Motor planning in the human posterior parietal and dorsal premotor cortices includes visuomotor prediction

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Abstract

The dorsal premotor and posterior parietal cortices have been linked to motor planning by electrophysiological recordings and brain imaging. Interestingly, these areas also show increased responses when visual feedback does not match the executed movements, which may indicate an adaptation of the brain's body representation to a nonstandard visuomotor mapping. Here, we tested whether brain regions that plan a movement also encode predictions about the visuomotor mapping expected during execution. Thus, we combined a delayed movement task with a virtual reality based manipulation of visuomotor congruence during functional magnetic resonance imaging (fMRI). After a delay period, participants executed one of two possible left hand movements; visual movement feedback was provided via a virtual hand model controlled by a data glove. During the delay, a cue specified the to-be-executed movement (or left it ambiguous); and the upcoming mapping of the virtual to real hand movements (congruent or incongruent). Premotor and posterior parietal brain areas showed increased activity, during the delay, when movements were planned (cued > uncued) and when an incongruent > congruent visuomotor mapping was cued. Moreover, there was a significant interaction between both effects in the left anterior intraparietal sulcus (aIPS), the left superior parietal lobe (SPL), and the bilateral dorsal premotor cortex (PMd); each showing strongest activation when specific movements were planned under an expected visuomotor incongruence. These results suggest that motor planning in the dorsal premotor and posterior parietal cortex entails a prediction of the resulting visual movement consequences, which can anticipate nonstandard visuomotor mappings.

Introduction

The idea that the brain employs predictive 'forward' models has been fruitfully applied to study the neuronal mechanisms underlying body representation for action (Wolpert & Kawato, 1998; Desmurget et al., 1999; Blakemore et al., 1998, 2001; Adams et al., 2013; Parr et al., 2021). One key assumption is that by means of such forward models, the brain predicts the sensory consequences of planned movements. A large body of research has focused on identifying the neural substrate of these sensorimotor predictions, and their relation to circuits involved in motor planning *per se*.

The neuronal basis of motor planning has been impressively illuminated with delayed movement paradigms: Electrophysiological recordings in monkeys have uncovered planning related neuronal activity in premotor areas when the immobile animal prepared movements (Ames et al., 2014; Churchland et al., 2006, 2010; Crammond & Kalaska, 1989, 2000; Ferraina & Bianchi, 1994; Kaufman et al., 2014; Shen & Alexander, 1997; Tanji & Evarts, 1976). A similar encoding of planned movements has been observed in the monkey posterior parietal cortex (PPC; Crammond & Kalaska, 1989; Ferraina & Bianchi, 1994; Schaffelhofer et al., 2015; Townsend et al., 2011). Human brain imaging studies have identified analogous preparatory responses in the ventral and dorsal premotor cortex, including the SMA, and in the PPC (Toni et al., 1999; Brass & von Cramon, 2002, 2004; Gallivan et al., 2013; Ariani et al., 2015, 2018; Gertz & Fiehler, 2015; Lindner et al., 2010). This delay period activity resembles that observed during motor execution (Ames et al., 2014; Lotze et al., 1999) and is thought to encode specific aspects of motor planning, such as movement direction (Crammond & Kalaska, 1989; Fernandez-Ruiz et al., 2007) or effector selection (Bernier et al., 2012; Hoshi & Tanji, 2002). Some researchers have put forth that motor planning may also include a prediction of the sensory consequences of planned actions (Kuang et al., 2015; Pilacinski et al., 2018).

One example of such a prediction is how visual body movements map onto motor signals. Notably, the above fronto-parietal areas have been implied in processing this visuomotor mapping. Thus, movements under visuomotor incongruence were associated with increased responses in premotor

and posterior parietal cortices, alongside temporoparietal and cerebellar regions (Balslev et al., 2005; Brass et al., 2001; Limanowski et al., 2017; Limanowski & Friston, 2020; Nahab et al., 2011; Ohata et al., 2020; Van Kemenade et al., 2017, 2019; cf. de Lange et al., 2006; Zimmermann et al., 2012). This has been interpreted as an adaptation of the body model, to learn how to move under novel 'nonstandard' visuomotor mappings. Notably, the brain areas showing this 'reactive' visuomotor adaptation closely match those associated with movement planning as per the above studies; i.e., including the PMd and areas in the SPL and aIPS of the PPC. Yet, it is unclear whether motor planning in these brain regions also entails a *prediction* of visuomotor mapping.

Here, to test this, we combined a delayed movement paradigm with a virtual reality based manipulation of visuomotor congruence inside an MR scanner: Participants had to execute one of two possible hand movements after a delay, during which the movement type and the visuomotor mapping could be cued (Fig. 1). Thus, our design allowed us to assess the hemodynamic correlates of motor planning and visuomotor predictions; as well as their potential anatomical overlap and interaction. We expected stronger premotor and posterior parietal activations during cued > uncued movements. Moreover, we hypothesized that preparing for 'nonstandard' mappings would require a recalibration of the default (life-long) predictions of the body model; hence we expected stronger activations during the preparation for incongruent > congruent visuomotor mappings. Thirdly, we hypothesized that both preparatory processes should interact; i.e., movement planning should require more neuronal resources when expecting an incongruent visuomotor mapping. Lastly, we expected the (cued) preparatory processes to influence activity in fronto-parietal areas during subsequent movement execution.

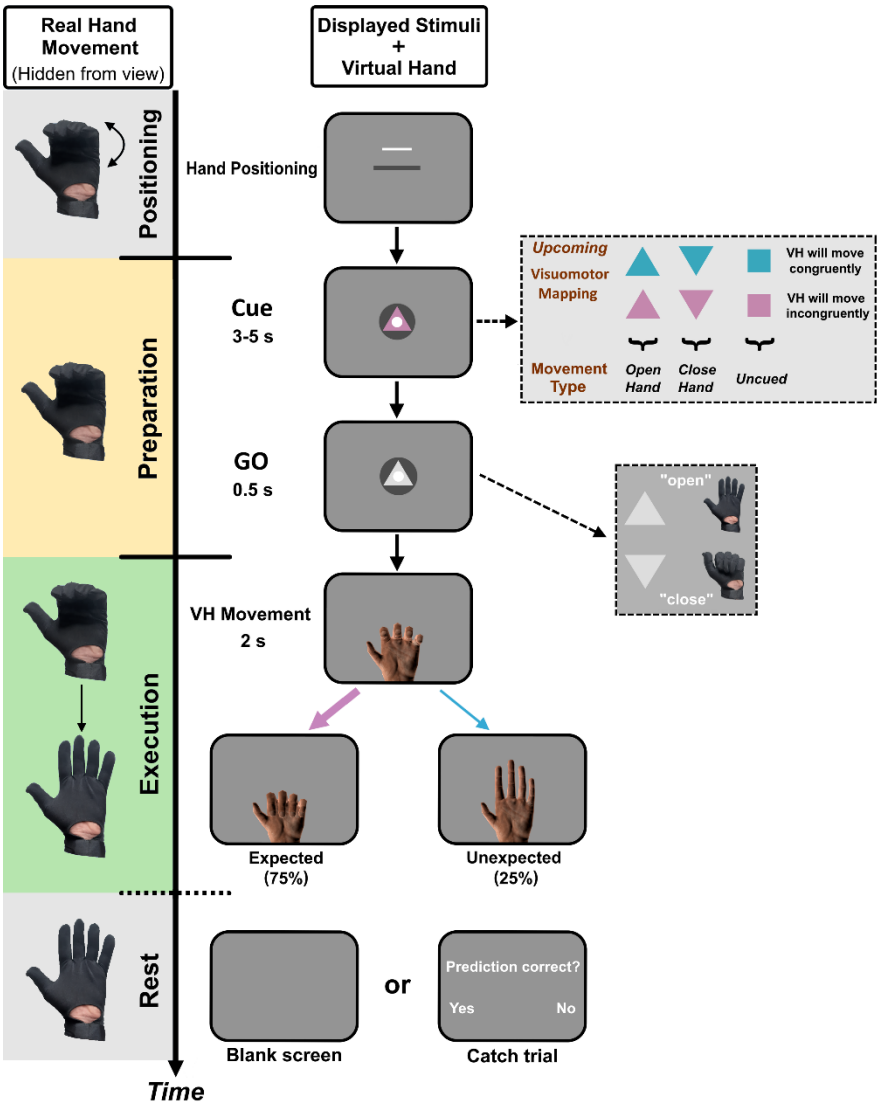

Figure 1. Experimental task design. The participants' real hand movements (left, hidden from view) were measured via a data glove and fed to a virtual hand (VH) model presented on screen (right). In each trial, participants had to execute one of two possible movements (open or close their hand) after a variable delay, starting from a neutral position (hand half-way closed). During the delay (preparation phase), we presented a visual cue that could provide two kinds of predictive information: Firstly, the cue's *shape* could specify the movement type to be executed after the delay (up- or downward triangle = open or close their hand) or leave it ambiguous (square = upcoming movement unknown). Secondly, the cue's *color* indicated the to-be-expected visuomotor congruence; i.e., whether the virtual hand would next reflect the real hand movement (here: cyan cue) or the respective opposing movement (here: pink cue). Thus, we orthogonally manipulated processes related to motor planning and visuomotor prediction, respectively. After a GO signal and appearance of the virtual hand on screen, the participants then executed the instructed hand movement while maintaining central fixation. In this particular example, the participant was cued that she would need to open her hand (triangle pointing upwards) and that the virtual hand would move incongruently during execution (pink cue), i.e., close. To ensure task engagement and attention to the cues, participants had to monitor and, in occasional catch trials, report whether the virtual hand movement matched the color-cued predictions (in 25% of trials, the virtual hand mapping was invalidly cued). In this figure, the visual cues have been enlarged for display purposes.

Materials and Methods

Participants

30 healthy, right-handed volunteers (18 female, mean age = 25.4 years, range 19-35) participated in the experiment after signing informed consent. The experiment was approved by the ethics committee of the Technische Universität Dresden and conducted in accordance with this approval.

Experimental design and procedure

Participants lay comfortably inside an MR scanner. On their left hand, they wore an MR-compatible data glove (5DT Data Glove 14 Ultra MRI), which measured each finger's flexion via sewn-in optical sensors. The glove data were fed to a photo-realistic virtual hand model, which was thus controllable in real-time by the participants' hand movements. The participants' real hand was placed outside of their view; i.e., during the entire experiment, participants only saw the virtual hand, but not their real hand. Furthermore, a response pad (2-Button Fiber Optic Response pad, Current Designs) was placed in the participant's right hand, on their lap, for them to give feedback during the experiment. Prior to the experiment, the glove was calibrated carefully, and the virtual hand model's finger flexion was adjusted to closely match the real hand posture and movement range according to the participant's perception. If necessary, the calibration was adjusted between scanning runs. Through a mirror on the head coil, participants saw a screen (1024 x 768 pixels resolution), onto which a projector displayed the virtual reality environment; i.e., the instructions, cues, and the virtual hand model. The virtual environment was created with the Blender 3D graphics software package (https://www.blender.org, Version 2.79) and its Python programming interface. The experimenter observed the virtual display (via a mirrored screen) at all times, thus ensuring task compliance.

The participants' task was to perform, in each trial, one of two types of cued hand movements (open or close, from a neutral starting position, see below) after an instructed delay. During movement, the virtual hand model moved congruently or incongruently to the participants' actual hand movements. Each trial consisted of two periods – a *preparation phase,* in which participants were cued with regards

to the upcoming movement (i.e., inducing motor preparation and visuomotor expectations, see below); followed by an *execution phase*, where participants executed the hand movements, while receiving (condition-specific, see below) visual movement feedback from the virtual hand model. See Figure 1 for an example trial.

Before each trial, participants had to bring their real, unseen hand to the neutral starting position (i.e., fingers half-way closed). For this, a small white bar was presented on screen, whose vertical position was controlled by the participants' hand posture via the data glove (i.e., the degree to which the hand was opened or closed). Participants had to align this bar with a central target (another bar, see Fig.1). If successful, the trial started; the bar was then replaced by a central white fixation dot. Participants were instructed to keep their gaze on this fixation dot throughout the entire trial; i.e., until the end of the movement phase.

After 1 second with only the fixation dot visible, a cue was presented and remained visible throughout the delay period (3 to 5 s jittered, pseudo-randomized, evenly distributed across conditions). This cue could provide participants with two kinds of predictive information: The *type of the upcoming movement* (i.e., hand opening or closing) and the *congruence of the virtual and real hand movements* during this movement (see below). These two predictions were coded by cue shape and color, respectively. Thus, in half of all trials, the cue *shape* specified the movement that the participant would need to execute next. Specifically, in 25% of trials an upward-pointing triangle informed participants that they would have to *open* their hand, while in another 25% a downward-pointing triangle informed them they would have to *close* their hand. In the remaining half of all trials, the cue was square-shaped and, thus, did not reveal the to-be-executed movement type in advance. In other words, only in half of the trials participants were able to generate a specific motor prediction about the movement they would have to execute after the delay period.

Furthermore, the *color* of the cue was predictive of whether, during the upcoming movement, the virtual hand would move congruently (i.e., reflecting the participants' real hand movement) or incongruently (performing the respective opposite movement type) with the participant's real hand

movements. Note that the movements of the virtual hand were controlled in real time by the participant in both cases, ensuring matching kinematics; In the incongruent conditions, the values fed to the hand model from the glove were simply inverted so that an opening movement would close the virtual hand, and vice versa. The cue colors (pink and cyan) were counter-balanced across participants. Following the preparatory period, a 'Go' signal (white triangle, centrally presented) appeared. Again, the pointing direction of this triangle instructed participants to open (triangle pointing up) or close (triangle pointing down) their hand. Note that, if the prior cue had not yet specified the movement type (i.e., square-shaped cue), the participants would only now know which movement they should execute. Participants were instructed to execute the movement as soon as the 'Go' signal disappeared (after 500 ms) and, instead, the virtual hand model was presented on the screen. This was done to ensure that participants did not start to move reflexively before the virtual hand was visible. Participants then had to execute the hand movement fluently, for which they had up to 2 s (if no movement was made during that period, the trial ended). Participants were instructed to make similar movements in all conditions and, after movement, to keep the hand in the final position (completely opened or closed) until the end of the trial. Then, the virtual hand disappeared again and a blank screen was shown for 2 s. As in the preparation phase, participants still had to maintain fixation on the central dot during and post execution. In a prior training session, participants were able to practice the movements and familiarize themselves with all conditions. In sum, this experimental setup resulted in a factorial design with the factors *Movement type* (Cued, Uncued) and *Visuomotor mapping* (Congruent, Incongruent). In other words, movement planning was orthogonal to expectations about visuomotor congruence.

Finally, we designed our experiment so that movements were not visually guided, as in delayed reach to target tasks, hence the visuomotor predictions pertained exclusively to the mapping of executed and observed hand movements. One implication of this was that visual movement feedback from the virtual hand was not relevant to movement execution per se. To ensure that participants nevertheless paid attention to the cues and, consequently, generated the respective visuomotor expectations

(rather than, for instance, simply waiting for the 'Go' signal), participants had to observe and, occasionally, verify if the virtual hand behavior matched the predictive visuomotor congruency color-cue (cf. Yon et al., 2018). Thus, in 25% of trials, the virtual hand moved contrary to the color-cued expectation (e.g., the virtual hand moved congruently although the cue had predicted it to move incongruently; but cues indicating the own movement type were always valid). In subsequent occasional catch trials (i.e., all "surprising" invalidly cued trials, and the same number of validly cued trials, balanced across all other conditions), a test question ("Prediction correct?") was presented centrally on the screen alongside two response options ("Yes"/"No"). Participants had to choose between those by pressing one of the response device buttons twice. If they did so within 1.5 s, feedback (i.e. "right" or "wrong") was shown for 0.5 s, otherwise they were visually instructed to respond faster the next time. To increase motivation, participants received an additional monetary reward of up to 5 € depending on the proportion of correct answers. Thus, the design for the execution phase entailed *Visuomotor cue validity* (Valid, Invalid), as another nested factor (below). This manipulation also allowed us to examine neuronal responses to expectation violation; i.e., by comparing invalidly with validly cued catch trials.

Overall, each trial lasted between 8.5 and 15 s. For each participant, we recorded 8 runs of 32 trials (6.5-8.5 mins run length) each, resulting in 256 trials and around 60 mins scanning time in total (depending on hand positioning and response times). Participants were free to rest as much as they wanted in between the individual scanning runs.

Behavioral data analysis

We tested for systematic differences in movement onset, duration, or amplitude between conditions; using the participants' hand movement data from the glove sensors (averaged over all fingers but the thumb). We segmented the continuous data to select the execution phase time window of each trial, then re-adjusted values to a zero baseline, i.e. the mean hand position during the 500 ms before presentation of the 'Go' signal. Movement onset was defined as the time point within the window where hand velocity first surpassed a threshold of more than 5 standard deviations from the baseline.

Correspondingly, the movement end was marked as the time point where hand velocity first fell again below this threshold. Movement duration and amplitude, respectively, were defined as the time difference and amplitude difference between movement onset and -end. A three-way ANOVA with the factors *Movement type* (Cued, Uncued), *Visuomotor mapping* (Congruent, Incongruent), and *Visuomotor cue validity* (Valid, Invalid), was used to test for differences between conditions. All analyses were performed using MATLAB (MathWorks).

fMRI data preprocessing and analysis

The fMRI data were recorded with a 3T scanner (MAGNETOM Prisma; Siemens) equipped with a 32-channel head coil. T2*-weighted images were acquired using an echo-planar imaging sequence (GRAPPA acceleration factor = 3, multi-band factor = 6, TR = 869 ms, TE = 38 ms, flip angle = 58°, voxel size = 2.4 mm^3, matrix size = 88 x 88, 60 interleaved slices). Depending on the length of the individual session (see above), 3000-4000 functional image volumes were recorded per participant. Additionally, for each participant we recorded a T1-weighted anatomical image (3D, voxel size = 0.9 x 0.9 x 0.9 mm^3, FOV = 272 x 272 mm, 240 slices, TR = 2.4 s, TE = 2.2 ms, flip angle = 8°) and two GRE field maps (64 layers, voxel size 2 x 2 x 2 mm^3; matrix size = 88 x 88; TR = 698 ms, TE_1 = 5.19 ms, TE_2 = 7.65 ms, flip angle 54°), after the second and sixth scanning run, respectively. All fMRI preprocessing steps and analyses were performed using MATLAB (MathWorks) and SPM12 (Wellcome Trust Centre for Neuroimaging, University College London; https://www.fil.ion.ucl.ac.uk/spm). The functional images were realigned and unwarped using voxel displacement maps calculated from the two field maps (the first map was used for runs 1 to 4, the second for runs 5 to 8). These images were then co-registered with the individual T1 image, spatially normalized to MNI space via previously estimated deformation fields, resliced to 2 mm^3 voxels, and smoothed with an 8 mm full with at half maximum Gaussian kernel. The T1 images were also normalized (but not smoothed) and averaged to create a group averaged structural image.

For each participant, a general linear model (GLM) was fitted to the preprocessed data with stick (0 s duration) regressors modeling the stimuli and movements, respectively: For the preparation phase,

four regressors were created for each combination of the two factors *Movement type* (Cued, Uncued) and *Visuomotor mapping* (Congruent, Incongruent), and set to the onset of the prediction cue. For the execution phase, twelve regressors were created for each combination of the three factors *Movement type* (Cued, Uncued), *Visuomotor mapping* (Congruent, Incongruent), and *Visuomotor cue validity* (Valid, Invalid; see above), and set to the onset of the movement execution phase including the virtual hand presentation. The six realignment parameters were added as noise regressors to each run, alongside a session constant. Two additional block regressors of no interest were included: one modeling the initial hand positioning (duration from trial start until the correct hand position was reached and the fixation dot presented), and one modeling the occasional catch trials (duration from the presentation of the question until the end of the feedback presentation). On the first (single participant) level, T-contrast images were created for each regressor vs baseline. These first-level contrast images were entered into group-level GLMs using a flexible factorial design, in which the group (second-level) T- and F-contrasts were calculated. We thereby used separate 2x2 GLMs with the aforementioned factors to evaluate those main effects and interactions during the preparation and execution phases, respectively. Note that the execution phase contained trials in which the cued visuomotor mapping (but not the cued movement type) was violated. Therefore, when comparing the effect of congruent vs incongruent cued visuomotor mappings during the execution phase, we calculated the GLM using only validly cued trials; whereas we pooled over validly and invalidly cued trials when comparing cued vs uncued movements (because the visuomotor mapping cue violation was irrelevant for this comparison). Finally, to assess potential 'surprise effects' during execution associated with invalidly cued movements, we calculated an analogous group-level GLM using first-level T-contrasts where invalidly cued catch trials in each condition were weighted with +1 and validly cued ones with -1.

Activations in the whole brain obtained from the group-level contrasts were assessed for statistical significance using a voxel-wise threshold of $p<0.05$, family-wise error corrected ($p_{FWE}<0.05$). In two cases, we had specific regions of interest defined a priori by orthogonal contrasts, and restricted the

search space accordingly, thus applying a small volume correction under the same voxel-wise threshold of $p_{FWE}<0.05$ for those results: Firstly, we expected an interaction of motor and visuomotor planning in brain regions showing a response to both individual effects. Therefore, we defined the search space for these interaction effects based on all (whole-brain) significant voxels obtained from the null conjunction of the respective main effects (see Fig. 2A,C). For completeness, we also tested for, and show the corresponding whole-brain results. Secondly, based on the previously reported overlap between action planning and execution (Lotze et al., 1999; Ames et al., 2014), we expected that brain regions involved in motor or visuomotor planning would also show condition specific effects during movement execution. Therefore, for the analysis of responses during the execution phase, we restricted the search space for effects to all significant voxels obtained from each respective analogous contrast during the preparation phase (see Fig. 2A,C). As we did not have any specific prediction about the directionality of response differences during movement execution, we used non-directional F contrasts in this case. The significant activation differences resulting from the group level contrasts are presented as renders on SPM12's template brains, or superimposed onto the group averaged normalized structural image. The displayed significant activations contain only voxels surviving the chosen threshold of $p_{FWE}<0.05$; any statistical maps displayed at $p<0.001$, uncorrected, were included solely to demonstrate that the obtained significant activations were very focal; i.e., did not spread into other, nonrelated areas. For anatomical reference, we used the SPM Anatomy toolbox (Eickhoff et al., 2005).

Results

All participants showed very good task performance; i.e., all performing >97% correct movements (on average, only one incorrect movement per recording session) and correctly identifying >93% of the catch trials (on average >98% of responses were correct). The participants' hand movements were, overall, very comparable across conditions. Importantly, there was no significant effect of visuomotor mapping (congruent vs incongruent) on movement onset, duration, or amplitude of the hand movements. Likewise, motor planning (cued vs uncued) had no significant effect on movement amplitude or duration. On average, movements in cued trials were initiated slightly earlier than in uncued trials ($F_{(2,29)} = 7.85$, p=0.006); the same was found for movements in validly > invalidly cued trials ($F_{(2,29)} = 12.12$, p<0.001). However, all of these temporal differences were smaller than 60 ms, and are therefore unlikely to have meaningfully influenced the observed highly significant BOLD signal differences. Movements in validly cued trials were on average 145 ms longer than in invalidly cued trials; $F_{(2,29)} = 19.31$, p<0.001); however, this effect was comparable across experimental factors (i.e., no significant interaction; $F_{(2,29)} = 0.02$), hence our contrasts of interest were also likely unaffected by this. In sum, the participants' behavior suggested that they engaged in motor planning and visuomotor prediction during scanning, as required; and that they executed relatively comparable hand movements across conditions.

In our fMRI analysis, our primary aim was to identify brain areas involved in both motor and visuomotor planning and prediction; i.e., we first looked for corresponding activation differences during the delay phase. Based on our first hypothesis, we contrasted the delay phase of trials in which a specific movement type could be prepared – based on the cue shape – with trials in which this was not possible (i.e., movement type cued > uncued). As expected, this contrast revealed significantly stronger (p_{FWE}<0.05) activations in the bilateral fronto-parietal cortices; with the strongest effect in the left aIPS, and furthermore in the right aIPS, the bilateral dorsal PMd, the left ventral premotor cortex (PMv), the bilateral SPL, and the bilateral lateral occipital cortices (LOC, including area V5). See Table 1 and Figure 2A for details. The converse contrast (i.e., delay phase of uncued > cued movement types) revealed

244 significantly stronger activations in the primary and secondary somatosensory cortices, the left frontal
245 pole, and in the bilateral medial temporal lobes (MTL, see Table 1 and Fig. 2B).

246 Then, we tested our second hypothesis; i.e., that fronto-parietal areas would also show increased
247 responses during the delay phase of trials in which an incongruent > congruent mapping of the virtual
248 hand movements relative to the real hand movements was cued; because here, predictions of the
249 body model would need updating. Indeed, during delay phases with cues predicting an incongruent >
250 congruent mapping, there was significantly stronger activation of premotor (the bilateral PMd, and the
251 left preSMA and PMv) and posterior parietal (the left aIPS and the bilateral SPL) areas, as well as the
252 right anterior cerebellum, see Figure 2C and Table 1. No significantly increased activations were
253 observed for the inverse contrast, cued congruent > incongruent visuomotor mapping.

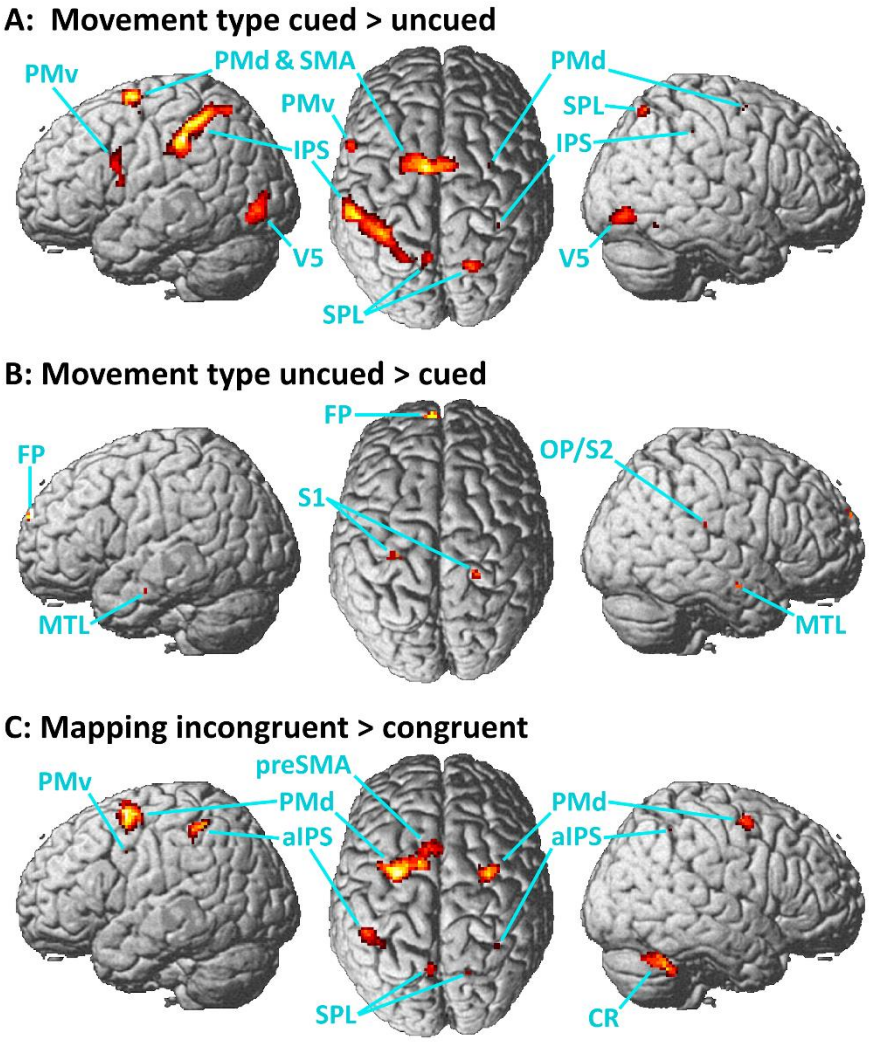

Figure 2. Brain activations related to motor planning and visuomotor prediction during the delay. (A) Renders of voxels showing significantly (p_{FWE}< 0.05) stronger activation when contrasting the delay phase of trials in which the to-be-executed movement type was cued, with trials in which this was left ambiguous (uncued). **(B)** Renders of voxels showing significantly (p_{FWE}< 0.05) stronger activation in the converse contrast. **(C)** Renders of voxels showing significantly (p_{FWE}< 0.05) stronger activation during the delay phase of trials in which the cue color predicted incongruent, compared with congruent visuomotor mapping. PMd = dorsal premotor cortex, PMv, = ventral premotor cortex, (a)IPS = (anterior) intraparietal sulcus, SPL = superior parietal lobule, FP = frontal pole, S1 = primary somatosensory cortex, S2 = secondary somatosensory cortex, OP = parietal operculum, MTL = medial temporal lobe, CR = cerebellum. See Table 1 for details.

Table 1. Brain areas showing significant main effects during the delay.

Movement type cued > uncued (CC+IC)-(CU+IU)		*MNI*			*Peak*	
Anatomical location	*Voxels*	*x*	*y*	*z*	*T*	p_{FWE}
L. Lateral occipital cortex (V5)	183	-40	-82	-4	7.66	<0.001
L. Intraparietal sulcus (aIPS & pIPS)	860	-38	-38	46	7.52	<0.001
L. Superior frontal gyrus (PMd & SMA)	546	-12	-4	66	7.35	<0.001
R. Lateral occipital cortex (V5)	130	38	-86	-10	7.30	<0.001
L. Precentral/inferior frontal gyrus (PMv)	90	-58	10	30	6.45	<0.001
R. Superior parietal lobe (BA 7A)	80	16	-66	60	6.45	<0.001
L. Superior parietal lobe (BA 7A)	50	-8	-60	54	6.02	0.002
R. Anterior intraparietal sulcus	58	34	-36	42	5.90	0.003
R. Fusiform gyrus	4	42	-58	-12	5.58	0.009
R. Middle frontal gyrus (PMd)	2	30	-4	60	5.17	0.038
Movement type uncued > cued (CU+IU)-(CC+IC)		*MNI*			*Peak*	
Anatomical location	*Voxels*	*X*	*y*	*z*	*T*	p_{FWE}
L. Pre-/postcentral gyrus (S1/M1)	52	-30	-24	48	6.18	<0.001
L. Frontal Pole	18	-6	62	28	5.72	0.005
R. Parietal operculum (OP/S2)	14	46	-30	20	5.64	0.007
R. Postcentral gyrus (S1)	11	24	-38	64	5.47	0.013
R. Medial temporal lobe (MTL)	5	56	-8	-18	5.35	0.020
L. Medial temporal lobe (MTL)	2	-54	-10	-22	5.16	0.039
L. Parietal operculum (OP/S2)	1	-40	-22	20	5.10	0.048
Mapping incongruent > congruent (IC+IU)-(CC+CU)		*MNI*			*Peak*	
Anatomical location	*Voxels*	*x*	*y*	*z*	*T*	p_{FWE}
L. Paracingulate gyrus and Superior frontal gyrus (preSMA/PMd)	584	-12	12	54	6.80	<0.001
R. Cerebellum (Lobule VI)	233	36	-56	-32	6.67	<0.001
R. Superior/middle frontal gyrus (PMd)	141	32	-2	56	6.46	<0.001
L. Anterior intraparietal sulcus	84	-48	-42	54	6.24	<0.001
L. Precuneus (BA 7A)	43	-8	-60	52	5.60	0.008
R. Superior parietal lobe (BA7A)	4	18	-66	56	5.24	0.030
R. Intraparietal sulcus	4	36	-48	50	5.22	0.032
R. Paracingulate gyrus	1	8	22	36	5.18	0.037
L. Anterior intraparietal sulcus	5	-38	-40	42	5.17	0.038
R. Lingual gyrus	2	38	-56	-16	5.17	0.039
L. Precentral gyrus (PMv)	1	-40	2	38	5.17	0.039
L. Middle frontal gyrus (PMv)	1	-38	4	36	5.11	0.046

CC = Congruent-Cued, CU = Congruent-Uncued, IC = Incongruent-Cued, IU = Incongruent-Uncued.

Next, we specifically tested for brain areas that would jointly encode both preparatory processes in our design; i.e., those related to motor planning and visuomotor mappings. Therefore, we calculated a null conjunction of the two contrasts comparing delay phases of cued > uncued movement types and incongruent > congruent cued visuomotor mappings (Fig. 2A,C), which detected voxels showing significant activation in both individual comparisons. The conjunction (Fig. 3A and Table 2) revealed that identical voxels within the left aIPS, the bilateral SPL, and the bilateral PMd were significantly activated when participants anticipated a specific movement type or an incongruent visuomotor mapping. At a more liberal threshold (p<0.001, uncorrected), such overlaps were also detected in the right IPS, the bilateral PMv, the SMA, the bilateral LOC/V5, and the bilateral cerebellum.

Having established anatomical correspondence of the main effects in the PMd, aIPS, and SPL, we evaluated our third hypothesis; i.e., that of an interaction effect of both kinds of preparatory processes in fronto-parietal areas. Thus, we tested whether, and which of the brain areas exhibiting a significant response to both experimental manipulations (cued > uncued movement type, C-U; and incongruent > congruent visuomotor mapping, I-C) would also show an interaction effect (IC-IU)-(CC-CU). In other words, we tested for a relatively stronger activation by movement planning (cued > uncued movements) under expected incongruence > congruence. Indeed, the bilateral PMd, the left aIPS, and the left SPL, as identified in the null conjunction, each showed a significant corresponding interaction effect, see Figure 3B and Table 2. The interaction was characterized by a strong relative increase in activation for delay phases in which the cue predicted a specific movement type with incongruent mapping of the virtual hand expected (see the plotted contrast estimates in Fig. 3B). No other significant effects were found in the whole brain. Even at a threshold of p<0.001, uncorrected, the interaction effects were specifically localized to the bilateral PMd, the left aIPS, and the left SPL; i.e., no other notable clusters appeared (see the inlay in Fig. 3B).

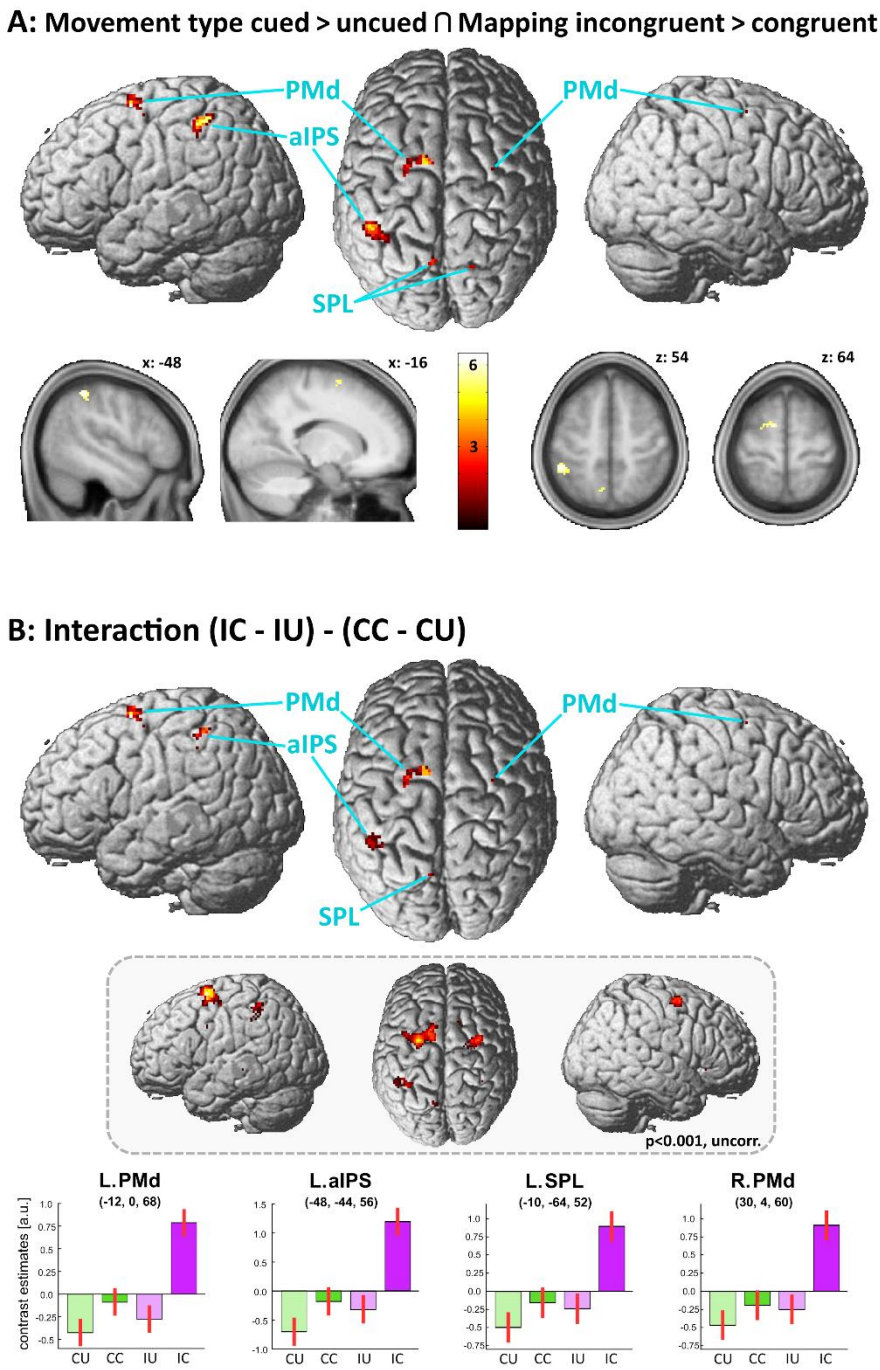

Figure 3. Shared neural substrates of motor and visuomotor preparation. (A) Renders and slice overlays of voxels with significantly (p_{FWE}< 0.05) increased activation during delays with cued > uncued movement type *and* delays with predicted incongruent > congruent visuomotor mapping; i.e., a null conjunction of the contrasts shown in Figs. 2A and 2C. **(B)** Voxels showing a significant (p_{FWE}< 0.05) interaction between those effects, within the areas identified by the null conjunction. The uncorrected whole-brain render (inlay) shows the anatomical restriction of the interaction effect to those areas. The bar plots show the mean-centered contrast estimates at each respective peak voxel with associated 90% confidence intervals. CC = Congruent-Cued, CU = Congruent-Uncued, IC = Incongruent-Cued, IU = Incongruent-Uncued. aIPS = anterior intraparietal sulcus, PMd = dorsal premotor cortex, SPL = superior parietal lobule. See Table 2 for details.

Table 2. Significant activations obtained from the null conjunction of main effects and the interaction effect.

Null conjunction (CC+IC)-(CU+IU) ∩ (IC+IU)-(CC+CU)		*MNI*			*Peak*	
Anatomical location	*Voxels*	*x*	*y*	*z*	*T*	p_{FWE}
L. Anterior intraparietal sulcus	83	-48	-42	54	6.24	<0.001
L. Superior frontal gyrus (PMd)	59	-12	2	64	6.00	<0.001
L. Precuneus/superior parietal lobe	15	-8	-60	52	5.60	0.002
R. Superior parietal lobe	4	18	-66	56	5.24	0.014
L. Precentral gyrus (PMd)	5	-26	-8	56	5.21	0.012
L. Anterior intraparietal sulcus	5	-38	-40	42	5.17	0.012
R. Middle frontal gyrus (PMd)	1	30	-4	60	5.17	0.031
Interaction (IC-IU)-(CC-CU)		*MNI*			*Peak*	
Anatomical location	*Voxels*	*x*	*y*	*z*	*T*	p_{FWE}
L. Superior frontal gyrus (PMd)	52	-12	0	68	4.42	0.004
R. Middle frontal gyrus (PMd)	1	30	-4	60	3.96	0.043
L. Superior frontal gyrus (PMd)	5	-26	-6	58	3.93	0.030
L. Anterior intraparietal sulcus	24	-48	-44	56	3.75	0.010
L. Superior parietal lobe (aIPS)	4	-38	-40	-42	3.68	0.032
L. Precuneus/superior parietal lobe	4	-10	-64	52	3.49	0.032

CC = Congruent-Cued, CU = Congruent-Uncued, IC = Incongruent-Cued, IU = Incongruent-Uncued.

Subsequently, we looked at condition-specific activation differences during the movement execution phase; which would indicate specific effects of the cues presented during the prior delay phase. Thus, we looked for activation differences within brain areas showing the corresponding condition-specific differences during the delay phase (cf. Fig. 2, see Methods for details). Firstly, we tested for differential activations during movements in trials where a specific movement type was cued in advance, compared with trials where the movement type was uncued until the 'Go' signal. The left PMd and the left aIPS showed significantly different activation levels between those trial types (F-test, see Table 3). Specifically, all regions showed increased activation levels in trials where the movement type was left uncued compared with trials where it was cued in advance (see contrast estimate plots in Fig. 4A; a post-hoc T-test on cued > uncued movements confirmed that these activation differences were significant at $p_{FWE}<0.05$). No other significantly different activations were found. At more liberal thresholds ($p<0.001$, uncorrected, see Fig. 4A inlay), further activations appeared in areas along the

IPS, the right PMd, and the SMA; thus, the topography overall closely resembled that showing significant activation differences during planning (Fig. 2A).

Analogously, we next tested for activation differences during movement execution relatable to the cued visuomotor mapping (congruent vs incongruent virtual hand movement; only validly cued trials). Here, we found significantly different activations in the bilateral PMd and left preSMA (Table 3). Activations of those regions were relatively increased during movements with incongruent compared with congruent visuomotor mapping (Fig. 4B). In a whole-brain analysis, we found further significant activation differences in the bilateral anterior insulae (L.: F = 28.75, x = -32, y = 22, z = 0; R.: F = 33.80, x = 32, y = 26, z = 0); again, showing increased activation by movement with incongruent > congruent visuomotor mapping (Ts = 5.36/5.81, p_{FWE}<0.05). There was, furthermore, a statistical trend in the right MTL (F = 27.17, p_{FWE}=0.081, x = 64, y = -8, z = -8; which reached significance in a post-hoc T-test comparing movements with congruent > incongruent visuomotor mapping, T = 5.21, p_{FWE}<0.05). At more liberal thresholds (p<0.001, uncorrected, see Fig. 4B inlay), the bilateral aIPS, among other regions, also showed activation differences. The identified significant activation differences did not overlap (i.e., no significant voxels when masking one effect with the other), and there were no significant interaction effects.

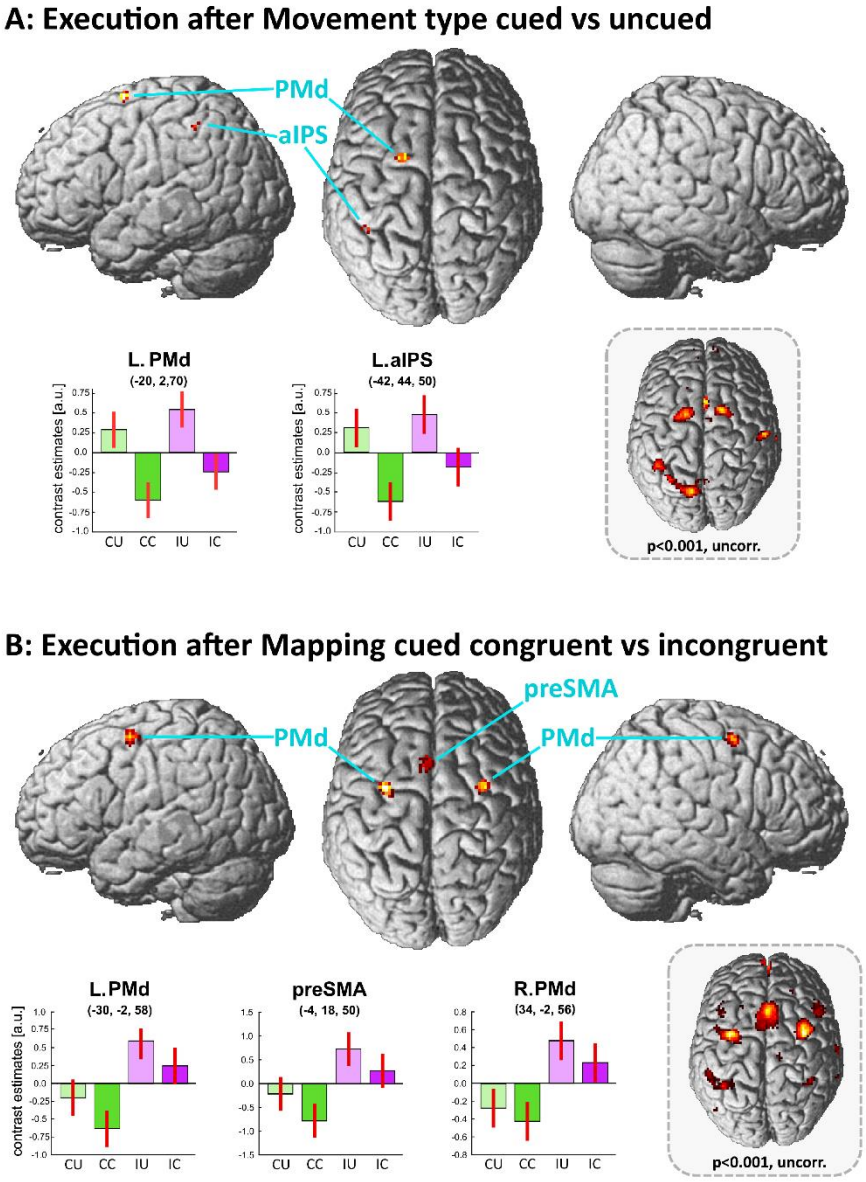

Figure 4. Brain activation differences during movement execution related to prior movement planning and visuomotor predictions. (A) Renders of voxels showing significantly (p_{FWE}< 0.05) different activations during movement execution in trials where the movement type had been cued in advance versus when it was left ambiguous (uncued). **(B)** Renders of voxels showing significantly (p_{FWE}< 0.05) different activation during movement execution in trials where congruent vs incongruent visuomotor mapping had been cued. The renders show the results of (non-directional) F-contrasts within a search space defined a priori by the respective delay phase contrast, see Methods for details. The bar plots show the mean-centered contrast estimates at each respective peak voxel with associated 90% confidence intervals. The uncorrected renders (inlays) are only included to illustrate the specificity of the identified effects within the whole brain. CC = Congruent-Cued, CU = Congruent-Uncued, IC = Incongruent-Cued, IU = Incongruent-Uncued. aIPS = anterior intraparietal sulcus, PMd = dorsal premotor cortex, preSMA = pre-supplementary motor area. See Table 3 for details.

Table 3. Brain areas showing significant activation differences during movement execution related to prior (cued) movement planning and visuomotor congruence predictions.

Execution after Movement type cued vs uncued		*MNI*			*Peak*	
Anatomical location	*Voxels*	*x*	*y*	*z*	*F*	p_{FWE}
L. Superior frontal gyrus (PMd)	61	-20	2	70	22.63	0.005
L. Superior parietal lobule (aIPS)	65	-42	-44	50	17.64	0.031
Execution after Mapping cued congruent vs incongruent		*MNI*			*Peak*	
Anatomical location	*Voxels*	*x*	*y*	*z*	*F*	p_{FWE}
L. Middle frontal gyrus (PMd)	164	-30	-2	58	27.78	<0.001
R. Middle frontal gyrus (PMd)	74	34	-2	56	27.25	0.001
L. Paracingulate gyrus (preSMA)	98	-4	18	50	20.16	0.009

305 Lastly, we tested for potential 'expectation violation' effects resulting from the manipulation of
306 visuomotor cue validity. We found significantly increased activations during movements where the
307 visuomotor mapping violated the cued expectations, compared with validly cued mappings, in a wide
308 network of brain areas that has previously been established as processing sensory surprise and general
309 error detection (Ullsperger et al., 2014; cf. Quirmbach & Limanowski, 2022); i.e., the medial frontal
310 and cingulate cortices, the left inferior frontal gyrus, the right anterior cerebellum, and in bilateral
311 posterior temporal and inferior parietal areas; further significant activations encompassed the bilateral
312 primary sensory and motor cortices, the thalamus, and the bilateral putamen. Cue violation effects
313 were detectable but not significant (p<0.001, uncorrected) in voxels of the left aIPS and SMA that
314 showed significant preparation effects. There were no significant differences in violation-related
315 activations between conditions, nor any significant interaction effects.

Discussion

Using a delayed movement task, virtual reality, and fMRI, we identified overlapping and interacting neuronal correlates of motor planning and visuomotor prediction. Firstly, delay period activity in the premotor cortex (PMd, PMv, and the SMA) and the PPC (IPS and SPL) increased during movement planning. This supports previous reports of motor planning in the PMd and PMv (Churchland et al., 2006, 2010; Crammond & Kalaska, 1994; Michaels et al., 2018; Schaffelhofer et al., 2015; Townsend et al., 2011), the PPC (Ferraina & Bianchi, 1994; Kuang et al., 2015), and the SMA (Brass & von Cramon, 2004; Gallivan et al., 2013). Secondly, the PMd, aIPS, SPL, and preSMA increased activity during the preparation for incongruent visuomotor mappings. Those were the same areas in which previous studies had shown adaptation to visuomotor incongruence (Limanowski et al., 2017; Limanowski & Friston, 2020; Nahab et al., 2011; Ogawa et al., 2006; Ohata et al., 2020). In other words, while previous work has demonstrated *reactive* adjustments of the fronto-parietal body model, our results show an *anticipatory* adjustment of the model's (visuomotor) predictions.

Thirdly, we observed an overlap of delay period responses during motor planning and visuomotor prediction in the bilateral PMd, the left aIPS, and the left SPL, and their significant interaction effect. In all four regions, the relative activation by motor planning was significantly enhanced when incongruent visuomotor mappings were expected. Thus, planning a movement associated with a nonstandard visuomotor mapping indeed required the most neuronal resources—likely, because the body model's default predictions needed to be updated. This result supports the hypothesis that the same (fronto-parietal) brain areas that plan movements also represent their sensory consequences (Kuang et al., 2015; Pilacinski et al., 2018); and suggest visuomotor prediction is an inherent component of motor planning.

Finally, brain regions involved in the preparatory processes also showed condition specific effects during movement execution. This aligns with findings that (pre)motor activity is highly similar during movement preparation and execution (Ames et al., 2014; Ariani et al., 2015, 2018; Lotze et al., 1999).

Interestingly, the left PMd and aIPS, which had increased activity during the preparation of (cued) movements showed the inverse pattern during execution; i.e., relatively decreased responses when the cued (planned) movement was executed. This suggests that without preparation, motor plans had to be created 'ad hoc' upon execution. Conversely, the bilateral PMd and the preSMA, which had shown increased responses when preparing for incongruent > congruent visuomotor mappings, showed the same effect during execution; i.e., stronger activation when moving under visuomotor incongruence. This corresponds to the typical fronto-parietal activation by movement under visuomotor incongruence (see above), and suggests that despite preparation, the nonstandard mapping still required relatively more fronto-parietal resources to control.

We observed the most prominent effects in the bilateral PMd and the left aIPS. Within the well-documented role of the PMd in motor planning and execution, it has been proposed that it is specifically involved in a process called "nonstandard sensorimotor mapping" (Wise et al., 1996); which includes accommodating spatial incongruencies between attentional, reach, and saccade targets. Our findings extend this view, because our "nonstandard" mapping solely pertained to the congruence between executed hand movements and visual feedback about the hand. Furthermore, the fact that we observed stronger PMd activation when one of the two alternative movements was prepared tentatively supports the view that, given multiple alternatives, the PMd plans one action at a time (Dekleva et al., 2018; Klaes et al., 2011; but cf. Cisek & Kalaska, 2002, 2005). Motor planning and visuomotor preparation were associated with slightly different peak activations within the PMd; in the superior and medial frontal lobes, respectively. This could imply a division of labor within the PMd, where superior parts plan movement and lateral-inferior parts anticipate the corresponding visuomotor mappings. Yet, the overlap and interaction of both preparatory responses in superior parts of the PMd suggests that these regions, specifically, are central to planning manual actions together with their anticipated sensory consequences.

Like the PMd, the left aIPS showed the strongest activation by motor planning and preparation for visuomotor incongruence, and an interaction between both. The aIPS is a key region of visuomotor

control (Desmurget et al., 1999; Grefkes & Fink, 2005) and an interface between hierarchical processing e.g. in the dorsal and ventral streams during visually guided action (Verhagen et al., 2012, 2013; cf. Fabbri et al., 2014). It constructs an upper limb representation based on visual and proprioceptive information (Ehrsson et al., 2004; Gentile et al., 2013; Limanowski & Blankenburg, 2015, 2016). Correspondingly, own body posture modulates IPS activity during motor imagery (de Lange et al., 2006) and action preparation (Zimmermann et al., 2012). Human aIPS responses are well documented during motor planning (e.g., Lindner et al., 2010) and movements under visuomotor incongruence (e.g., Brass et al., 2001; Limanowski et al., 2017). Our results now show a clear role of the left aIPS in planning movements under anticipation of their visual consequences.

Some of our effects were stronger in the left hemisphere; i.e., ipsilaterally to the executing hand. Work on visuo-proprioceptive integration has also highlighted the left PPC, independently of hand side (de Lange et al., 2006; Limanowski & Blankenburg, 2017). Likewise, the left PMd has been implied in sensorimotor integration and response selection during motor learning, independently of hand side (Hardwick et al., 2013). Moreover, the PPC, PMd, PMv, and preSMA code hand actions for the ipsilateral limb (Gallivan et al., 2013). Speculatively, body representation may be left-hemispherically biased.

Several other activations were noteworthy: The preparation for visuomotor incongruence increased activity in the right anterior cerebellum. The cerebellum, and specifically Lobule VI of the right hemisphere, increases activity when sensory feedback cannot be predicted by motor signals (Blakemore et al., 1998, 2001); and responds proportionally to the degree of mismatch between movements and their visual consequences (Leube et al., 2003; Limanowski et al., 2017; Van Kemenade et al., 2019). Our results align with the view that the cerebellum predicts sensory action consequences via forward modeling (Miall et al., 1993); specifically, we show that it updates visuomotor predictions ahead of movement execution.

Furthermore, different regions of the SMA were involved in motor vs visuomotor planning. The SMA responds to surprising action outcomes (Ulllsperger et al., 2014), including visuomotor incongruence

(e.g., Nahab et al., 2011; Ohata et al., 2020). Thereby it may register and correct visuomotor learning errors (Grafton et al., 2008; Limanowski et al., 2017). Our results extend this view; by suggesting an anticipatory visuomotor remapping in the SMA. Conversely, the preSMA responded to motor planning *per se*. This aligns with the long standing association of the (pre)SMA with motor planning and initiation (Cunnington et al., 1996; Sakai et al., 1999; Makoshi et al., 2011; Brass & von Cramon, 2002, 2004).

Motor planning also activated the PMv and visual areas around the V5. The PMv has been implied in motor planning (see above); and is key for representing the upper limb for action (Ehrsson et al., 2004; Graziano, 1999; Limanowski & Blankenburg, 2016). However, in contrast to the PMd, the PMv did not show significantly overlapping nor interacting responses during motor and visuomotor preparation. This matches findings that far more neurons in the dorsal, than in the ventral premotor cortex encode aspects of upcoming movements (Hoshi & Tanji, 2002). The V5 activation could indicate the generation of sensory expectations (cf. Aitken et al., 2020; Yon et al., 2018; Muckli et al., 2015) about visual motion from the hand. They could also have resulted from mental transformation of visual body posture (Bonda et al., 1995; Lamm et al., 2007). Conversely, delay responses in the sensorimotor cortex and the MTL increased when movements were uncued. This could be related to the maintenance of several possible movement plans in working memory; as the MTL and somatosensory cortex encode visual (Xie et al., 2023) and somatosensory working memory (Schmidt & Blankenburg, 2018), respectively. Finally, movements under incongruent > congruent mapping significantly activated the bilateral anterior insulae, in line with previous results (Grafton et al., 2008; Nahab et al., 2011; Quirmbach & Limanowski, 2022; Yomogida et al., 2010). However, the insula did not show any heightened preparatory activity during the preceding delay periods. Thus, it may detect visuomotor mismatches, rather than anticipating them.

Future work should clarify some remaining questions. Firstly, while the responses to ‘expectation violation’ included the typical mismatch detection areas (Ullsperger et al., 2014), we did not find any significant differences between conditions. This may have resulted from including only few such trials (as examining surprise was not our main aim). Furthermore, as we did not track fixation, we cannot

exclude potential eye movement influences on our results (cf. Gorbet & Sergio, 2016). Our non-spatial, non-goal directed movement task and the instructed central fixation rendered systematic eye movements useless and, thus, unlikely. Still, future studies should address both of these points.

To conclude, our results suggest that motor planning in the PMd and PPC involved predicting the accompanying mapping of visual feedback. Planning for nonstandard mappings required more neuronal resources, likely due to the need to update the default predictions of the body model.

References

Adams, R. A., Shipp, S., & Friston, K. J. (2013). Predictions not commands: active inference in the motor system. *Brain Structure and Function, 218*, 611-643.

Aitken, F., Turner, G., & Kok, P. (2020). Prior Expectations of Motion Direction Modulate Early Sensory Processing. *The Journal of Neuroscience*, *40*(33), 6389–6397. https://doi.org/10.1523/JNEUROSCI.0537-20.2020

Ames, K. C., Ryu, S. I., & Shenoy, K. V. (2014). Neural Dynamics of Reaching following Incorrect or Absent Motor Preparation. *Neuron*, *81*(2), 438–451. https://doi.org/10.1016/j.neuron.2013.11.003

Ariani, G., Wurm, M. F., & Lingnau, A. (2015). Decoding internally and externally driven movement plans. *Journal of Neuroscience, 35*(42), 14160-14171.

Ariani, G., Oosterhof, N. N., & Lingnau, A. (2018). Time-resolved decoding of planned delayed and immediate prehension movements. *Cortex*, *99*, 330–345. https://doi.org/10.1016/j.cortex.2017.12.007

Balslev, D., Nielsen, F. Å., Paulson, O. B., & Law, I. (2005). Right Temporoparietal Cortex Activation during Visuo-proprioceptive Conflict. *Cerebral Cortex*, *15*(2), 166–169. https://doi.org/10.1093/cercor/bhh119

Bernier, P.-M., Cieslak, M., & Grafton, S. T. (2012). Effector selection precedes reach planning in the dorsal parietofrontal cortex. *Journal of Neurophysiology*, *108*(1), 57–68. https://doi.org/10.1152/jn.00011.2012

Blakemore, S.-J., Frith, C. D., & Wolpert, D. M. (2001). The cerebellum is involved in predicting the sensory consequences of action: *Neuroreport*, *12*(9), 1879–1884. https://doi.org/10.1097/00001756-200107030-00023

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

Bonda, E., Petrides, M., Frey, S., & Evans, A. (1995). Neural correlates of mental transformations of the body-in-space. *Proceedings of the National Academy of Sciences*, *92*(24), 11180–11184. https://doi.org/10.1073/pnas.92.24.11180

Brass, M., Zysset, S., & von Cramon, D. Y. (2001). The Inhibition of Imitative Response Tendencies. *NeuroImage*, *14*(6), 1416–1423. https://doi.org/10.1006/nimg.2001.0944

Brass, M., & Von Cramon, D. Y. (2002). The role of the frontal cortex in task preparation. *Cerebral cortex, 12*(9), 908-914.

Brass, M., & Cramon, D. Y. V. (2004). Decomposing components of task preparation with functional magnetic resonance imaging. *Journal of cognitive neuroscience, 16*(4), 609-620.

Churchland, M. M., Afshar, A., & Shenoy, K. V. (2006). A Central Source of Movement Variability. *Neuron*, *52*(6), 1085–1096. https://doi.org/10.1016/j.neuron.2006.10.034

Churchland, M. M., Cunningham, J. P., Kaufman, M. T., Ryu, S. I., & Shenoy, K. V. (2010). Cortical Preparatory Activity: Representation of Movement or First Cog in a Dynamical Machine? *Neuron*, *68*(3), 387–400. https://doi.org/10.1016/j.neuron.2010.09.015

Cisek, P., & Kalaska, J. F. (2002). Simultaneous Encoding of Multiple Potential Reach Directions in Dorsal Premotor Cortex. *Journal of Neurophysiology*, *87*(2), 1149–1154. https://doi.org/10.1152/jn.00443.2001

Cisek, P., & Kalaska, J. F. (2005). Neural Correlates of Reaching Decisions in Dorsal Premotor Cortex: Specification of Multiple Direction Choices and Final Selection of Action. *Neuron*, *45*(5), 801–814. https://doi.org/10.1016/j.neuron.2005.01.027

Crammond, D. J., & Kalaska, J. F. (1989). Neuronal activity in primate parietal cortex area 5 varies with intended movement direction during an instructed-delay period. *Experimental Brain Research*, *76*(2). https://doi.org/10.1007/BF00247902

Crammond, D. J., & Kalaska, J. F. (2000). Prior Information in Motor and Premotor Cortex: Activity During the Delay Period and Effect on Pre-Movement Activity. *Journal of Neurophysiology*, *84*(2), 986–1005. https://doi.org/10.1152/jn.2000.84.2.986

Cunnington, R., Bradshaw, J. L., & Iansek, R. (1996). The role of the supplementary motor area in the control of voluntary movement. *Human Movement Science*, *15*(5), 627–647. https://doi.org/10.1016/0167-9457(96)00018-8

de Lange, F. P., Helmich, R. C., & Toni, I. (2006). Posture influences motor imagery: An fMRI study. *NeuroImage*, *33*(2), 609–617. https://doi.org/10.1016/j.neuroimage.2006.07.017

Dekleva, B. M., Kording, K. P., & Miller, L. E. (2018). Single reach plans in dorsal premotor cortex during a two-target task. *Nature Communications*, *9*(1), 3556. https://doi.org/10.1038/s41467-018-05959-y

Desmurget, M., Epstein, C. M., Turner, R. S., Prablanc, C., Alexander, G. E., & Grafton, S. T. (1999). Role of the posterior parietal cortex in updating reaching movements to a visual target. *Nature Neuroscience*, *2*(6), 563–567. https://doi.org/10.1038/9219

Ehrsson, H. H., Spence, C., & Passingham, R. E. (2004). That's My Hand! Activity in Premotor Cortex Reflects Feeling of Ownership of a Limb. *Science*, *305*(5685), 875–877. https://doi.org/10.1126/science.1097011

Eickhoff, S. B., Stephan, K. E., Mohlberg, H., Grefkes, C., Fink, G. R., Amunts, K., & Zilles, K. (2005). A new SPM toolbox for combining probabilistic cytoarchitectonic maps and functional imaging data. *NeuroImage*, *25*(4), 1325–1335. https://doi.org/10.1016/j.neuroimage.2004.12.034

Fabbri, S., Strnad, L., Caramazza, A., & Lingnau, A. (2014). Overlapping representations for grip type and reach direction. Neuroimage, 94, 138-146.

Fernandez-Ruiz, J., Goltz, H. C., DeSouza, J. F. X., Vilis, T., & Crawford, J. D. (2007). Human Parietal "Reach Region" Primarily Encodes Intrinsic Visual Direction, Not Extrinsic Movement Direction, in a Visual–Motor Dissociation Task. *Cerebral Cortex*, *17*(10), 2283–2292. https://doi.org/10.1093/cercor/bhl137

Ferraina, S., & Bianchi, L. (1994). Posterior parietal cortex: Functional properties of neurons in area 5 during an instructed-delay reaching task within different parts of space. *Experimental Brain Research*, *99*(1). https://doi.org/10.1007/BF00241423

Gallivan, J. P., McLean, D. A., Flanagan, J. R., & Culham, J. C. (2013). Where One Hand Meets the Other: Limb-Specific and Action-Dependent Movement Plans Decoded from Preparatory Signals in Single Human Frontoparietal Brain Areas. *The Journal of Neuroscience*, *33*(5), 1991–2008. https://doi.org/10.1523/JNEUROSCI.0541-12.2013

Gentile, G., Guterstam, A., Brozzoli, C., & Ehrsson, H. H. (2013). Disintegration of Multisensory Signals from the Real Hand Reduces Default Limb Self-Attribution: An fMRI Study. *The Journal of Neuroscience*, *33*(33), 13350–13366. https://doi.org/10.1523/JNEUROSCI.1363-13.2013

Gertz, H., & Fiehler, K. (2015). Human posterior parietal cortex encodes the movement goal in a pro-/anti-reach task. *Journal of Neurophysiology*, *114*(1), 170–183. https://doi.org/10.1152/jn.01039.2014

Gorbet, D. J., & Sergio, L. E. (2016). Don't watch where you're going: The neural correlates of decoupling eye and arm movements. *Behavioural Brain Research*, *298*, 229–240. https://doi.org/10.1016/j.bbr.2015.11.012

Grafton, S. T., Schmitt, P., Van Horn, J., & Diedrichsen, J. (2008). Neural substrates of visuomotor learning based on improved feedback control and prediction. Neuroimage, 39(3), 1383-1395.

Graziano, M. S. A. (1999). Where is my arm? The relative role of vision and proprioception in the neuronal representation of limb position. *Proceedings of the National Academy of Sciences*, *96*(18), 10418–10421. https://doi.org/10.1073/pnas.96.18.10418

Grefkes, C., & Fink, G. R. (2005). REVIEW: The functional organization of the intraparietal sulcus in humans and monkeys: Intraparietal sulcus in monkeys and humans, C. Grefkes and G. R. Fink. *Journal of Anatomy*, *207*(1), 3–17. https://doi.org/10.1111/j.1469-7580.2005.00426.x

Hardwick, R. M., Rottschy, C., Miall, R. C., & Eickhoff, S. B. (2013). A quantitative meta-analysis and review of motor learning in the human brain. *NeuroImage*, *67*, 283–297. https://doi.org/10.1016/j.neuroimage.2012.11.020

Hoshi, E., & Tanji, J. (2002). Contrasting Neuronal Activity in the Dorsal and Ventral Premotor Areas During Preparation to Reach. *Journal of Neurophysiology*, *87*(2), 1123–1128. https://doi.org/10.1152/jn.00496.2001

Kaufman, M. T., Churchland, M. M., Ryu, S. I., & Shenoy, K. V. (2014). Cortical activity in the null space: Permitting preparation without movement. *Nature Neuroscience*, *17*(3), 440–448. https://doi.org/10.1038/nn.3643

Klaes, C., Westendorff, S., Chakrabarti, S., & Gail, A. (2011). Choosing Goals, Not Rules: Deciding among Rule-Based Action Plans. *Neuron*, *70*(3), 536–548. https://doi.org/10.1016/j.neuron.2011.02.053

Kuang, S., Morel, P., & Gail, A. (2015). Planning Movements in Visual and Physical Space in Monkey Posterior Parietal Cortex. *Cerebral Cortex*, bhu312. https://doi.org/10.1093/cercor/bhu312

Lamm, C., Windischberger, C., Moser, E., & Bauer, H. (2007). The functional role of dorso-lateral premotor cortex during mental rotation. *NeuroImage*, *36*(4), 1374–1386. https://doi.org/10.1016/j.neuroimage.2007.04.012

Leube, D., Knoblich, G., Erb, M., Grodd, W., Bartels, M., & Kircher, T. T. (2003). The neural correlates of perceiving one's own movements. *NeuroImage*, *20*(4), 2084–2090. https://doi.org/10.1016/j.neuroimage.2003.07.033

Limanowski, J., & Blankenburg, F. (2015). Network activity underlying the illusory self-attribution of a dummy arm: Network Activity of Illusory Self-Attribution. *Human Brain Mapping*, *36*(6), 2284–2304. https://doi.org/10.1002/hbm.22770

Limanowski, J., & Blankenburg, F. (2016). Integration of Visual and Proprioceptive Limb Position Information in Human Posterior Parietal, Premotor, and Extrastriate Cortex. *The Journal of Neuroscience*, *36*(9), 2582–2589. https://doi.org/10.1523/JNEUROSCI.3987-15.2016

Limanowski, J., & Blankenburg, F. (2017). Posterior parietal cortex evaluates visuoproprioceptive congruence based on brief visual information. *Scientific Reports*, *7*(1), 16659. https://doi.org/10.1038/s41598-017-16848-7

Limanowski, J., & Friston, K. (2020). Attentional Modulation of Vision Versus Proprioception During Action. *Cerebral Cortex*, *30*(3), 1637–1648. https://doi.org/10.1093/cercor/bhz192

Limanowski, J., Kirilina, E., & Blankenburg, F. (2017). Neuronal correlates of continuous manual tracking under varying visual movement feedback in a virtual reality environment. *NeuroImage*, *146*, 81–89. https://doi.org/10.1016/j.neuroimage.2016.11.009

Lindner, A., Iyer, A., Kagan, I., & Andersen, R. A. (2010). Human Posterior Parietal Cortex Plans Where to Reach and What to Avoid. *The Journal of Neuroscience*, *30*(35), 11715–11725. https://doi.org/10.1523/JNEUROSCI.2849-09.2010

Lotze, M., Montoya, P., Erb, M., Hülsmann, E., Flor, H., Klose, U., Birbaumer, N., & Grodd, W. (1999). Activation of Cortical and Cerebellar Motor Areas during Executed and Imagined Hand Movements: An fMRI Study. *Journal of Cognitive Neuroscience*, *11*(5), 491–501. https://doi.org/10.1162/089892999563553

Makoshi, Z., Kroliczak, G., & Van Donkelaar, P. (2011). Human Supplementary Motor Area Contribution to Predictive Motor Planning. *Journal of Motor Behavior*, *43*(4), 303–309. https://doi.org/10.1080/00222895.2011.584085

Miall, R. C., Weir, D. J., Wolpert, D. M., & Stein, J. F. (1993). Is the Cerebellum a Smith Predictor? *Journal of Motor Behavior*, *25*(3), 203–216. https://doi.org/10.1080/00222895.1993.9942050

Michaels, J. A., Dann, B., Intveld, R. W., & Scherberger, H. (2018). Neural Dynamics of Variable Grasp-Movement Preparation in the Macaque Frontoparietal Network. *The Journal of Neuroscience*, *38*(25), 5759–5773. https://doi.org/10.1523/JNEUROSCI.2557-17.2018

Muckli, L., De Martino, F., Vizioli, L., Petro, L. S., Smith, F. W., Ugurbil, K., ... & Yacoub, E. (2015). Contextual feedback to superficial layers of V1. *Current Biology, 25*(20), 2690-2695.

Nahab, F. B., Kundu, P., Gallea, C., Kakareka, J., Pursley, R., Pohida, T., Miletta, N., Friedman, J., & Hallett, M. (2011). The Neural Processes Underlying Self-Agency. *Cerebral Cortex*, *21*(1), 48–55. https://doi.org/10.1093/cercor/bhq059

Ogawa, K., Inui, T., & Sugio, T. (2006). Separating brain regions involved in internally guided and visual feedback control of moving effectors: An event-related fMRI study. *NeuroImage*, *32*(4), 1760–1770. https://doi.org/10.1016/j.neuroimage.2006.05.012

Ohata, R., Asai, T., Kadota, H., Shigemasu, H., Ogawa, K., & Imamizu, H. (2020). Sense of Agency Beyond Sensorimotor Process: Decoding Self-Other Action Attribution in the Human Brain. *Cerebral Cortex*, *30*(7), 4076–4091. https://doi.org/10.1093/cercor/bhaa028

Parr, T., Limanowski, J., Rawji, V., & Friston, K. (2021). The computational neurology of movement under active inference. Brain, 144(6), 1799-1818.

Pilacinski, A., Wallscheid, M., & Lindner, A. (2018). Human posterior parietal and dorsal premotor cortex encode the visual properties of an upcoming action. *PLOS ONE*, *13*(10), e0198051. https://doi.org/10.1371/journal.pone.0198051

Quirmbach, F., & Limanowski, J. (2022). A Crucial Role of the Frontal Operculum in Task-Set Dependent Visuomotor Performance Monitoring. *Eneuro*, *9*(2), ENEURO.0524-21.2021. https://doi.org/10.1523/ENEURO.0524-21.2021

Sakai, K., Hikosaka, O., Miyauchi, S., Sasaki, Y., Fujimaki, N., & Pütz, B. (1999). Presupplementary Motor Area Activation during Sequence Learning Reflects Visuo-Motor Association. *The Journal of Neuroscience*, *19*(10), RC1–RC1. https://doi.org/10.1523/JNEUROSCI.19-10-j0002.1999

Schaffelhofer, S., Agudelo-Toro, A., & Scherberger, H. (2015). Decoding a Wide Range of Hand Configurations from Macaque Motor, Premotor, and Parietal Cortices. *The Journal of Neuroscience*, *35*(3), 1068–1081. https://doi.org/10.1523/JNEUROSCI.3594-14.2015

Schmidt, T. T., & Blankenburg, F. (2018). Brain regions that retain the spatial layout of tactile stimuli during working memory – A 'tactospatial sketchpad'? *NeuroImage*, *178*, 531–539. https://doi.org/10.1016/j.neuroimage.2018.05.076

Shen, L., & Alexander, G. E. (1997). Preferential Representation of Instructed Target Location Versus Limb Trajectory in Dorsal Premotor Area. *Journal of Neurophysiology*, *77*(3), 1195–1212. https://doi.org/10.1152/jn.1997.77.3.1195

Tanji, J., & Evarts, E. V. (1976). Anticipatory activity of motor cortex neurons in relation to direction of an intended movement. *Journal of Neurophysiology*, *39*(5), 1062–1068. https://doi.org/10.1152/jn.1976.39.5.1062

Toni, I., Schluter, N. D., Josephs, O., Friston, K., & Passingham, R. E. (1999). Signal-, Set- and Movement-related Activity in the Human Brain: An Event-related fMRI Study. *Cerebral Cortex*, *9*(1), 35–49. https://doi.org/10.1093/cercor/9.1.35

Townsend, B. R., Subasi, E., & Scherberger, H. (2011). Grasp Movement Decoding from Premotor and Parietal Cortex. *The Journal of Neuroscience*, *31*(40), 14386–14398. https://doi.org/10.1523/JNEUROSCI.2451-11.2011

Ullsperger, M., Danielmeier, C., & Jocham, G. (2014). Neurophysiology of Performance Monitoring and Adaptive Behavior. *Physiological Reviews*, *94*(1), 35–79. https://doi.org/10.1152/physrev.00041.2012

Van Kemenade, B. M., Arikan, B. E., Kircher, T., & Straube, B. (2017). The angular gyrus is a supramodal comparator area in action–outcome monitoring. *Brain Structure and Function*, *222*(8), 3691–3703. https://doi.org/10.1007/s00429-017-1428-9

Van Kemenade, B. M., Arikan, B. E., Podranski, K., Steinsträter, O., Kircher, T., & Straube, B. (2019). Distinct Roles for the Cerebellum, Angular Gyrus, and Middle Temporal Gyrus in Action–Feedback Monitoring. *Cerebral Cortex*, *29*(4), 1520–1531. https://doi.org/10.1093/cercor/bhy048

Verhagen, L., Dijkerman, H. C., Medendorp, W. P., & Toni, I. (2012). Cortical Dynamics of Sensorimotor Integration during Grasp Planning. *The Journal of Neuroscience*, *32*(13), 4508–4519. https://doi.org/10.1523/JNEUROSCI.5451-11.2012

Verhagen, L., Dijkerman, H. C., Medendorp, W. P., & Toni, I. (2013). Hierarchical Organization of Parietofrontal Circuits during Goal-Directed Action. *The Journal of Neuroscience*, *33*(15), 6492–6503. https://doi.org/10.1523/JNEUROSCI.3928-12.2013

Wise, S. P., di Pellegrino, G., & Boussaoud, D. (1996). The premotor corte× and nonstandard sensorimotor mapping. *Canadian Journal of Physiology and Pharmacology*, *74*(4), 469–482. https://doi.org/10.1139/cjpp-74-4-469

Wolpert, D. M., & Kawato, M. (1998). Multiple paired forward and inverse models for motor control. *Neural networks, 11*(7-8), 1317-1329.

Xie, W., Chapeton, J. I., Bhasin, S., Zawora, C., Wittig, J. H., Inati, S. K., Zhang, W., & Zaghloul, K. A. (2023). The medial temporal lobe supports the quality of visual short-term memory representation. *Nature Human Behaviour*, *7*(4), 627–641. https://doi.org/10.1038/s41562-023-01529-5

Yomogida, Y., Sugiura, M., Sassa, Y., Wakusawa, K., Sekiguchi, A., Fukushima, A., Takeuchi, H., Horie, K., Sato, S., & Kawashima, R. (2010). The neural basis of agency: An fMRI study. *NeuroImage*, *50*(1), 198–207. https://doi.org/10.1016/j.neuroimage.2009.12.054

Yon, D., Gilbert, S. J., de Lange, F. P., & Press, C. (2018). Action sharpens sensory representations of expected outcomes. *Nature Communications*, *9*(1), 4288. https://doi.org/10.1038/s41467-018-06752-7

Zimmermann, M., Meulenbroek, R. G. J., & de Lange, F. P. (2012). Motor Planning Is Facilitated by Adopting an Action's Goal Posture: An fMRI Study. *Cerebral Cortex*, *22*(1), 122–131. https://doi.org/10.1093/cercor/bhr098