the preparatory phase (appearance of white triangle - PREP regressor), at the onset of the joystick movement (start of 216 movement - MOV regressor), and at the onset of the response screen ("yes" vs. "no", RESP regressor). To examine brain regions whose activity fluctuated with trial-by-trial confidence, we took a parametric 218 modulation approach (e.g. Fleming et al., 2018; Pereira et al., 2020): the "MOV" regressor event regressors were modulated by four additional parametric factors (Wood et al., 2008) representing in order, the trial-by-220 trial values of the angle of the deviation, of the detection response "yes" vs. "no", of the peak cursor error, and of the confidence rating, leading to the following regression equation:

BOLD ~ deviation_angle + detection_response + peak_cursor_error + confidence

However, we also replicated our results using four single regressor models (BOLD ~ deviation_angle, BOLD

~ detection_response, BOLD ~ peak_cursor_error, BOLD ~ confidence). To account for head motion-related variance, we included the six differential parameters derived from the realignment process [x, y, and z translations (in millimeters) plus pitch, roll, and yaw rotations] as regressors of no interest. Low-frequency signal drifts were filtered using a cut-off period of 128s. Global scaling was applied, with each fMRI value rescaled to a percentage value of the average whole-brain signal for that scan.

Contrast images from one-sample t-tests corresponding to each event (PREP, MOV, RESP) and their parametric modulators, were fed into a second-level random-effect analysis. All second-level results are reported at a significance-level of p<0.05 using cluster-extent family-wise error (FWE) correction with a voxel-height threshold of p < 0.001. In Figure 3, activations are displayed at a cluster-size threshold of 30 voxels, using MRIcroGL (http://www.cabiatl.com/mricrogl/). Data and analysis scripts from this study will be made freely available upon acceptance.

238 Results

Participants correct for deviations regardless of detection

For both detected (hits) and undetected (misses) deviations, all trajectories correctly ended on the 240 target (Figure 1B) showing that participants always adjusted to the experimentally induced 242 deviations. Reconstructions of what trajectories would be without deviation for hits and misses confirmed that participants would have clearly missed the target, even for miss trials (Figure 1C), 244 showing that they corrected for deviations even when not reporting them. We also assessed the relation between the lateral angle of the joystick (i.e. corrective motor command) and the cursor 246 position (i.e. visual feedback). For this, we cross-correlated cursor position and joystick angle vectors across every trial, averaged over trials and participants, and observed that the strongest 248 correlation occurred with a lag of -0.45 s ± 0.01 s (mean ± 95% confidence interval; Figure 1D). Furthermore, this correlation was significant for detected (t(30) = -41.30, p < 0.001) and undetected 250 (t(30) = -36.06, p < 0.001) deviations, showing that participants corrected deviations regardless of whether they reported them or not.

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Detection responses rely on cursor error

A one-up/two-down staircase procedure was used throughout the experiment, resulting in an average deviation angle of 20.59° ± 2.03 overall. The detection performance was 67.71 % ± 1.74 correctly reported deviations (d' = 1.69 ± 0.14), indicating that participants' performance was well above chance level. Participants were conservative in their response (c = 0.37 ± 0.08, t(30) = 4.63; p < 0.001). For deviated trials, neither small variations in the imposed deviation angle due to the staircase procedure (t(5160) = 0.91, p = 0.36), nor the index of the trial (t(5160) = -0.11; p = 0.91) had an effect on detection responses. We therefore considered perceptual difficulty to be constant over time, which is standard in perceptual metacognition (e.g. Fleming et al., 2010).

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When analyzing cursor position over time, we computed the horizontal distance between the cursor and the midline as an (unsigned) measure of *cursor error* (Figure 1E). We then regressed detection responses using cursor error and trial type (deviated vs. non-deviated) as fixed effects (generalized mixed effect models for every time point). We found a significant interaction effect during the first 0.85 s of the movement (p < 0.05; corrected), indicating that during this time, the relation between detection responses and cursor error depended on whether the trial was actually deviated or not. Furthermore, there was a main effect of cursor error without an interaction in a

later time window up to 1.63 s after movement onset (p < 0.05) and a main effect of trial type during the whole movement (p < 0.001), suggesting that during this part of the movement, cursor error had similar influence on detection responses regardless of whether the trial was deviated or not, with an additive bias due to trial type. We verified that cursor error also had an effect on detection responses in deviated trials (p < 0.05 between 0.49 and 1.94 s) and for undeviated trials (p < 0.05 between 0 and 1.61 s), confirming that the effect of cursor error on detection responses was genuine.



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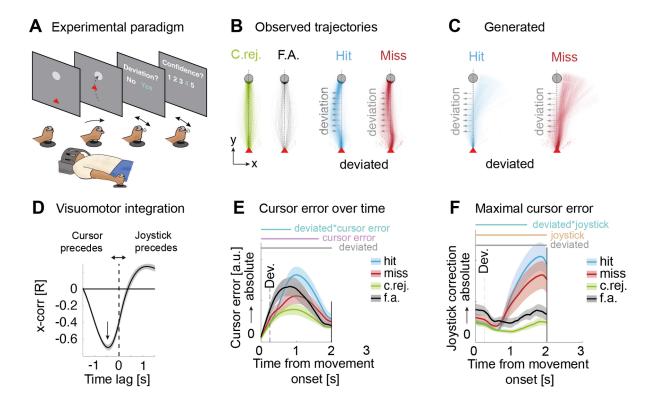


Figure 1. Experimental paradigm and detection responses. A) Participants started every trial by using the joystick to bring a visible cursor (red triangle) to a target (circle) on top of the screen. A deviation was applied to the cursor in 79% of the trials, titrated so as to reach 71% of detection accuracy. Titrated detection rates can be found in Figure 1-1. After reaching the target, participants reported whether the cursor was deviated or not (detection) and how confident they were about their answer. B) Trajectories of the cursor for correct rejections (green), false alarms (black), hits (blue) and misses (red). Note that deviations could be towards the left or the right, but right deviation trials are mirrored and pooled with left trials for display purposes. C) Generated trajectories obtained by recomputing the cursor position had there been no deviation for hits (blue) and misses (red). D) Cross-correlation between cursor error and iovstick lateral position. The vertical arrow indicates the time lag at which cross-correlation is strongest. E) Cursor error over time for different signal detection theory categories: hits (blue), misses (red), correct rejections (green) and false alarms (black). The significant (p < 0.05; FDR corrected) main effects of cursor error (respectively, of deviation) over time is depicted by the purple (respectively, grey) line; and the significant interaction effects between deviated trials and cursor error is depicted by the cyan line. Model comparison, peak cursor error distributions and discriminability analyses can be found in Figures 1-2, 1-3, 1-4 and 1-5. F) Idem, for joystick correction over time. In all panels, shaded areas indicate 95% confidence intervals.

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Our results are consistent with a threshold operation on the visual feedback, with higher cursor error leading to deviation detection (hit and false-alarms; Figure 1E). Therefore, detection responses should be best explained by the peak cursor error over the time course of the movement (i.e. deviations are detected if the cursor error reaches a threshold value at some point during the trial). Indeed, this model had a better Bayesian Information Criterion (BIC) than models with cursor error sampled at single time points (Figure 1-1A), as well as other measures of visual feedback (Figure 1-1B). Similarly, models based on putative motor or proprioceptive feedback vielded worse BIC (Figure 1-1C). The two main effects in this model were significant (peak cursor error: t(6403) = 5.31; p < 0.001; trial type: t(6403) = 7.47; p < 0.001) and there was no significant interaction (t(6403) = -1.32; p = 0.19), confirming that the occurrence of deviations did not change how visual information (quantified by peak cursor error) is integrated into detection responses, but nevertheless influenced conscious detection (deviation was more frequently reported on deviated than non-deviated trials overall). Nonetheless, the information carried by the peak cursor error would not have been sufficient for participants to have such performance (Figures 1-2 and 1-3), showing that they must have relied on additional signals, whether those were based on visual, motor or proprioceptive information.

Confidence scales with peak cursor error

We then examined confidence ratings across signal detection theory categories (Figure 2A). To understand how visual information is integrated into confidence ratings, we regressed confidence using various summary statistics of cursor error over time (Figure 2B). Our baseline model investigated the relation between detection responses and confidence, and thus included only a predictor for trial type (deviated vs. non-deviated), as well as for detection response (to model the fact that confidence is conditioned to the response; interaction effect: z = 8.98, p < 0.001). We then determined the best model in terms of BIC, which was obtained by adding a predictor for peak cursor error over time (peak err.). This model showed a lower BIC compared to the baseline model with a single predictor for detection response (Figure 2C; Δ BIC = -313.80; p < 0.001). Alternative models, such as including the cursor error at the onset of the deviation (onset err.), the average (signed) cursor position (avg. pos.), or the average of the cursor error (avg. err.), yielded lower improvements in BIC.

Using the winning model, we found an interaction between peak cursor error and detection responses (Figure 2D-E; z = 4.69, p < 0.001), showing that confidence ratings were influenced by

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the peak cursor error conditioned to the detection response (i.e. when the peak cursor error is high, confidence in detected deviations is high but confidence in undetected deviations is low). There was also an interaction between trial type and peak cursor error (z = 4.20, p < 0.001) and between detection response and trial type (z = 7.087, p < 0.001) but no triple interaction between detection response, trial type, and peak cursor error (z = -1.38, p = 0.17). These results show that participants rated their confidence by conditioning the peak cursor error to their conscious detection, with a confidence bias for non-deviated trials that depended on their response (e.g. more confident for correct rejections versus misses; less confident for false alarms vs. hits).

To better understand the relation between confidence and peak cursor error, we fitted the data independently for deviated and non-deviated trials. We confirmed the interaction of response and peak cursor error for both trial types (deviated: z = 5.77, p < 0.001; non-deviated: z = 5.76, p < 0.001). Importantly, and contrary to the hypothesis of limited monitoring, we also found that confidence was significantly related to cursor error size for all trial categories (p < 0.01 for hits, misses, correct rejections, and false alarms). Together, these results show that confidence increases with peak cursor error when participants report a deviation but decreases with peak cursor error when participants do not report a deviation, independently of whether the deviation was actually due to an experimental manipulation (e.g. during misses) or to their own intrinsic visuomotor variability (e.g. during correct rejections) (Figure 2D-E).

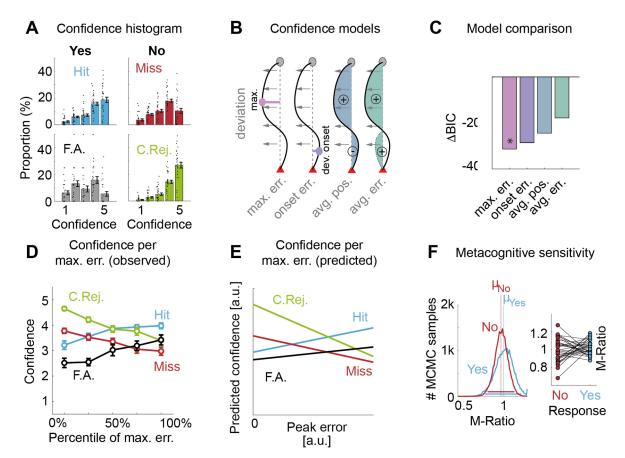


Figure 2. Confidence ratings and metacognition. A) Distribution of confidence ratings for hits (blue), misses (red) and correct rejections (green). Each black dot represents the data of one participant. B) Schematic depiction of the four regressors used for the four confidence regression models tested: peak err.: peak cursor error; onset. err: cursor error at the onset of the deviation; avg. pos.: cursor position (signed) averaged along the trajectory; avg. err.: cursor error (unsigned) averaged along the trajectory. C) Improvement in BIC (compared to a model with no cursor information). Note that the peak err. model shows the largest improvement (*). Additional model comparisons can be found in Figure 2-1. D) Confidence for different percentiles of peak cursor error (peak err.) for hits (blue), misses (red) and correct rejections (green). E) Fixed effects predictions of confidence for comparable levels of peak error (normalized) for hits (blue), misses (red), correct rejections (green) and false-alarms (black). F) Hierarchical Bayesian estimation of response-specific metacognitive efficiency using the M-Ratio. Left: posterior probability for "yes" (blue) and "no" (red) responses Vertical lines show the mean M-Ratio and horizontal bars show the 95% confidence interval. Right: Single participant values of the M-Ratio. In all panels, shaded areas and whiskers indicate 95% confidence intervals.

Preserved metacognitive efficiency for unreported deviations

Finally, to confirm that participants reliably monitored their visuomotor actions, we estimated their (metacognitive) efficiency by measuring to what extent the information available to the detection decision was used to scale their confidence. For this, we fitted a response-specific hierarchical Bayesian model based on signal detection theory (Fleming, 2017) which estimates metacognitive efficiency for "yes" and "no" responses while controlling for task performance (this model used all "yes" and "no" trials in the fitting procedure). Results from this analysis revealed a metacognitive efficiency of 0.96 for the "no" responses (correct rejections and misses), indicating that participants efficiently used all information available for the decision to adjust their confidence ratings.

Metacognitive efficiency for "Yes" responses was similar (0.99; Figure 2F). These results show that metacognitive efficiency was optimal in the sense that confidence ratings were as informative as what would be expected based on detection performance, and thus confirm that reporting deviations does not lead to better metacognitive efficiency.

Brain correlates of visuomotor performance

To investigate the neural substrate of the cognitive processes described above, we used trial-by-trial measures (confidence, response, peak cursor error, and deviation angle) as parametric regressors to model the fMRI BOLD signal during each movement. These regressors showed only limited correlation among themselves (maximal absolute mean R = 0.41; Figure 3-1). First, we found positive relationships between the BOLD signal and detection responses in the right primary visual cortex, meaning that activity increases when participants detected the deviations (Figure 3A; Table 1). We found no significant negative relationships. We also found that larger peak cursor error yielded widespread activity in visual, motor, and subthalamic regions, as well as in the left insula, cingulate, and lateral prefrontal cortex (right inferior frontal gyrus and anterior prefrontal cortex (aPFC); Figure 3B; Table 1). Smaller cursor error yielded no differential activity beyond the statistical threshold and we did not find any neural correlate of deviation angle.

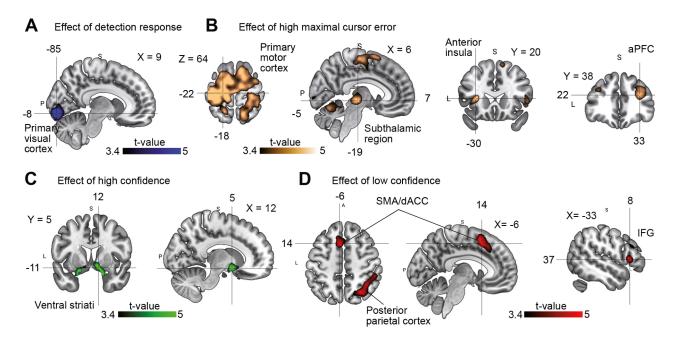


Figure 3. fMRI results. Statistical maps of parametric modulation contrast for A) explicit detection ("yes" responses), B) high peak cursor error, C) high confidence and D) low confidence. Note that colors represent different parametric regressors and are independent from Figure 1. Results are displayed at p < 0.001 uncorrected, but all clusters displayed were significant after FWE correction (p < 0.05). aPFC: anterior prefrontal cortex; SMA: supplementary motor area; dACC: dorsal anterior cingulate cortex. IFG: inferior frontal gyrus. See text Tables 1 and 2 for other brain activations. Correlation between regressors can be

found in Figure 3-1. Figure 3-2 shows beta values averaged across participants for each level of confidence are shown for each ventral striatum using MarsBar (Brett et al., 2002)..

Table 1. Summary of whole brain regions' activation for response and peak cursor error

Brain region	MNI Co	ordinate	s	Cluster	Significance			
	mm (xyz)		extent					
				(voxels)				
"Yes" responses								
Right primary visual cortex	9	-85	-8	602	T= 6.64, p _{FWEc} < 0.001			
High peak cursor error								
Left primary motor cortex	-18	-22	64	3563	T= 8.18, p _{FWEc} < 0.001			
Right inferior occipital gyrus	45	-67	1	927	T= 6.17, p _{FWEc} < 0.001			
Left anterior insula	-30	20	7	632	T= 5.33, p _{FWEc} < 0.001			
Right subthalamic region	6	-19	-5	285	T= 5.26, p _{FWEc} < 0.001			
Right lateral anterior prefrontal cortex	33	38	22	229	T= 5.13, p _{FWEc} < 0.001			
Right mid-cingulate gyrus	15	-19	37	106	T= 4.98, p _{FWEc} = 0.028			
Right inferior frontal gyrus	48	29	1	279	T= 4.47, p _{FWEc} < 0.001			
Left calcarine cortex	-12	-85	-8	147	T= 4.41, p _{FWEc} = 0.008			
Left superior occipital gyrus	-21	-79	28	108	T= 4.16, p _{FWEc} = 0.026			
No surviving voxels for the contrasts: Low peak error, No responses; $p_{FWEc} = p$ corrected for multiple								
comparisons at the cluster level								

400 Brain correlates of confidence

We then turned to confidence and found positive relationships with the BOLD signal, meaning that higher confidence was related to increased bilateral ventral striatum activity, extending to the left amygdala (Figure 3C; Table 2). Conversely, we found negative relationships, meaning that lower confidence was associated with increased activity in the left supplementary motor area (SMA), extending to the dorsal anterior cingulate cortex (dACC), together with the left inferior and middle frontal gyri, as well as the right posterior parietal cortex (Figure 3D; Table 2).

Table 2. Summary of whole brain regions' activation for confidence

MNI Coordinates mm (xyz)				Significance
			(voxels)	
12	5	-11	103	T=5.85, p _{FWEc} = 0.04
-21	-1	-17	96	T= 5.80, p _{FWEc} =0.04
-15	8	-14		T=4.69
-6	14	49	221	T=5.33, p _{FWEc} = 0.00
-51	20	4	119	T=4.97, p _{FWEc} = 0.02
-33	8	37	134	T=4.51, p _{FWEc} = 0.01
36	-49	40	403	T=5.43, p _{FWEc} < 0.00
	-15 -6 -51	mm (xyz) 12 5 -21 -1 -15 8 -6 14 -51 20	mm (xyz) 12 5 -11 -21 -1 -17 -15 8 -14 -6 14 49 -51 20 4	mm (xyz) extent (voxels) 12

412 Discussion

We studied the behavioral and neural correlates of detection and confidence in a visuomotor reaching task with perturbations. We found that while participants often reported not being aware of deviations applied experimentally to the trajectory of their movement, their metacognitive efficiency was not impaired by this reported lack of awareness. Thus, they adjusted confidence judgments to the accuracy of their detection responses even when reporting no deviations. Furthermore, regression model selection revealed that regardless of whether participants were aware of the deviation or not, their judgment relied on a summary of visual feedback (i.e. peak cursor error), whose magnitude correlated with activity in a specific visuomotor brain network. Finally, we uncovered neural activity patterns associated with confidence, with high confidence engaging subcortical areas in the ventral striatum, and low confidence engaging a cortical network in medial and lateral frontal cortex as well as posterior parietal cortex.

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In terms of detection responses, we found that participants tended to report an experimentally 426 induced deviation when the visible cursor error was high, and conversely did not report one when the cursor error was low. We interpret these detection reports as awareness of the deviation 428 although as with any measure based on introspection, it is conceivable that participants had partial awareness while reporting being unaware (Mudrik & Deouell, 2022). These findings are consistent 430 with awareness of a deviation occurring when cursor error exceeds a threshold: when the peak cursor error is higher than this threshold, a deviation is reported. Other regression models of 432 detection responses or confidence could not fit the data as well, whether they were based on other measures of visual feedback, or on putative proprioceptive signals (indexed by joystick position). 434 Still, a part of the variance of participants' performance was not explained by the peak cursor error, suggesting that participants use other dimensions of the visual feedback not captured by the peak 436 cursor error, or other motor or proprioceptive signals. This idea is in line with previous works showing that participants at least partially rely on additional information, possibly stemming from 438 the proprioceptive inputs (Farrer et al., 2008) and/or the comparison of the perceived cursor position relative to a self-generated prediction, based on an efferent copy of their motor command 440 (Wolpert et al., 1995). The later assumption agrees well with past research on motor control and agency (Haggard, 2017). As the contribution of these different signals is still unclear in the context 442 of motor control (e.g. Kasuga et al., 2022), future studies will be required to disentangle their contribution to deviation detection and its associated confidence.

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To further assess how well participants monitored their movements, we examined their metacognitive efficiency when they reported being unaware of deviations that they nonetheless successfully corrected. Remarkably, metacognitive efficiency was similar when participants reported deviations and when they did not, suggesting that even if the visuomotor information was not enough to report a deviation, it could still be harnessed to rate confidence. Moreover, we found that confidence increased with peak cursor error when participants reported the deviation, and instead decreased with peak cursor error when participants did not report the deviation. This behavior reveals a judicious use of visuomotor signals to guide confidence, irrespective of the reported awareness of the deviation. We therefore surmise that participants were able to consciously monitor their unfolding movements by having access to at least a summary of visuomotor cues that guided their explicit detection and confidence responses, similar to what could occur for internally accumulated sensory signals (Pereira et al., 2021). The factors that constitute the evidence used to compute confidence are still unknown. Since metacognitive efficiency was as good as expected considering detection performance, it is possible that they directly derive from the decisional signal used for detection responses. Therefore, our findings question the notion that small deviations are corrected mostly in the absence of awareness (Blakemore & Frith, 2003; Custers & Aarts, 2010): people might be unaware of some deviations that they correct, but they still have a calibrated 'feel' of their performance.

Our finding of preserved metacognition for "no" responses thus sharply contrasts with visual 464 metacognition studies describing lower metacognition for putatively unaware stimuli (Kanai et al., 466 2010; Mazor et al., 2020; Pereira et al., 2021). Considering that the factors responsible for metacognitive inefficiency are still unclear (Shekhar & Rahnev, 2021), we can only speculate on 468 why metacognitive performance does not decrease for unaware deviations in our task. Confidence for unaware visual stimuli was proposed to depend on monitoring attention instead of perceptual 470 evidence (Kanai et al., 2010; Mazor et al., 2020). According to this view, confidence for aware and unaware stimuli might involve different mechanisms. In other studies, reduced metacognitive 472 efficiency for unaware stimuli was accounted for by a single mechanism (Kellij et al., 2021; Pereira et al., 2021), based on the fact that the variances for noise and stimuli differ. It is therefore possible 474 that, in our study, equal variance between the noise and the signal allowed metacognition to be preserved for "no" responses. Indeed, the absence of response-specific differences in 476 metacognitive sensitivity suggests that neither unequal variance nor response-specific

metacognition are good candidates to explain our data. It is therefore possible that unequal variance occurs only in perceptual metacognition studies with perceptual uncertainty on the stimulus (which are either weak or embedded in noise). In our study, there is no perceptual uncertainty on peak cursor error, it is simply smaller for unaware deviations, therefore not leading to unequal variance nor lower metacognitive sensitivity for unaware deviations.

Our fMRI results showed extended activations associated with increasing peak cursor error, involving sensorimotor regions, as well as occipital areas, anterior prefrontal and mid-cingulate cortex, insula, inferior frontal gyrus, and subthalamic regions. These results suggest the existence of widespread action-monitoring processes (Limanowski et al., 2017), possibly responsible for the integration of visual and proprioceptive feedback signals with motor action planning. Interestingly, the aPFC – including the frontal pole and posterior regions of Brodmann area 46 (Neubert et al., 2014) – has been extensively linked to perceptual metacognition in studies using voxel-based morphometry (Fleming et al., 2010), TMS (Rahnev et al., 2016) or patients with focal lesions (Fleming et al., 2014). In our study, activity in the aPFC was modulated by the peak cursor error, and not by the confidence regressor, suggesting that the aPFC might not be involved in confidence per se but rather in monitoring the performance of actions. Further in line with our interpretation, patients with prefrontal lesions reported fewer deviations than healthy controls despite similar corrective behavior in a task similar to ours (Slachevsky et al., 2001). In sum, our finding of increased aPFC activity reflecting cursor errors and not confidence pleads in favor of a role of the aPFC for monitoring action performance rather than the accuracy of decisions.

Finally, we found that low confidence was associated with higher activity in a network of medial frontal cortex, left inferior and middle frontal gyri, and right posterior parietal cortex, providing novel support for a role of fronto-parietal regions in metacognitive processes via graded confidence computation (Hebart et al., 2016; Vaccaro & Fleming, 2018), extending here to the motor rather than purely perceptual domain. Conversely, high confidence engaged the ventral striatum, again corroborating fMRI findings in the perceptual domain (Hebart et al., 2016; Guggenmos et al., 2016; Mazor et al., 2020). Apart from its well-known involvement in reward-based learning (Daniel & Pollmann, 2014), the ventral striatum also computes pseudo-reward prediction errors – defined as reward predictions errors related to the subjectively perceived progress in a given task, rather than merely driven by external (e.g. monetary) reward (Westbrook et al., 2016). Our results therefore dovetail with a broader putative role of the ventral striatum for valuation information predicting

reward (Schultz et al., 1992; Daniel & Pollmann, 2014), whereby in the absence of feedback, the valuation information corresponds to confidence (Daniel & Pollmann, 2014). Taken together, these findings support a key role of the ventral striatum in monitoring decisional signals for confidence (Daniel & Pollmann, 2014; Hebart et al., 2016; Vaccaro & Fleming, 2018) that can be used to adapt subsequent behavior even in absence of external feedback (Guggenmos et al., 2016).

To conclude, our study sheds new light on both cognitive and neural mechanisms that underpin the monitoring of visuomotor behavior: participants base their detection and confidence reports on at least some summary statistic of visual feedback. We also map these monitoring and correcting processes to activity in an extended brain network including the aPFC, calling for a revision of its role in tracking confidence only. Importantly, although participants did report not being aware of some deviations, their confidence ratings were still calibrated to their actual performance on a trialby-trail basis and guided by the same summary statistics as detection responses. These results may offer a plausible explanation for a paradox: that humans perform corrective actions in the absence of awareness but are good at attributing actions to themselves or to an external agent (de Vignemont & Fourneret, 2004). We argue that even if participants are unaware of their corrections, they can still accurately report their confidence through an efficient summary statistic of action parameters. They only become aware that something is wrong when that summary statistic exceeds what could be expected from their own intrinsic motor variability. Elucidating these mechanisms bears important clinical implications as deficits in the awareness of action have been linked to psychiatric diseases (Blakemore & Frith, 2003) such as schizophrenia (Frith et al., 2000; Voss et al., 2010). Our methodology should catalyze future research in the visuomotor domain to uncover metacognitive deficit in schizophrenia, or more generally, psychosis spectrum (Rouy et al., 2021), and what is the underlying defective process. It will be important to examine whether these clinical populations employ the same mechanisms to compute confidence as we describe here, and if so, how deficits in such mechanisms relate to specific pathophysiologic dimensions (positive i.e. psychotic and negative i.e. amotivational symptoms) and to particular brain substrates.

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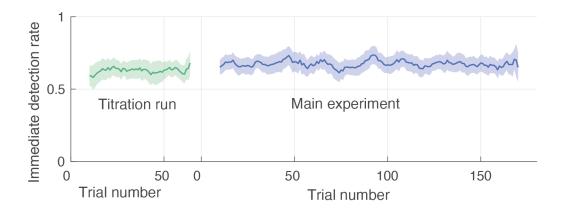
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Extended data



Staircase convergence. Immediate detection rate estimated using a 10-trial running average excluding catch trials for the 62 trials titration run (80 trials in total) in green and the main experiment in blue. All participants had a minimum of 8 reversals missing a deviation in trial n-1 and detecting it in trial n or detecting a deviation in trial n-1 and missing it in trial n) during the titration run showing good convergence. There are not differences between the number of reversals in the first (36.13 \pm 1.45) and second run (35.45 \pm 1.46) of the main experiment (z = 0.41, p = 0.68).

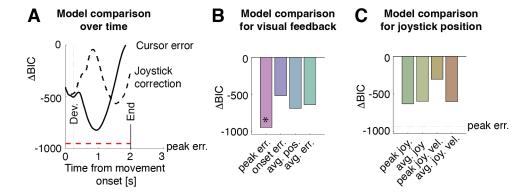
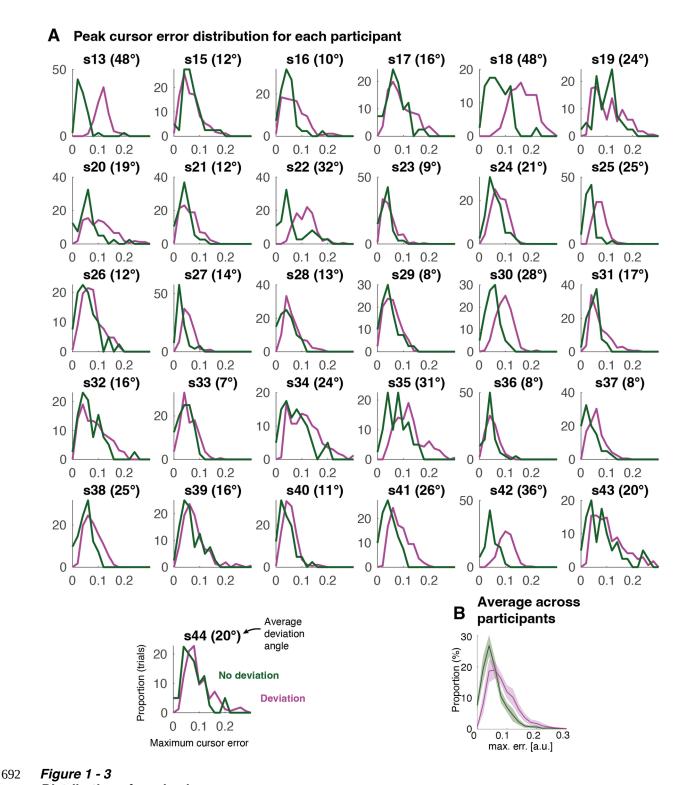


Figure 1 – 2 Regression model comparison

Bayesian information criteria (BIC) difference of different models compared to a model with only trial type (deviated or non deviated) as fixed effect. The lower the BIC, the better the model. A) BIC differences compared to the baseline model with no cursor error for models using the cursor error (solid trace) or the joystick correction (absolute value of the lateral position of the joystick; dashed line) at different times from movement onset. The horizontal purple dashed shows the BIC difference when using the peak cursor error, which is consistently lower. B) BIC differences for different measures of cursor position: peak err.: maximal cursor error; onset. err: cursor error at the onset of the deviation; avg. pos.: cursor position (signed) averaged along the trajectory; avg. err.: cursor error (unsigned) averaged along the trajectory. The asterisk shows the best model (peak cursor error; peak err.) C) BIC differences for different measures of joystick position: peak joy.: peak joystick horizontal position, avg. joy.: joystick horizontal position averaged the trajectory, peak joy. vel.: peak joystick horizontal velocity, avg. joy. vel.: joystick horizontal velocity averaged the trajectory. The horizontal purple dashed line shows the BIC difference when using the peak cursor error (peak err.), which is consistently lower.



Distribution of maximal cursor error

A) For deviated (light blue) and non-deviated (dashed black) trials for every participant. The average deviation angle (i.e. easiness of the task) obtained through the staircase procedure is displayed in the title of each panel. Only participants who failed to reach a low average deviation angle showed highly separable distributions (e.g. s13, s18, s42). B) Idem, but averaged across participants. Shaded area represents the

95% confidence interval.

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A AROC for each participant

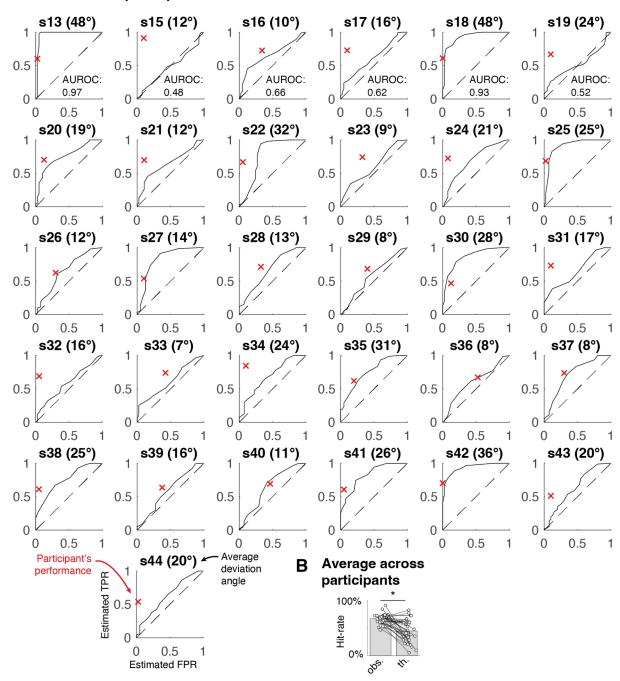


Figure 1 - 4
Receiving operating curve (ROC) analysis for detection.

A) To compare individual participants' performances against the information contained in the maximal cursor error, we estimated the ROC curve (black trace) by sliding the criterion along the horizontal axis in Figure 1 - 2 while computing true positive rate (estimated TPR) and false positive rate (estimated FPR). The dashed black trace represents the theoretical ROC curve for random performance (i.e. for non-separable distributions of maximal cursor error between deviated and non-deviated trials). We then displayed the actual performance from each participant in terms of TPR and FPR (red cross). If participants would rely only on the maximal cursor error to detect deviations, we would expect their performance to be under (or close to) the estimated ROC curve. This was the case only for a few participants (e.g. s30, s36, s40). These results indicate that most participants used additional information to detect deviations. We obtained very similar results using other indices (see Figure 2B) such as cursor error at deviation onset, averaged cursor position, and averaged cursor error, suggesting that participants did not use another more integrative strategy either, even based on other visual cues from the cursor. B) Across participants, this theoretical hit-rate, corresponding to the theoretical performance that could be achieved using peak cursor error alone, was much lower (th.; $42\% \pm 4$) than the observed hit-rate (obs.; $67\% \pm 2$; t(30) = 5.16; p < 0.001. Similar results

were obtained using other summary statistics of cursor error over time (Figure 2B), such as cursor error at the onset of the deviation (onset err.), the average (signed) cursor position (avg. pos.), or the average of the cursor error (avg. err.). These result suggest that participants could not have reached the observed detection performance relying on the peak cursor error information alone. C) Between-participant correlation between the estimated area under the ROC curve (AUROC) quantifying the information contained in the maximal cursor error and the average deviation angle achieved by the staircase procedure. This relation shows that the less good participants were at the task (high deviation angle), the more information they could use from the maximal cursor error.

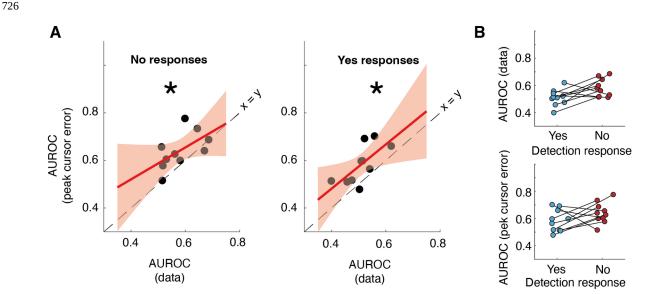


Figure 1 – 5.

Receiving operating curve (ROC) analysis for confidence. A. Simulated AUROC (vertical axis) compared to AUROCs in the data (horizontal axis) for yes (detected; left) and no (undetected; right) responses. Each point represents one of the 10 participants for which we had enough false alarms. Red lines represent the regression line with shaded 95 % confidence intervals. B. Differences of AUROC in the data (top) and simulated from the peak cursor error (bottom) between yes and no responses for each participant confirming the absence of evidence for an increase in metacognitive sensitivity for detected deviations (Yes responses).

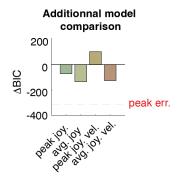


Figure 2 – 1

Additional model comparison: BIC differences for different (unsigned) measures of joystick position: peak joy.: peak joystick horizontal position, avg. joy.: joystick horizontal position averaged the trajectory, peak joy. vel.: peak joystick horizontal velocity, avg. joy. vel.: joystick horizontal velocity averaged the trajectory. The horizontal purple dashed shows the BIC difference when using the peak cursor error, which is consistently lower.

CORRELATION	Angle	Detection	Peak error	Confidence
Angle	1.00			
Detection	0.41 ± 0.02	1.00		
Peak error	0.30 ± 0.03	0.37 ± 0.04	1.00	
Confidence	-0.11 ± 0.03	0.02 ± 0.03	-0.04 ± 0.04	1.00

Figure 3 – 1
Correlation table of the four parametric regressors used in our fMRI.

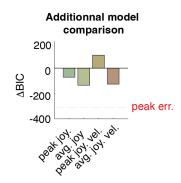


Figure 3 – 2

Beta values averaged across participants for each level of confidence. For each subject, we modeled each level of confidence as an individual condition. Thus each subject had 5 regressors, one regressor for condition. Using MarsBar (Brett et al., 2002), we then extracted BOLD estimates for each confidence level with a sphere (radius of 3 mm) around the peak voxel for the left (MNI: 12, 5, -11) and right ventral striatum (MNI: -15, 8, -14) of each participant.