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A crucial role of the frontal operculum in task-set dependent visuomotor performance monitoring

Abbreviated title: Set-dependent visuomotor performance monitoring

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Abstract

For adaptive goal-directed action, the brain needs to monitor action performance and detect errors. The corresponding information may be conveyed via different sensory modalities; for instance, visual and proprioceptive body position cues may inform about current manual action performance. Thereby, contextual factors such as the current task set may also determine the relative importance of each sensory modality for action guidance. Here, we analysed human behavioural, functional magnetic resonance imaging (fMRI), and magnetoencephalography (MEG) data from two virtual reality (VR)-based hand-target phase matching studies to identify the neuronal correlates of performance monitoring and error processing under instructed visual or proprioceptive task sets. Our main result was a general, modality-independent response of the bilateral frontal operculum (FO) to poor phase matching accuracy, as evident from increased BOLD signal and increased gamma power. Furthermore, functional connectivity of the bilateral FO to the right posterior parietal cortex (PPC) increased under a visual vs proprioceptive task set. These findings suggest that the bilateral FO generally monitors manual action performance; and, moreover, that when visual action feedback is used to guide action, the FO may signal an increased need for control to visuomotor regions in the right PPC following errors.

Key words: Action; frontal operculum; sensorimotor integration; performance monitoring; visuo-propriceptive integration

Significance statement: The brain uses feedback from the senses to guide behaviour and correct errors. During hand movements, this feedback can come from seen and felt hand positions. Here, we used brain scanning to show that brain regions in the frontal operculum responded to action errors in a hand-target matching task, when either seen or felt hand positions are task relevant. Furthermore, when the seen hand position had to be prioritized for the task, these regions increased their communication with the right posterior parietal cortex, which is known to guide hand

movements based on visual cues. These results suggest a crucial role for the frontal operculum in monitoring hand actions; in particular, when vision is task relevant.

1 Introduction

2 To effectively perform goal-directed action in the environment, the brain needs to monitor motor
 3 performance and detect errors, so that it can enable adaptive changes in behaviour (Diedrichsen,
 4 2005; Klein et al., 2007; Suminski et al., 2007; Ullsperger et al., 2014). During performance
 5 monitoring, the predicted outcome of one's actions selected based on current goals (i.e., task set) is
 6 compared with actual sensory feedback, and behavioural changes are initiated if a mismatch
 7 between both is detected (Ullsperger et al., 2014). The neurofunctional basis of performance
 8 monitoring and error correction has been illuminated by recent brain imaging and
 9 electrophysiological work. Specifically, a 'salience network' comprising, among others, the dorsal
 10 anterior cingulate cortex, the bilateral insular cortex and the inferior frontal gyri, is assumed to
 11 integrate sensory input, responding to behaviourally salient stimuli—behavioural errors—with
 12 increased activation (Seeley et al., 2007; Sridharan et al., 2008; Ham et al., 2013; Uddin, 2021).
 13 Thereby regions like e.g. the frontal operculum (FO, also anterior insular cortex, IC (Sridharan et al.,
 14 2008; Higo et al., 2011; Klein et al., 2013; Cieslik et al., 2015; Billeke et al., 2020)) may signal a need
 15 for increased cognitive control to the executive control network, consisting (among other regions) of
 16 the lateral prefrontal cortices, the PPC, supplementary motor area (SMA), and the inferior parietal
 17 lobule (Ullsperger et al., 2010; Uddin, 2021). This network, in turn, may direct attentional resources
 18 to the relevant stimuli, driving behavioural adaptations (Sridharan et al., 2008; Menon and Uddin,
 19 2010).

20 Notably, action performance and error may be conveyed via different sensory modalities; in manual
 21 action, for instance, via visual and proprioceptive cues about body position. In the context of body
 22 representation for action, visual and proprioceptive body position cues can be weighted depending
 23 on the current context; e.g., based on their relative relevance for the specific task at hand (van Beers

24 et al., 1999; Sober and Sabes, 2005; Lebar et al., 2017). Recently, we have used VR to examine this
25 contextual sensory weighting during action under conflicting visual (virtual) and proprioceptive (real,
26 unseen) body position feedback. Our fMRI and MEG studies (Limanowski and Friston, 2020;
27 Limanowski et al., 2020) specifically shed light on the effects of adopting a visual vs proprioceptive
28 attentional set during goal-directed manual action tasks, demonstrating that participants can
29 prioritise either modality over the other; and we observed corresponding changes of neuronal gain in
30 the respective sensory (visual and proprioceptive) brain regions.

31 Here, we capitalized on the novel task design of these studies. Firstly, we aimed to investigate the
32 neuronal correlates of performance monitoring in this ecologically valid VR-based goal-directed
33 grasping task; and to compare the results to previous work using more abstract study designs.
34 Secondly, as the original studies had demonstrated behavioural and neuronal effects of an
35 experimentally controlled task set prioritizing vision vs proprioception, another goal of our analysis
36 was to determine whether performance monitoring would be modality specific (i.e., involve different
37 brain regions when vision vs proprioception was task relevant) or modality general. Based on the
38 above literature, we expected task inaccuracy to be reflected by activity in the performance
39 monitoring network and, potentially, also in fronto-parietal attentional areas. Furthermore, in
40 contrast to the original MEG results, which had suggested low oscillatory frequencies (in the beta
41 band) as encoding an attentional task set (Limanowski et al., 2020), we expected high frequencies to
42 reflect error processing (in line with assumptions of the predictive coding framework, cf. Friston et
43 al., 2015). We therefore re-analysed the behavioural, fMRI, and MEG data from our above studies,
44 correlating participants' task performance with hemodynamic and oscillatory activity; and testing for
45 differences in brain connectivity.

46 Materials and Methods

47 Participants

48 For this study, we re-analysed fMRI and MEG data acquired by (Limanowski and Friston, 2020;
49 Limanowski et al., 2020). Healthy, right-handed volunteers with normal or corrected-to-normal vision
50 participated in both experiments after providing written informed consent. The fMRI study included
51 16 subjects (8 female, mean age 27, range 21-37), the MEG study included 18 subjects (9 female,
52 mean age 29, range 21-39). Both experiments were approved by the local research ethics committee
53 (University College London) and conducted in accordance with these approvals.

54 Experimental design and task

55 Participants wore an MR compatible data glove (5DT Data Glove MRI, 1 sensor per finger, 8 bit
56 flexure resolution per sensor, 60 Hz sampling rate, communication with the PC via USB) on their right
57 hand. The glove measured each finger's flexion via sewn-in optical fibre cables, and was carefully
58 calibrated prior to scanning to fit each participant's movement range. Recorded hand movement
59 data was used to control a photorealistic virtual hand (VH) model, moving in accordance to the
60 participant's hand movements and presented as part of a virtual reality task environment. This
61 virtual environment, consisting of the VH, a fixation dot and task instructions, was created in the
62 open-source 3D computer graphics software Blender (<http://blender.org>). The environment was
63 presented via a projector on a screen (for details see Limanowski and Friston, 2020; Limanowski et
64 al., 2020).

65 Participants were instructed to perform repetitive right-hand grasping movements, paced by
66 oscillatory (0.5 Hz) size changes (12%) of the central fixation dot: Thus, participants had to match the
67 fully open hand position with the biggest dot size and, conversely, the fully closed hand with minimal
68 dot size. Choosing the fixation dot as a target for the phase matching was done to ensure fixation
69 (see Limanowski & Friston, 2020; Limanowski et al., 2020 for the corresponding eye tracking analyses
70 that support this) and to prevent participants from looking away from the VH—this was necessary

71 since we wanted the visual action feedback (from the hand) to be comparable across VH and RH
 72 conditions (while it was effectively a distractor in the RH condition). However, note that what was
 73 tracked was an oscillatory size change; i.e., a rather abstract quantity. In other words, the task was a
 74 phase matching task rather than a visuo-spatial pursuit task; with this, we aimed to minimize the
 75 visual bias implicit in the design. Participants performed the task in movement blocks of 32 s (16
 76 close-and-open movements; the last movement was signalled by brief blinking of the fixation dot),
 77 separated by 16 s rest periods during which only the fixation dot was visible. All participants trained
 78 extensively before scanning. Note that this task was not designed to investigate visuomotor
 79 adaptation or learning, but maintaining hand-target phase matching during a sustained visual vs
 80 proprioceptive attentional task set.

81 In half of the conditions, a lag was introduced to the virtual hand's movements to evoke visuomotor
 82 incongruence; i.e., the virtual hand movements lagged behind the actually executed movements. In
 83 the fMRI experiment, a lag of 267 ms was introduced in the second half of each movement block; this
 84 delay length was chosen based on the results of a previous study that showed this amount of lag was
 85 well perceptible and could be adapted to with recurrent grasping movements (Limanowski et al.,
 86 2017). Since a pre-test for the subsequent MEG study showed that the behavioural effects observed
 87 in the fMRI study were slightly stronger when introducing longer delays, in this experiment a lag of
 88 500 ms was presented in separate delay blocks. However, differences in the amount of lag did not
 89 change the nature of the task; and the behavioural results were comparable across fMRI and MEG
 90 experiments (see Limanowski & Friston, 2020 and Limanowski et al., 2020). Before the start of each
 91 movement block, participants were instructed to match the phase of the fixation dot with either the
 92 seen VH model, or their unseen real hand. The virtual hand was visible in both conditions. Under
 93 incongruence, only one modality could be aligned with the target phase, which resulted in a
 94 misalignment of the other one; when trying to align their unseen real hand with the dot's phase,
 95 participants therefore had to ignore the movements of the virtual hand. Note that it was visual *hand*
 96 *movement* that was therefore task-relevant or irrelevant, not visual information per se (which

included the visually presented target dot). The task instruction ('VIRTUAL' or 'REAL') were presented 2.5 s before the start of each movement block for 2 s, and throughout the block, the colour of the fixation dot reminded participants of the current condition. In the fMRI experiment (Limanowski and Friston, 2020), we additionally varied the visibility (high or low) of the virtual hand during half of the movement blocks. However, we found no differences in performance between different visibility levels; and in our present reanalysis, there were no significant differences between visibility levels either. Therefore, we present the differential fMRI task contrasts in terms of VH vs RH task, summing over high and low visibility levels in each condition. In sum, despite minor technical differences between fMRI and MEG experiments, both can be described as a balanced 2 x 2 factorial design with the factors *task* (VH vs RH) and *congruence* (congruent vs incongruent).

Behavioural Data Analysis

In our previous analyses, we examined the neuronal correlates of the instructed task set; and only analysed condition specific differences in average performance (Limanowski and Friston, 2020; Limanowski et al., 2020). In the present study, we examined the neuronal correlates of phase matching *accuracy* (i.e., *fluctuations* around those average performances). All analyses were performed using MATLAB (MathWorks, Natick, MA, United States).

To quantify hand-target phase matching (in)accuracy, we calculated the root mean square error (RMSE) of the difference between the target position (i.e., the position within the oscillatory cycle) and the position of the task relevant hand (i.e., the position within the grasping cycle, averaging the recorded finger position data per hand). Thus, the virtual hand position was evaluated for the VH condition movements and the real hand position for the RH condition. For construction of the fMRI/MEG regressors, we binned the resulting RSME values into 1 s time windows, each centred on a time point of minimum or maximum target size, corresponding to the hand fully closed or opened if moved synchronously with the target. To focus on within-subject fluctuations in performance, rather than between-subject differences, the overall RSME across the entire experiment was normalized for each single subject (i.e. minimum and maximum performance error value was equal across

123 participants; 0 and 1, respectively). The resulting RSME values were assigned to one regressor per
 124 experimental condition (VH congruent, VH incongruent, RH congruent, RH incongruent), and de-
 125 meaned separately to reflect only variation around the condition mean. To evaluate if phase
 126 matching differed between conditions, we calculated a two-way repeated measures ANOVA with the
 127 factors *task set* (VH or RH) and *congruence* on the RSME values.

128 The amplitude of the hand movement at each time point was calculated via a cubic spline
 129 interpolation of the respective minimum and maximum hand position values in each time window.
 130 The resulting time series was de-meaned per condition as well, and used as noise regressor for the
 131 following fMRI and MEG analysis (see below). We also calculated the mean values of hand
 132 movement velocity, acceleration and jerk per subject and condition. For each of these movement
 133 parameters (including amplitude) we calculated a two-way repeated measures ANOVA with the
 134 factors *task set* (VH or RH) and *congruence* to evaluate condition-specific differences. Note, however,
 135 that the calculated RSME values implicitly captured all potential differences in movement
 136 characteristics as they imply a deviation from the optimal movement trajectory; therefore, these
 137 differences are considered negligible, and reported here: Movement amplitude was found to be
 138 significantly higher for condition RH than VH in both data sets (ANOVA, Main effect of task set, $F_{(1,15)}$
 139 $= 7.705$, $p = 0.014$ for fMRI; $F_{(1,17)} = 8.038$, $p = 0.011$ for MEG); in the fMRI data, movement amplitude
 140 was also significantly higher for incongruent than congruent trials ($F_{(1,15)} = 6.499$, $p = 0.022$). Mean
 141 amplitude values with associated standard deviation for the fMRI data set were: VH_congruent =
 142 0.607 (0.088), VH_incongruent = 0.640 (0.079), RH_congruent = 0.644 (0.098), RH_incongruent =
 143 0.664 (0.094). Mean amplitude values with associated standard deviation for the MEG data set were:
 144 VH_congruent = 0.696 (0.101), VH_incongruent = 0.681 (0.108), RH_congruent = 0.722 (0.089),
 145 RH_incongruent = 0.721 (0.119). Furthermore, in the fMRI study data (but not in the MEG study
 146 data), movement velocity was, on average, significantly higher for RH than VH ($F_{(1,15)} = 6.726$, $p =$
 147 0.020); and higher in trials with delayed compared to congruent seen movements ($F_{(1,15)} = 5.044$, $p =$
 148 0.040); mean velocity values with associated standard deviations: VH_congruent = 0.0106 (0.0014),

149 VH_incongruent = 0.0111 (0.0013), RH_congruent = 0.0112 (0.015), RH_incongruent = 0.0114
 150 (0.0015). It should be noted that, although significant, these differences were very small; there were
 151 no significant effects of acceleration or jerk. For completeness, we also tested for correlations
 152 between performance error and movement amplitude, velocity, acceleration, and jerk by calculating
 153 the Pearson correlation coefficients for each participant; and testing it for significance (i.e.,
 154 significant difference from zero) with a t-test on the group level. Similarly, we calculated the
 155 correlation between performance error and fMRI head movements (realignment parameters), via
 156 subject-level Pearson correlation and group-level t-test, adjusted for multiple comparisons for the six
 157 realignment parameters. On average, phase matching accuracy correlated significantly, but only
 158 weakly, with movement amplitude (mean Pearson's $r = .27$ for fMRI data; mean $r = .18$ for MEG data,
 159 both $t_{S(17)} > 5$, $ps < 0.05$); and it also correlated significantly—again, very weakly—with velocity,
 160 acceleration, and jerk (highest $r = .178$, lowest $r = .073$; all $ps < 0.05$ for fMRI and MEG data). Phase
 161 matching did not significantly correlate with the fMRI realignment parameters (all $|r| < 0.02$, *n.s.*).

162 FMRI Data Preprocessing and Analysis

163 All analyses were performed using MATLAB (MathWorks, Natick, MA, United States) and SPM12.6
 164 (Wellcome Trust Centre for Neuroimaging, University College London,
 165 <https://www.fil.ion.ucl.ac.uk/spm/>).

166 We reused the pre-processed fMRI data by Limanowski and Friston, 2020. The fMRI data had been
 167 acquired using a 3T scanner (Magnetom TIM Trio, Siemens), equipped with a 64-channel head coil.
 168 T_2^* -weighted images were acquired using gradient echo-planar imaging sequences
 169 (voxel size = $3 \times 3 \times 3 \text{ mm}^3$, matrix size = 64×72 , TR = 3.36 s, TE = 30 ms, flip angle = 90°).

170 We fitted a general linear model (GLM, 128 s high-pass filter) to each participant. Each condition (VH,
 171 RH) was modelled with a boxcar function as a 32 s movement block; we added a parametric
 172 modulator (1/-1) to each condition encoding the first half of each block as congruent (-1) and the
 173 second half as incongruent (1) movement periods. Additionally, we included a regressor encoding the

(de-measured) RSME values for each conditions; the values were re-sampled to match the 3.36 s scan length prior to this. Regressors modelling the task instructions and movement amplitude were added to the GLM alongside the realignment parameters as regressors of no interest.

For each subject, we calculated contrast images of each RSME regressor against the baseline. These were then entered into a group-level flexible factorial design, with the factors *task* (VH or RH) and *congruence* (congruent, incongruent), and an additional factor modelling the subject constants. To assess potential differences between congruent and incongruent movement periods, we calculated separate first-level GLMs, in which the RSME values of the second movement half were inverted; this effectively encoded the contrast congruent-incongruent. The resulting contrast images were entered into an analogous group-level GLM as described above.

Group-level results were assessed for statistical significance using a voxel-wise threshold of $p < 0.05$, family-wise error (p_{FWE}) corrected for multiple comparisons. We projected the resulting statistical maps onto the mean normalized structural image or rendered it on SPM12's brain template. The unthresholded T-maps corresponding to the contrasts reported here can be inspected online at <https://neurovault.org/collections/GGWQTGSI>. For anatomical reference we used the SPM Anatomy toolbox (Eickhoff et al., 2005).

MEG Data Preprocessing and Analysis

MEG signals had been acquired using a 275-channel whole-head setup with third-order gradiometers (CTF Omega, CTF MEG International Services LP, Coquitlam, Canada) at a sampling rate of 600 Hz. Following the original analysis by (Limanowski et al., 2020), the MEG data were high-pass filtered (1 Hz), downsampled to 300 Hz, and epoched into trials of 2 s each (each corresponding to a full target oscillation/grasping cycle).

In the main (sensor space) MEG data analysis, we looked for spectral power differences under 'steady-state' assumptions; i.e., treating the spectral profile as a 'snapshot' of performance dependent responses as manifest in quasi-stationary power spectra (Moran et al., 2008; Donner and

199 Siegel, 2011; Friston et al., 2019). We computed trial-by-trial power spectra in the 0-98 Hz range
 200 using a multi-taper spectral decomposition (Thomson, 1982) with a spectral resolution of ± 2 Hz. The
 201 spectra were log-transformed, converted to volumetric scalp x frequency images—one image per
 202 trial—with two spatial and one frequency dimension (Kilner and Friston, 2010), and smoothed with a
 203 Gaussian kernel with full width at half maximum of 8 mm x 8 mm x 4 Hz. The resulting images were
 204 entered into a general linear model (GLM) using a within-subject ANOVA with the respective RSME
 205 values as a covariate (first-level analysis). As in the fMRI analysis, movement amplitude was
 206 moreover included as a covariate of no interest to capture movement related fluctuations. Contrast
 207 images were then calculated for each condition's accuracy covariate. These contrast images were
 208 then entered into a group-level GLM using a flexible factorial design including the two within-subject
 209 experimental factors (task and congruence), and a factor modelling the between subject variance.
 210 The statistical parametric maps obtained from the respective group-level contrasts were evaluated
 211 for significant effects using a threshold of $p < 0.05$, family-wise error (p_{FWE}) corrected for multiple
 212 comparisons at the peak (voxel) level.

213 As a post-hoc analysis, source localization of trial-by-trial correlation of gamma band power with
 214 performance error was performed using a variational Bayesian approach with multiple sparse priors
 215 (Litvak and Friston, 2008). Source localization was performed in the 34-88 Hz range (which was the
 216 range of effects in the spectral analysis thresholded at $p < 0.001$, uncorrected). As we had already
 217 performed an analogous localization on the fMRI data (see above), we could use the superior spatial
 218 acuity of fMRI to improve MEG source localization; i.e., the fMRI activations (thresholded at $p <$
 219 0.001 , uncorrected) were used as empirical (spatial) priors for the Bayesian inversion routine
 220 (Henson et al., 2010; López et al., 2014). For comparison, we also reconstructed the sources using a
 221 Bayesian beamforming approach (Belardinelli et al., 2012). This produced very similar results; i.e., the
 222 strongest effects were localized to the bilateral inferior frontal gyri, including the FO (a further,
 223 weaker source was localized to the primary visual cortex). The results of this source localization were
 224 summarized as 3D images and entered into a group-level t-test. Since the significance of the effects

on spectral responses had already been established with the sensor space analysis, the ensuing statistical parametric maps were displayed at a threshold of $p < 0.05$, uncorrected, rendered on SPM's smoothed average brain template. The unthresholded T-map corresponding to the source localization can be inspected online at <https://neurovault.org/collections/GGWQTGSI>.

FMRI functional connectivity analysis

In our main analysis (see above), we identified brain areas that showed a significant response to phase matching inaccuracy. The fMRI and MEG results consistently highlighted the bilateral FO (while further fMRI activations were found in the dorsal premotor cortex, PMd, and the dlPFC).

In our original analyses (Limanowski and Friston, 2020; Limanowski et al., 2020), the FO did not show any task specific effects (i.e., activity differences between VH and RH tasks) per se, neither did the SMA or the dlPFC. However, following the clear response of the FO to poor task performance in general, we now asked whether these areas would change their connectivity to other (potentially, task relevant) brain areas depending on whether the inaccuracy was registered during the VH or RH task; i.e., while participants focused either on visual (VH) or proprioceptive (RH) action feedback.

To answer this question, we used psychophysiological interaction (PPI) analysis for fMRI data. This analysis aims to explain neuronal activity of other brain areas in terms of an interaction between psychological factors (the specific task condition) and physiological factors (the BOLD signal time course in the region of interest (Friston et al., 1997; O'Reilly et al., 2012)). The resulting interaction (PPI) reveals voxels in the brain that increase their connectivity with a specific seed region in a given context; e.g., in a specific task condition. Note that task dependent changes in connectivity per se (i.e., between VH and RH task sets) were identified in both fMRI and MEG data sets (Limanowski and Friston, 2020; Limanowski et al., 2020). However, in the fMRI data, the SPM approach allowed us to select a spatially isolated volume of interest (i.e., voxels from the FO) that was not part of the original connectivity analysis. This was not analogously possible for the MEG data, which in the original

249 connectivity analysis were modelled on the whole-scalp level (Limanowski et al., 2020). Therefore,
250 we limited the connectivity analysis to the fMRI data.

251 For the PPI analysis, we calculated separate GLMs with concatenated runs for each participant, and
252 thus identified subject-specific peaks of the main effects observed on the group level. The individual
253 peaks were defined as the maximum effect within a 10 mm radius sphere of the respective group-
254 level maximum (see Table 1). From these individual peaks, we extracted the BOLD signal of the seed
255 regions as the first eigenvariate of activity across all voxels in a 4 mm radius sphere centred on the
256 participant-specific peak. For three subjects where no effect could be identified for the specific PMd
257 seed region as well as one case where no effect was found for the dIPFC region, we resorted to the
258 group level maximum for seed region localization.

259 The SPM12.6 PPI routine was then used to form the interaction between the psychological factor and
260 the seed region's summarized BOLD signal time course. Note that while the seed regions were
261 identified per their significant response to phase matching inaccuracy (Fig. 2), our psychological
262 factor was the task set; i.e., the instructed hand modality at the beginning of each movement block
263 (VH vs RH; pooled over different levels of virtual hand visibility, see above). After forming the
264 interaction term, a second GLM was constructed for each participant, including the interaction, the
265 seed region's extracted signal, the task set and the realignment parameters as regressors of no
266 interest.

267 On the group-level, the connectivity of the bilateral FO was evaluated using a paired t-test; i.e., a
268 GLM including the PPI contrast images of the left and right FO of each participant, and another factor
269 modelling the between-participant variance. We also tested whether the other two regions showing
270 significant responses to phase matching inaccuracy (PMd and dIPFC) would exhibit connectivity
271 changes, using a similar approach.

Figure 1. Phase matching task. Participants controlled a photorealistic virtual hand model (VH) with a data glove worn on their right hand. In all experimental conditions, the real hand (RH) was occluded from view, while the VH was visible at all times. Participants had to match the oscillatory phase of a virtual target (fixation dot), changing its size sinusoidally at 0.5 Hz) with grasping movements (i.e., open at maximum target size, closed at minimum size). Thereby, participants were instructed to match the target's oscillatory phase with the grasping movements of *either* the VH *or* the unseen RH (while ignoring the movements of the VH). These instructions induced a specific task set, in which either visual or proprioceptive hand movement information was task relevant. In half of all trials, RH and VH moved congruently ('congruent'), while in the other half of the trials ('incongruent'), the movements of the VH were delayed with respect to the actually executed movements (RH); this introduced visuo-proprioceptive incongruence. Reprinted from Limanowski et al. (2020).

272 Results

273 Behavioural results

274 In both studies, participants reported allocating their attention to the respective instructed hand; in
 275 line with the assumption that the task instructions would create a visual vs proprioceptive task set.
 276 Both VH and RH tasks were perceived as comparably difficult, with the incongruent conditions being
 277 judged as more difficult in each case. Moreover, in both studies, participants were able to follow the
 278 task instructions; i.e., to keep the instructed modality's (vision or proprioception) grasping
 279 movements significantly better aligned with the phase of the dot than the non-instructed modality.
 280 See the original studies (Limanowski et al., 2020; Limanowski & Friston, 2020) for details.

281 Our analysis was aimed at identifying the neuronal correlates of fluctuations of performance
 282 (i.e., fluctuations around condition specific mean performances). For completeness, we still report
 283 the condition-specific RMSE means and standard deviations; for the fMRI data set those were:
 284 VH_congruent = 0.265 (0.045), VH_incongruent = 0.244 (0.041), RH_congruent = 0.273 (0.058),
 285 RH_incongruent = 0.257 (0.061)); for the MEG data set those were: VH_congruent = 0.213 (0.045),
 286 VH_incongruent = 0.244 (0.040), RH_congruent = 0.206 (0.041), RH_incongruent = 0.322 (0.095).
 287 Overall, participants performed slightly better in the VH than the RH task; although this difference
 288 was statistically significant only for the MEG study data (ANOVA, Main effect of task set, $F_{(1,17)} =$
 289 7.136,
 290 $p = 0.016$). In the MEG study, RMSE was significantly higher for incongruent than congruent trials in
 291 both data sets (ANOVA, $F_{(1,17)} = 30.026$, $p < 0.001$); in the fMRI data, RMSE was higher for congruent
 292 than incongruent trials ($F_{(1,15)} = 6.820$, $p < 0.05$). In sum, the behavioural results and self-reports
 293 showed that participants could follow the task instructions; that this induced the desired cognitive-
 294 attentional task set; and that behaviour in the VH vs RH tasks was comparable across fMRI and MEG
 295 studies.

296 FMRI results

297 In our main fMRI analysis, we sought to identify brain regions in which neuronal activity correlated
 298 with phase matching (in)accuracy (Fig. 2). A significant ($p_{\text{FWE}} < 0.05$) main effect of inaccuracy was
 299 observed in the bilateral FO, the left dorsal premotor cortex (at uncorrected thresholds, this
 300 activation cluster spanned to the left SMA), and the left dlPFC (see Table 1 and Fig. 2). More liberal
 301 thresholds
 302 ($p < 0.001$, uncorrected) revealed further activation clusters in the right middle and superior frontal
 303 gyri, the precuneus, the midcingulate cortex (MCC), the right middle temporal gyrus (MTG), and
 304 bilaterally in the cerebellum (cf. the render in Fig. 2). Conversely, a significant main effect of accuracy
 305 was found in the left pre- and postcentral gyrus, corresponding to the primary motor cortex (M1). No
 306 other comparisons (i.e., contrasting the effects of accuracy between task conditions, delay, or visual
 307 salience levels; see Methods) yielded significant effects. At uncorrected thresholds ($p < 0.001$), voxels
 308 in several brain areas showed a stronger correlation with task inaccuracy under the VH task than
 309 under the RH task; namely, in the MCC, the bilateral FO, the right MTG, the left cerebellum, the right
 310 dlPFC, and the bilateral posterior parietal cortex (PPC, peak within the intraparietal sulcus, IPS).

Figure 2. BOLD signal increases related to phase matching inaccuracy. The renders (left) and slice overlays (right) show brain areas in which hemodynamic activity was correlated with the relative inaccuracy of hand-target phase matching (displayed at $p < 0.001$, uncorrected). Significant activations ($p_{\text{FWE}} < 0.05$; voxels outlined in blue on the slice overlays) were located in the bilateral FO, the left SMA, and the left dlPFC.

Table 1. Significant ($p_{FWE} < 0.05$) activations for all reported fMRI contrasts.

Anatomical location	Voxels	MNI (x, y, z)			Peak T	Peak p_{FWE}
Correlation with phase matching inaccuracy						
L. Insula (FO)	1	-26	20	12	5.92	0.012
L. Superior frontal gyrus (PMd)	13	-16	4	70	5.90	0.014
L. Middle frontal gyrus / frontal pole (dlPFC)	2	-26	44	24	5.80	0.018
R. Insula (FO)	3	30	22	12	5.72	0.023
Correlation with phase matching accuracy						
L. Pre- and postcentral gyrus (M1)	6	-32	-18	38	6.18	0.006
	3	-28	-22	66	5.78	0.019
	1	-24	-24	62	5.49	0.044

MEG results

The MEG sensor space analysis revealed that phase matching inaccuracy was associated with significantly increased spectral power in the gamma frequency range over mid-frontal sensors (main effect; peak at 52 Hz, $T = 5.31$, $p_{FWE} < 0.05$; see Fig. 3A). These spectral effects were source-localized to the bilateral inferior frontal gyri, including the bilateral FO (Fig. 3B). No other spectral power comparisons yielded statistically significant results; but there was a statistical trend suggesting inaccuracy was associated with reduced alpha (8 Hz) power over posterior sensors ($T = 4.61$, $p_{FWE} = 0.069$).

Figure 3. Spectral power increases related to phase matching inaccuracy. **A:** The ‘glass brain’ (maximum intensity) projections show the sensor level scalp-frequency maps of spectral power correlated with the relative inaccuracy of hand-target phase matching (the darkest voxels show the strongest effect along the respective projection; the maps are thresholded at $p < 0.001$, effects significant at $p_{FWE} < 0.05$ are outlined in blue; the top plots have one frequency dimension, 0 - 98 Hz, and one spatial dimension, P - A = posterior-anterior, L - R = left-right; the bottom plot has two spatial dimensions). **B:** Renders (left) and slice overlay (right) showing the corresponding source localization of the correlation to regions around the FO.

319 Functional connectivity analysis

320 The above fMRI activations and source-localized MEG gamma power consistently suggested that
 321 periods of poor phase matching activated the bilateral FO, in line with previous literature that had
 322 established this region’s role in error processing and performance monitoring (see Introduction).
 323 However, we did not find any significant difference between conditions (i.e., between visual and
 324 proprioceptive task sets). Therefore, we next performed a connectivity (PPI) analysis on the fMRI
 325 data to explore whether task relevant brain areas would change their connectivity to the FO
 326 depending on the instructed task condition (VH or RH).

327 This analysis revealed a significantly increased coupling of several brain areas with the bilateral FO
 328 during the VH task > RH task, most strongly expressed in the right inferior parietal lobe (IPL, see Fig.
 329 4A and Table 2). The increase in coupling with the right IPL was evident for both the left and right FO
 330 independently, as revealed by an additional ‘null’ conjunction analysis (Fig. 4B; a conjunction of
 331 voxels activated in the PPI with the left FO and PPI with the right FO, each thresholded at $p < 0.001$,
 332 uncorrected). Correspondingly, there were no significant differences in coupling between the left and
 333 right FO. A supplementary analysis testing for potential coupling differences with the FO during

334 VH_incongruent vs VH_congruent yielded no significant effects, either. There were no significant
 335 connectivity changes with the FO under the RH task > VH task. No significant changes in connectivity
 336 were observed in analogous analyses calculated for the PMd or the dIPFC, the other two brain
 337 regions showing significant effects in the main analysis (see above).

Figure 4. Task-dependent connectivity changes of the bilateral FO. **A:** Brain areas showing increased coupling with the bilateral FO during the VH task relative to the RH task (displayed at $p < 0.001$, uncorrected). The strongest effects were located in the right IPL (voxels significant at $p_{FWE} < 0.05$ are outlined in blue). **B:** A corresponding 'null' conjunction contrasts confirmed this increased task dependent coupling with the right IPL for the left and right FO independently (each PPI contrast thresholded at $p < 0.001$, uncorrected).

Table 2. Brain areas showing significant ($p_{FWE} < 0.05$) coupling increases with the bilateral FO during the VH task > RH task.

Anatomical location	Voxels	MNI (x, y, z)			Peak T	Peak p_{FWE}
R. Inferior parietal lobe / supramarginal gyrus (IPL/SMG)	15	56	-32	38	10.71	0.002
R. Postcentral gyrus (S1)	4	54	-14	44	9.26	0.012
R. Precentral Gyrus (M1)	1	4	-24	48	9.02	0.017
R. Temporal Pole	2	52	20	-22	8.83	0.022
	2	40	22	-24	8.68	0.027

338 Discussion

339 We used data from a virtual reality-based hand-target phase matching task to identify the
 340 hemodynamic and oscillatory correlates of performance (i.e., phase matching accuracy) monitoring
 341 under instructed task relevance of visual or proprioceptive hand position feedback. The specific
 342 design of this task, with continuous goal-directed movements and the experimentally controlled
 343 switching of attentional task set created a novel, ecologically valid context for performance
 344 monitoring.

345 Our main result was a general, modality-independent response of the bilateral FO to poor phase
 346 matching accuracy, as evident from increased BOLD signal levels and increased gamma power.
 347 Furthermore, connectivity of the bilateral FO to the right PPC/IPL increased while participants
 348 executed the phase matching task with the visible virtual hand, compared to when they executed it
 349 with the real, unseen hand.

350 The observed general *BOLD signal increase* in the bilateral FO with task (phase matching) inaccuracy
 351 replicates observations of previous studies using more abstract study designs, where BOLD signal in
 352 the FO increased in response to performance errors. For instance, the FO was activated by error trials
 353 vs correct trials in the Simon task (Danielmeier et al., 2011; Ham et al., 2013); in an antisaccade task
 354 (Klein et al., 2007); and in a flanker task (Eichele et al., 2008). Similarly, FO error-related BOLD signal
 355 increases were observed in visuomotor adaptation tasks (Grafton et al., 2008) and in response to
 356 tactile ‘oddball’ stimuli (Allen et al., 2016). Some studies found activation of the FO correlated
 357 positively with task performance (Wager et al., 2005; Bunge et al., 2015). This could, however, be
 358 explained with an general underlying function of FO activation in performance monitoring; acting not
 359 as an error signal per se, but as part of a mechanism to improve performance in response to errors
 360 (cf. Eichele et al., 2008). Thus, it has been proposed that neuronal activity in the FO may indicate the
 361 need for increased allocation of attentional resources to specific stimuli to achieve task-appropriate
 362 behaviour (Ham et al., 2013; Langner and Eickhoff, 2013; Cieslik et al., 2015; Uddin, 2021).
 363 Additionally, due to FO’s reciprocal connections to multiple sensory, limbic, and association areas

364 (Sridharan et al., 2008), it may act as crucial ‘relay’ station for switching between different task
 365 relevant networks, e.g. switching from default network to executive control network (Klein et al.,
 366 2007; Sridharan et al., 2008; Menon and Uddin, 2010; Ullsperger et al., 2010).

367 The *spectral correlates* of task inaccuracy were expressed in the gamma frequency range, thus
 368 confirming the potential role of high-frequency oscillations for conveying error signals (Friston et al.,
 369 2015). Furthermore, notably in agreement with the BOLD signal increases, they were source-localized
 370 to the bilateral FO (as part of larger sources in the IFG). A general correspondence and spatial co-
 371 localization of the BOLD signal and gamma power has been established in previous studies (Brovelli
 372 et al., 2005; Foucher et al., 2003; notably, including co-localization of responses in the insula, cf.
 373 Castelhana et al., 2014). Our findings align with previous studies that reported increases in
 374 intracranially recorded gamma activity in the FO following (stop-signal) task errors (Bastin et al.,
 375 2016). Moreover, gamma band activity per se is often interpreted as indicating enhanced processing
 376 of attended (e.g., task relevant) sensory information (Jensen et al., 2007; Hipp et al., 2012; Siegel et
 377 al., 2012; Clayton et al., 2015). In other studies, increased gamma power (over mid-frontal sensors)
 378 during response competition has been interpreted as indicating increased cognitive control (Grent-’t-
 379 Jong et al., 2013). A Granger causality analysis by (Chand and Dhamala, 2017) suggested that, during
 380 perceptual decision making, the FO may exert causal influence over fronto-parietal areas within the
 381 gamma band.

382 In sum, and in light of the above literature, our fMRI and MEG results suggest that the FO is involved
 383 in performance monitoring during goal-directed hand movements, corroborating its role as
 384 suggested by previous studies in other, non-motor tasks. Notably, while most of the above studies
 385 used trial-by-trial designs, our study featured continuous movements; thus, our results complement
 386 previous literature in showing that the FO shows similar responses in task settings requiring ‘on-line’
 387 performance monitoring and adjustment during manual actions. Specifically, we propose that FO
 388 activation (expressed through BOLD signal and gamma power increase) may have indicated a
 389 reaction to task inaccuracy or error, and a corresponding need for behavioural adjustment.

390 Tentatively, this interpretation is supported by the fact that posterior alpha power behaved opposite
 391 to gamma; i.e., it decreased with increasing inaccuracy (although this effect did not reach statistical
 392 significance, see Results). It is well established that posterior alpha inversely correlates with attention
 393 and task engagement (Yamagishi et al., 2003; Sauseng et al., 2005; Thut, 2006; Bacigalupo and Luck,
 394 2019).

395 In addition to increased activation of the bilateral FO, our fMRI connectivity analysis revealed that
 396 these areas also increased their *functional coupling* with the right PPC (peak located in the IPL) during
 397 the VH task (phase matching with vision) compared with the RH task (phase matching with
 398 proprioception). An fMRI study by Higo et al. (2011) used a task requiring attention to faces, houses,
 399 or body parts; and found that the FO increased its functional coupling with visual areas processing
 400 the respective task relevant stimulus category. In our case, however, the FO's connectivity increase
 401 was not with primary and secondary visual cortices, which had shown task (attentional set)
 402 dependent activity increases in our previous studies (Limanowski and Friston, 2020; Limanowski et
 403 al., 2020). Instead, FO coupling increased with the IPL of the right PPC; an area that is involved in
 404 more high-level processes including multisensory and sensorimotor integration, and visuo-spatial
 405 attention (Wolpert et al., 1998; Andersen and Buneo, 2002; Malhotra et al., 2009).

406 We propose that this result is related to the fact that visual hand movements were task relevant in
 407 the VH task, but had to be ignored in the RH task (where phase matching was done with
 408 proprioception). Thus, visual hand movements were essential for correcting phase matching error in
 409 the VH task, but irrelevant in the RH task. Notably, FO connectivity was not significantly different
 410 during periods of visuo-proprioceptive incongruence; neither did we find significant differences
 411 between congruent and incongruent conditions in the main fMRI GLM analysis. This suggests that the
 412 observed VH > RH task dependent connectivity difference was related to the task-relevant hand
 413 feedback modality being vision > proprioception per se, rather than to (in)congruence between
 414 vision and proprioception. This interpretation fits with previous work showing that the right PPC,
 415 specifically areas in the right IPL, are critical hubs for executing and correcting visually guided arm

416 movements (Desmurget et al., 1999; Culham et al., 2003; Wenderoth et al., 2004; Culham and
 417 Valyear, 2006; Ogawa et al., 2007; Lane et al., 2011).

418 Potentially, this effect might have been enhanced by intrinsic differences between the modalities in
 419 relation to visuo-proprioceptive integration and error detection; i.e., it might have been easier for
 420 participants to notice a phase matching error when focusing on visual action feedback (VH task) than
 421 when focusing on proprioception (RH task). This could have been due to visual body position
 422 estimates being intrinsically less variable than proprioceptive ones (cf. van Beers et al., 1999); and
 423 because the visual body position was easier to compare to, and to integrate with, the visually
 424 presented target (in the VH task) than the proprioceptive body position (in the RH task). However,
 425 note that the target quantity was not visuo-spatial but abstract; i.e., the oscillatory growing-and-
 426 shrinking phase of the fixation dot. When we lowered the statistical threshold of the main GLM
 427 analysis to $p < 0.005$, uncorrected, the bilateral FO (the PPI seed regions) and the right PPC (the PPI
 428 target region) showed a stronger correlation with task inaccuracy under the VH task compared with
 429 the RH task. Although this was a weak effect, it could mean that overall, errors were more easily
 430 processed (in those areas) in the VH task. Interestingly, participants performed slightly worse in the
 431 RH than in the VH task, which could support the interpretation that proprioceptive performance
 432 monitoring was less efficient than when vision was used. This may also fit with previous reports of
 433 increased BOLD signal in the FO for error trials of which participants were aware, compared to
 434 unaware errors (Klein et al., 2007; Harsay et al., 2018). Specifically, Harsay et al. (2018) also observed
 435 increased functional connectivity of the FO to the PPC (bilaterally, in addition to the bilateral S1)
 436 during aware > unaware errors.

437 In sum, we suggest that the increased connectivity between the FO and the right PPC during the
 438 VH > RH task indicates the FO signalling an increased need for control and attentional and/or
 439 behavioural adjustment (following poor performance) to visuomotor regions in the right PPC; which
 440 could also be related to how easily those performance deficits could be detected.

441 The above speculations could also explain why we did not observe any connectivity increases of the
 442 FO during the RH > VH task. Accordingly, this could be because participants were less aware of their
 443 phase matching (in)accuracy when performing the task with the unseen real hand. Future work
 444 should evaluate this possibility with specific task designs.

445 Besides activations in the bilateral FO, we also found BOLD signal increases due to poor phase
 446 matching in the PMd (spanning to the SMA at uncorrected thresholds) and in the dlPFC (at the
 447 junction of middle frontal gyrus and frontal pole). Both areas have been strongly implied in
 448 performance monitoring in other contexts, albeit implying the SMA specifically rather than the more
 449 lateral PMd (Ullsperger et al., 2014). The SMA has been shown to respond to unexpected stimuli, e.g.
 450 surprising action outcomes (Sakai et al., 1999; Krakauer et al., 2004; Ullsperger et al., 2010; Scangos
 451 et al., 2013). Furthermore, BOLD signal in the SMA and in the PMd has previously been reported to
 452 correlate with positional error in a visuomotor learning task (Grafton et al., 2008) and in a continuous
 453 hand-target tracking (Limanowski et al., 2017). In line with the interpretation provided in these
 454 studies, the PMd (and, uncorrected, SMA) activation we observed may indicate an updating of
 455 movement plans in response to poor detected phase matching. Similarly, the lateral PFC is
 456 considered a crucial part of sensorimotor hierarchy (Benchenane et al., 2011; Sokhadze et al., 2012),
 457 and is thought to contribute to performance monitoring and error detection; e.g., by preparing
 458 attentional task sets and comparing behavioural output against them (Ullsperger and von Cramon,
 459 2004; Danielmeier et al., 2011; Cieslik et al., 2015; Smith et al., 2019). In our experiment, the dlPFC
 460 activation could imply similar underlying ‘high level’ functions.

461 Conversely, we observed that BOLD signal in the contralateral M1 correlated positively with task
 462 accuracy. This effect could be related to the fact that higher task accuracy coincided with more
 463 pronounced hand movements and, thus, also with associated changes in movement velocity,
 464 acceleration, and jerk. Future work will have to clarify whether differences in movement trajectories
 465 contribute to differential M1 activation as observed here. However, we had included movement
 466 amplitude as a regressor of no interest in our first-level GLMs, which should have largely accounted

467 for this potential bias. Alternatively, this observation also aligns with the M1's known role in motor
468 learning (Hardwick et al., 2013; Spampinato and Celnik, 2017; Panico et al., 2021); with previous
469 findings that M1 activity correlated with visuomotor adaptation performance (Della-Maggiore and
470 McIntosh, 2005) or with visuomotor target tracking performance (Ogawa et al., 2006); and with the
471 fact that a perturbation of the M1 via transcranial magnetic stimulation (TMS) resulted in reduced
472 sensorimotor adaption (Orban de Xivry et al., 2011).

473 Finally, our results should be compared to previous studies with some caution, since our task was
474 designed around continuous movements; therefore, we could not isolate specific time points—and
475 neuronal correlates—that would clearly correspond to specific cognitive or motor processes like e.g.
476 error detection or correction. Future trial-by-trial task designs should therefore try to validate our
477 interpretation.

478 In conclusion, our results suggest a critical role for the bilateral FO in performance monitoring during
479 goal-directed manual action; and that following errors in visually guided manual action specifically,
480 the FO may signal an increased need for control to visuomotor regions in the right PPC.

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666

Real hand (RH)

Virtual hand (VH)

Target
(fixation dot)

0.5 Hz

Hand movements

A

B