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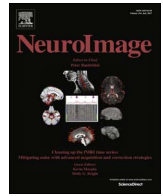
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Representational precision in visual cortex reveals outcome encoding and reward modulation during action preparation

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ABSTRACT

According to ideomotor theory, goal-directed action involves the active perceptual anticipation of actions and their associated effects. We used multivariate analysis of fMRI data to test if preparation of an action promotes precision in the perceptual representation of the action. In addition, we tested how reward magnitude modulates this effect. Finally, we examined how expectation and uncertainty impact neural precision in the motor cortex. In line with our predictions, preparation of a hand or face action increased the precision of neural activation patterns in the extrastriate body area (EBA) and fusiform face area (FFA), respectively. The size of this effect of anticipation predicted individuals' efficiency at performing the prepared action. In addition, increasing reward magnitude increased the precision of perceptual representations in both EBA and FFA although this effect was limited to the group of participants that learned to associate face actions with high reward. Surprisingly, examination of representations in the hand motor cortex and face motor cortex yielded effects in the opposite direction. Our findings demonstrate that the precision of representations in visual and motor areas provides an important neural signature of the sensorimotor representations involved in goal-directed action.

Introduction

Sensorimotor interactions with the environment provide organisms with information about the consequences of their actions. Such information is critical for developing outcome-directed, goal-driven behavior. According to ideomotor theory (Harleß, 1861; James, 1890; Lotze, 1852), goal-directed action involves the anticipation of the action's perceptual consequences. This prediction has been confirmed in numerous behavioral studies (Elsner and Hommel, 2001; Shin et al., 2010; Waszak et al., 2012). There is also a growing literature beginning to reveal how perceptual and affective features of intended outcomes are processed in the brain (Daw and O'Doherty, 2014; Elsner et al., 2002; Jessup and O'Doherty, 2014; Kühn et al., 2011, 2010; McNamee et al., 2013; Melcher et al., 2008; Valentin et al., 2007). The present

study focused on the nature of the perceptual representations in visual cortex. Kühn et al. (2011) have shown that category-specific perceptual regions code the outcome of intended actions, whereby the preparation of hand versus face actions activates category-specific areas that have traditionally been associated with the perception of face stimuli (FFA) and body parts (including hands; EBA) (Downing et al., 2001), respectively.

Here we address the question whether perceptual representations of anticipated action outcomes in EBA and FFA show an additional signature of enhanced neural encoding. We used multivariate analysis of fMRI data to examine the consistency, or precision, of patterns of activity in the EBA and FFA across trials. Our choice of analysis is motivated by previous research demonstrating that representational precision has important functional implications in neural processing

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(Churchland et al., 2011, 2010, 2006; Schurger et al., 2015, 2010; Warren et al., 2016, 2015). Furthermore, the multivariate measure of precision we use does not depend on a uniform increase of brain activity in all voxels of a given brain area. Thus, as earlier work using multivariate techniques has shown, it allows us to characterize changes in neural processing even in cases when the change is not detectable using univariate approaches (Etzel et al., 2016; Xue et al., 2010).

Neurophysiological studies in animals have shown that measures of representational precision are a signature of information encoding in many parts of the cortex (Churchland et al., 2011, 2010, 2006). M.M. Churchland and colleagues demonstrated that the variability of firing rates of neurons in the premotor cortex decreases as a decision is formed Churchland et al. (2006), and this type of variability decreases across the whole brain at onset of any type of stimulus (2010). In humans, Schurger and colleagues demonstrated that neural consistency is a hallmark of conscious perception, both between (2010) and within (2015) trials. Here we attempt to demonstrate for the first time that modulations in representational consistency can also be region specific. More specifically, we examined representational consistency to determine whether anticipation of a hand or face action increases the precision of representations in the associated perceptual area, i.e. the EBA or FFA (see Fig. 1).

The second goal of the present study was to test whether the neural consistency of sensorimotor codes during action preparation is modulated by the reward value of a particular outcome (see Fig. 1C, middle and right panel). Recent work suggests that reward motivation impacts the signal-to-noise ratio of representations of task sets in frontoparietal brain regions (Etzel et al., 2016). This finding is consistent with longstanding theoretical accounts (Botvinick and Braver, 2015; Kruglanski et al., 2002; Simon, 1967). Based on recent behavioral evidence, we predict that neural representations of perceptual outcomes should be more precise specifically when the related actions are associated with reward (Allman et al., 2010; Eder and Dignath, 2015; Muhle-Karbe and Krebs, 2012) (Fig. 1C middle panel). Alternatively, potential reward might have a more general neuromodulatory effect related to motivational significance, whereby increases in catecholergic-mediated gain improve the signal-to-noise ratio of neural processing across the brain (Aston-Jones and Cohen, 2005; Nieuwenhuis et al., 2005; Servan-Schreiber et al., 1990). Such an effect may provide a general boost in stability or precision (Warren et al., 2016, 2015) (Fig. 1C right panel). Interestingly, Warren, Holroyd, (2011, 2012) argued that brain-wide increases in signal-to-noise ratio should have a differential impact across brain regions, such that brain regions more engaged in signal processing should have a greater change in activity than less engaged regions. Thus, region-specific effects of reward on neural precision do not necessarily discount a role of neuromodulators in this effect.

Finally, we also investigated the precision of motor representations of planned actions. In our task, participants were cued as to whether they would be required to make either a hand or face action three to six seconds later. Critically, during this cue period, participants did not know exactly which hand action (left or right button press) or face action (“smile” or “kiss”) they would make, only whether they would use their hands or their face. We expected that representations of potential actions would be strongly instantiated in motor cortex relative to the same action representations when they were not anticipated. However, the impact that such a change should have on representational precision is not clear. One possibility is that strong representation of both actions simultaneously should promote consistency between trials. Another possibility is that the uncertainty concerning which action would ultimately be cued would provoke greater variability, reducing precision. Notably, A.K. Churchland et al. (2011) showed that firing rates of neurons in the primate lateral intraparietal area are more variable when monkeys are cued with four versus two potential decision outcomes. Furthermore, within trials, firing rates in this area get more variable as a perceptual decision is

formed. They hold that neural variability is a natural outcome of the stochastic accumulation and integration of evidence (Miller and Wang, 2006). Though our participants do not make protracted decisions based on noisy evidence, they do consider multiple decision outcomes. Also potentially relevant is that information encoded in perceptual areas versus motor areas involves different levels of abstraction (Wurm and Lingnau, 2015). For example, representations in the FFA and surrounding regions are distributed and overlapping (Haxby et al., 2001). In contrast, representation of left versus right hand responses will be lateralized and, consequently, discrete. Warren et al. (2016) demonstrated that the effect of neural gain on representational precision varies according to pattern overlap. Thus, if action relevance were to increase representational precision through modulation of gain either locally (Destexhe et al., 2003), or across the brain (Warren et al., 2016), we would expect precision to increase more in perceptual regions than motor regions. However, a change in precision in motor cortex opposite to that observed in perceptual areas would work against an interpretation of these effects as being mediated by brain-wide changes in signal-to-noise ratio.

To foreshadow our somewhat counterintuitive results, we found that whereas considering motor actions increased representational precision in perceptual areas associated with the action (EBA versus FFA), it decreased representational precision in associated motor areas (hand motor cortex versus face motor cortex). Furthermore, with some caveats, we found evidence that increasing reward magnitude increases representational precision in perceptual areas, but decreases representational precision in motor areas, apparently enhancing the effect of action-area congruence.

Material and methods

Participants

Thirty-one healthy right-handed volunteers (age 19–27 years; 8 males) with normal vision and no dental braces participated in the study. The experiment was approved by the medical ethics committee of the Leiden University Medical Center, and all participants gave written informed consent. The experiment took approximately two hours, and participants were paid 25 euros. One participant was excluded from analyses because of a hardware failure during data collection. Participants were randomly assigned to one of the two action-reward mapping groups: Half of the participants (n=15) learned to associate face actions with high reward and hand actions with low reward. The other half of the participant (n=15) learned to associate hand actions with high reward and face actions with low reward.

Experimental paradigm and design

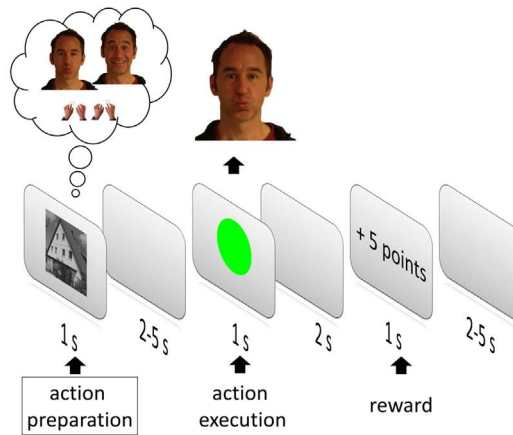
Fig. 1B shows the trial structure of the task. Each trial started with a cue presented for 1 s showing the picture of a house. There were two possible house pictures, each cuing a different condition. The house cues instructed participants to either respond with a face or hand action as soon as the subsequent target was presented (see Fig. 1A). Note that the brain response to this action-preparation phase is the focus of the analyses described in this paper. After a blank screen of jittered duration between 2 and 5 s, the target specifying the to-be-performed action was presented for 1 s. The three possible actions in the context of a hand cue were a button press with the left index finger, a button press with the right index finger, or no action. The three possible actions in the context of a face cue were uncompressing the lips into a broad smile and raising both eyebrows (“smile”), compressing the lips into a kiss and lowering the eyebrows (“kiss”), or no action (Fig. 1A). Participants were instructed to respond quickly, but due to the difficulty of measuring the timing of face actions, we followed Kühn et al. (2011), and measured reaction times for the hand actions only. Following target presentation, there was a two-second blank screen,

A Experimental design:

	Cue		
Target		\$\$\$*	\$*
		—	—

*) Action-Reward mapping is counterbalanced

B Trial set-up:



C Predicted effects (during action preparation):

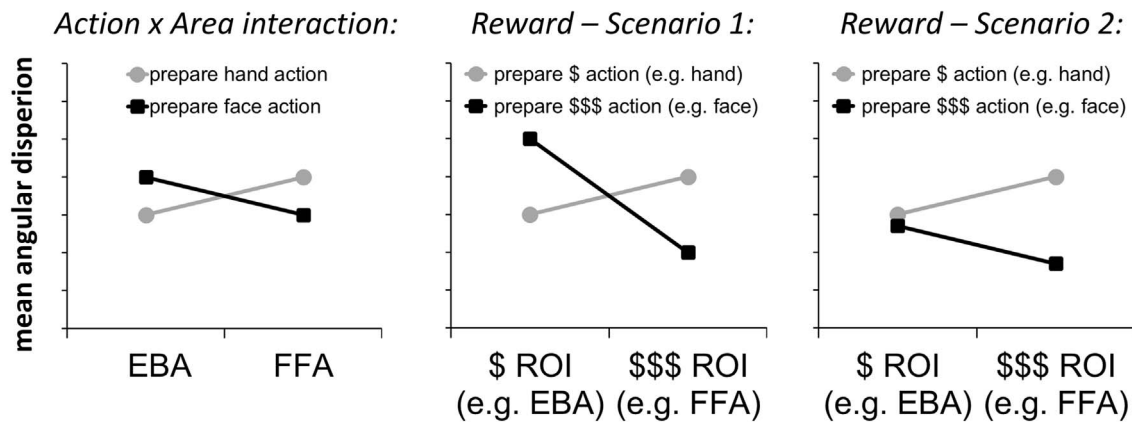


Fig. 1. **A.** Example of the study design. Participants were instructed to prepare a face or hand action (pictures show actions carried out by second author). These action modalities were associated with either low reward (\$) or high reward (\$\$\$). The action-reward mapping was counterbalanced across participants, so half of the participants learned to associate hand actions with more reward than face actions. The other half of the participants learned to associate face actions with more reward than hand actions (shown here in the example). Details about the cue-action and action-reward contingencies used in different blocks are presented in Table 1. **B.** Example of a trial presenting a cue that instructs participants to prepare a face action. To brain response to this action-preparation phase is the target of the analyses in this paper. The subsequent target indicated the action to be executed which was followed by feedback stimulus indicating the monetary reward gained. **C.** Illustration of predicted effects for the precision of neural perceptual representations in the EBA and FFA during the action preparation phase of a trial. We analyzed across-trial angular dispersion, a measure of the consistency of neural patterns across all trials. Note that less dispersion reflects more precision. We predicted that an action x ROI interaction (left panel) would reveal increased precision for congruent versus incongruent action-area combinations (i.e., more precision when preparing a face action in the visual cortex area involved in face processing (FFA), compared to the area involved in body parts processing (EBA); and vice versa for the preparation of a hand action). On top of this action x ROI interaction effect, reward might alter the consistency of the neural information in two ways: When preparing a high-reward action (e.g. a face action), 1) it might lead to a selectively more stable representation in the reward-related ROI only (e.g. FFA) (middle panel), or 2) it might lead to a more stable representation irrespective of the area (right panel).

and then a feedback screen. Participants received feedback indicating the reward (in points) for the current trial along with a running total (in points and euros). Between trials a blank screen was presented for a jittered duration of 2–5 s.

This task was a modified version of the paradigm utilized by Kühn et al. (2011). Extending the original study, we introduced reward feedback following action execution. This addition allowed us to associate different action modalities (hand vs. face) with different reward magnitudes. Participants were instructed that 4 eurocents would be paid for every point earned. Because we could not record the accuracy or timing of face actions, we always provided the reward feedback associated with the correct action. In order to encourage correct performance, we told participants that we recorded their actions via video, and that points gained for incorrect actions would be subtracted at the end of the experiment. However, all participants

received the same total amount at the end of the study (25 euros).

Outside the scanner, participants first practiced the task for 12 trials. Task instructions were provided on a computer screen and we presented a picture of the face actions required, accompanied by experimenter demonstration if necessary. The experimenter confirmed that participants understood the correct face actions before they were put in the scanner. Inside the scanner, we presented three separate blocks (in counterbalanced order), each containing 60 trials. Each block started with a repetition of task instructions and gave participants the mapping of house cue to action modality (hand or face). Each of the three blocks used two unique house cues with mapping counterbalanced across participants. Participants were not informed about the action-reward contingency. There were two groups of participants: Half of participants were randomly assigned to the condition in which face actions were associated with high reward, whereas the other half of

Table 1
Overview of different blocks used in experiment.

Action-reward group	Modality of action to be prepared Cue	Reward value	Action to be performed Cue + Target	Frequency + reward Cue + Target						Average reward Cue		
				block A		block B		block C		block A	block B	block C
\$\$\$ action = hand (N=15)	prepare face action	\$ (low)	"kiss"	40%	+1	25%	+2	40%	+1	+0.8	+4	+4
			"smile"	40%	+1	25%	+2	40%	+1			
			no action	20%	+0	50%	+6	20%	+16			
	prepare hand action	\$\$\$ (high)	left hand	40%	+5	25%	+6	40%	+3	+4	+4	+4
			right hand	40%	+5	25%	+6	40%	+3			
			no action	20%	+0	50%	+2	20%	+8			
\$\$\$ action = face (N=15)	prepare face action	\$\$\$ (high)	"kiss"	40%	+5	25%	+6	40%	+3	+4	+4	+4
			"smile"	40%	+5	25%	+6	40%	+3			
			no action	20%	+0	50%	+2	20%	+8			
	prepare hand action	\$ (low)	left hand	40%	+1	25%	+2	40%	+1	+0.8	+4	+4
			right hand	40%	+1	25%	+2	40%	+1			
			no action	20%	+0	50%	+6	20%	+16			

participants learned to associate hand actions with high reward. This action-reward mapping did not change across blocks and was included as a between-participants factor in the analyses reported (see Analytic Approach below).

As Table 1 shows, each of the three block used a different combination of action-reward contingency and proportion of no-action trials. This manipulation allowed us to explore the effect of incentive salience on perceptual and motor representations of expected actions. Across blocks, we varied the probability of reward, the magnitude of reward for each type of response, and the proportion of trials requiring no action. For example, in blocks A and C, no-action responses were infrequent (20%), and in block A no-action received no reward (0 points), whereas in block C no-action received high reward (12 points on average). This manipulation was exploratory – it was difficult to predict beforehand what would be the optimal combination of incentive salience and proportion of no-action trials. All analyses reported included block as a factor, and significant interactions with block are reported when significant. However, because the factor block never interacted significantly with any of the primary effects of interest, we do not discuss the effects of incentive salience and proportion of no-action trials in this paper.

After the experimental session, we employed a localizer scan in order to also report (as a supplementary analysis) the original univariate analyses on individual-specific voxels of interest in the EBA and FFA reported by Kühn et al. (2011). During the localizer task, participants passively viewed pictures of hands and faces. We used eight different male and female, black-and-white photographs as well as eight different black-and-white photographs of hands. All images were adjusted to assure the same average luminance. In a separate block, all house cue images were presented in random order so that we would be able to localize cue-specific brain activity (analysis not reported). House cue trials were modeled as nuisance regressors in the event-related design used for the localizer scan. All images were presented for 1 s and followed an inter-trial interval of jittered duration between 2 and 5 s.

In order to be able to explore the relationship between our primary neural outcomes and individual differences in reward sensitivity and impulsivity, participants filled out the following questionnaires (translated into Dutch) outside the scanner: the Behavioral Inhibition System/Behavioral Activation System (BIS/BAS) Scales (Franken et al., 2005), the Barratt Impulsivity Scale (BIS-11) (Patton et al., 1995), the Dickman Impulsivity Inventory (DII) (Claes et al., 2000), and the Substance Use Risk Profile Scale (SURPS) (Woicik et al., 2009). Note that impulsivity is a multidimensional construct, so we chose a

selection of scales that earlier have been related to individual differences in goal-directed behavior (Colzato et al., 2010; Hogarth et al., 2012; Wiers et al., 2010). Using a $p < .01$ threshold, we found that area-specific representational precision was associated with lower scores on the Behavioral Inhibition Scale, $r(28) = 0.482$, $p = 0.007$ (cf. Gentsch et al., 2015). However this result did not survive Bonferroni or FDR correction, and is therefore not discussed further. Correlations between trait measures and the effects of reward were not observed.

MRI data acquisition

Scanning was performed with a standard whole-head coil on a 3-T Philips Achieva MRI system (Best, The Netherlands) at the Leiden University Medical Center. During the task, three runs of 337 T2*-weighted whole-brain EPIs were acquired, including 2 dummy scans preceding each run to allow for equilibration of T1 saturation effects (TR = 2.2 s; TE = 30 ms, flip angle = 80°, 38 transverse slices, $2.75 \times 2.75 \times 2.75$ mm +10% interslice gap). The same sequence was run to acquire 360 EPIs for the localizer scan. Stimuli were projected onto a screen that was viewed through a mirror at the head end of the scanner. After the functional runs, a high-resolution EPI scan (TR = 2.2 ms; TE = 30 ms, flip angle = 80°, 84 transverse slices, $1.964 \times 1.964 \times 2$ mm) was acquired for registration purposes. This was followed by a 3D T1-weighted scan (TR = 9.8 ms; TE = 4.6 ms, flip angle = 8°, 140 slices, $1.166 \times 1.166 \times 1.2$ mm, FOV = $224.000 \times 177.333 \times 168.000$).

fMRI preprocessing

Preprocessing of the fMRI data was carried out using FEAT (fMRI Expert Analysis Tool) Version 5.98, part of FSL (FMRIB's Software Library, www.fmrib.ox.ac.uk/fsl) (Smith et al., 2004). The following preprocessing was applied: motion correction, slice-timing correction, brain extraction, spatial smoothing using a Gaussian kernel of FWHM 6.0 mm, grand-mean intensity normalization of the entire 4D dataset by a single multiplicative factor, and high-pass temporal filtering (Gaussian-weighted least-squares straight line fitting, with sigma = 60.0 s). Functional scans were registered to high-resolution EPI images, which were registered to T1 images, which were registered to the standard space of the MNI (Montreal Neurological Institute) with 2 mm resolution using FLIRT. The preprocessed data were individually inspected and this confirmed that individual runs were not affected by excessive motion and were registered correctly.

Regions of interests

The main analyses reported are restricted to predefined regions of interest (ROI) for the visual and motor cortex. For the FFA, EBA, and PPA we used bilateral masks that were based on category-selective group-level parcels resulting from group-constrained participant-specific analyses on an independent dataset of 30 participants (Julian et al., 2012). The Face Motor Cortex (FMC) and Hand Motor Cortex (HMC) were based on the contrast of the univariate event-related analysis in the current study that compared face action execution versus hand action execution, and vice versa, across participants and runs. In order to keep the size of these motor ROIs roughly comparable to the size of the perceptual ROIs, these masks were obtained by using a threshold at an uncorrected z -value of 5.5 ($p < 0.001$).

Multivariate analyses

In order to analyze the consistency of neural patterns over trials, we extracted the peak of the BOLD response (approximately six seconds after cue onset) from the preprocessed fMRI data. Analyses were run separately for each individual, run, and ROI. To quantify consistency, we treated each pattern of activity as a vector running from a zero origin to a point in multidimensional, representational space with coordinates defined by each value in the vector. This method yielded vectors with 4968 coordinates in the EBA, 1749 coordinates in the FFA, 1067 coordinates in the face motor cortex, 570 coordinates in bilateral hand motor cortex, 281 coordinates in left hand motor cortex, and 289 in right hand motor cortex. Thus, the representational space for each brain area had as many dimensions as there were voxels in the ROI. By treating activity patterns as vectors we were able to calculate the angular dispersion of all vector pairs within a given condition. Angular dispersion is a measure specifically optimized to characterize variability in space/direction (Fisher et al., 1987) and thus suited for conceptualizing pattern consistency as precision: similar patterns of activity will tend to cluster together in the representational space, like the arrows of an expert archer on a target. In principle, a similar type of analysis can be performed using correlation analysis, as in seminal work by Haxby et al. (2001), and as extensively developed by Kriegeskorte et al. (2008a), (b). However, the directionality inherent in the calculation of angular dispersion aligns well with the concept of precision, as it applies to the current work.

Angular dispersion was calculated across trials as described by Schurger et al. (2015), quantified as the length of the normalized vector sum, divided by the number of vectors summed, and presented as one minus this value so that lower values indicate lower angular dispersion, and greater precision. The raw activation values after preprocessing were z -scored across each voxel's time series separately before calculating angular dispersion. For each condition, angular dispersion was calculated between each pair of trials, for all possible pairs within the same condition and then averaged across all possible combinations to get the overall measure of angular dispersion. Calculating angular dispersion one pair of vectors at a time has the benefit that the inverse of angular dispersion between two vectors yields values that can be interpreted in terms of the relative direction of the two vectors.

Angular dispersion was calculated separately for conditions in which participants prepared face actions and hand actions. This allowed us to test the hypotheses depicted in Fig. 1C. We predicted that neural representations in the FFA would be more consistent (i.e. involve lower angular dispersion) when participants prepare a face action relative to a hand action, and vice versa for the EBA. We also predicted that reward would modulate these representations. Note that the approach presented here deviates from typical multivariate pattern analysis classification approaches that focus on determining if a pattern of activation in a given area is predictive of the manipulation in question. Such analyses would yield a summary statistic about the discrimination success of an area (also associated with methodological confounds on its own, cf. Todd et al., 2013), not a direct measure of

consistency or precision.

Finally, because there is a nonlinear relationship between signal-to-noise ratio and angular dispersion that can potentially confound the results when overall differences in mean activation are observed, we implemented a mean-matching procedure on the vector norms, as recently applied by Schurger et al. (2015) and described in detail by M.M. Churchland et al. (2010). To specify, our mean-matching procedure selected a subset of trials (pattern vectors) for which the mean vector norm was matched across both conditions. To do so, we only selected trials with the greatest common distribution of vector norms present for both conditions. Thus, each bin of this common distribution had a height equal to the smallest value for that same bin across both conditions. We then matched the distribution of the vector norms of the two conditions to this common distribution using a random selection of trials. The mean angular dispersion for both conditions was then calculated for this subset of trials. This procedure was repeated 5000 times with different random seeds, resulting in 5000 angular dispersion values per condition. The reported angular dispersion values represent the mean of these values.

Univariate analyses

Standard univariate analyses were run on the preprocessed fMRI data (see above) using FEAT (fMRI Expert Analysis Tool) Version 5.98. In native space, the fMRI time series were analyzed using an event-related approach in the context of the general linear model with local autocorrelation correction. The model was high-pass-filtered (Gaussian-weighted least-squares straight-line fitting, with $\sigma = 60.0$ s). The task model included the following regressors: two for the cue period (face action preparation and hand action preparation), and three for the target + reward period (face action execution, hand action execution, and no action required). This allowed us to probe for brain activity related to executing a particular action modality (face or hand) and receiving reward feedback (low or high), and brain activity related to preparing a particular action (face or hand) and anticipating (low or high) reward. All regressors used square-wave functions to represent the duration of the cue (1 s) or the time from target presentation to reward presentation (4 s), respectively. These regressors were convolved with a canonical HRF. Temporal derivatives of these regressors were also included. For the localizer task, a model using the same parameters included two regressors for the face and hand pictures and six regressors for the different house cues.

Relevant contrasts for the experimental task were combined across the three runs on a participant-by-participant basis using fixed-effects analyses. These second-level contrast images were then submitted to third-level mixed-effects group analyses. One group analysis was run to create masks of the hand and face motor cortex (see the section Regions of interest below) based on the effects of action modality (hand versus face actions) during the execution phase. Another group analysis probed brain activity in reward-related brain areas and analyzed the effect of reward during the anticipation and receipt of reward. This analysis modeled the interaction between reward value and action-reward mapping (see Results).

The supplementary analysis described in the Results section used univariate analyses based on the same ROIs that are used for the multivariate analyses. In addition, we also report an individual peak analysis that used the approach described by Kühn et al. (2011). For this analysis, peak voxels in the bilateral EBA and FFA for the Face > baseline and Hand > baseline contrasts in the localizer scan were manually identified first. Individual mean COPE values (arbitrary units) of the preparation contrasts of the experimental runs of spheres of 6 mm radius centered at these peak voxels were then extracted using featquery. These values were subsequently submitted to a repeated-measures ANOVA in SPSS. For some participants, no peak voxels could reliably be identified from the localizer scan, so the analyses reported only include 23 participants.

Statistical inference and thresholding

All analyses reported are restricted to the ROIs described above, except for the analyses that focused on brain activation during reward anticipation and feedback (see Results). Those analyses were restricted to key regions of the neural reward circuit (Haber and Knutson, 2010) by using small anatomically defined volumes of interest for the basal ganglia, frontal medial cortex, and amygdala (all based on FLS's Harvard-Oxford Structural Atlases). These analyses report small volume corrected (SVC) clusters in these areas with a height threshold of $z > 2.3$ and a cluster probability of $p < 0.05$, based on Gaussian random field theory (Worsley, 2001).

Analytic approach of ROI analyses

The analyses focused on the quality of neural representations in perceptual and motor regions during the preparation of an action with the face or hand, before the exact action was known (see Fig. 1). For each participant, either the face or the hand action was associated with higher levels of monetary reward (see also Table 1). To facilitate the interpretation of this counterbalanced design, we labeled the particular actions and ROIs in terms of whether they were associated with high or low reward (compare left versus middle panel in Fig. 1C). That is, for half of the participants, the EBA (the "hand area") and the hand action were labeled as a "low reward" ROI (\$ROI) and "low reward" action (\$action) respectively, whereas the FFA (the "face area") and the face action were labeled as a "high reward" ROI (\$\$\$ROI) and "high reward" action (\$\$\$action) respectively. For the other half of the participants this mapping was reversed. The same approach was used for the hand motor cortex (HMC) and the face motor cortex (FMC).

Unless otherwise noted, ANOVAs run on the perceptual and motor regions associated with the variable of interest included the within-participant factors ROI (low versus high reward), action (low versus high reward), and block (A, B and C), and the between-participant factor action-reward mapping (face or hand as high reward action). Greenhouse-Geisser correction was applied when assumptions of sphericity were violated. In these cases, we report corrected p-values and uncorrected degrees of freedom. All significant effects ($p < 0.05$) are reported.

The predicted effects are depicted in Fig. 1C. First, independent of reward, a ROI-specific action coding (Fig. 1C, left panel) should be evident by a significant interaction between ROI and action in the specified direction. Second, reward scenario 1 would result in a steeper slope (Fig. 1C, middle panel) for high reward action than low reward action, which could be calculated by the following contrast ($\$ROI^{\$action} - \$\$ROI^{\$action}$) - ($\$ROI^{\$action} - \$\$ROI^{\$action}$). Note however, that this comparison would involve comparing neural encoding between distinct brain areas, which would be confounded by anatomical differences between regions and potential variations in properties of the magnetic field across space. Thus, we cannot validly test for this outcome with our design, and we do not report this test in the results section.¹ Third, reward scenario 2 (Fig. 1C, right panel), would be evident by a significant main effect of action in the specified direction. Given these key predictions, the comparisons of particular cell means within the design are not informative, so we do not provide tests on simple effects. In the case that effects interacted with the between-participants factor action-reward mapping, we report follow-up ANOVAs that describe the particular effect for both groups separately.

¹ These considerations mean that we can only interpret changes within a particular ROI and accordingly, we report but do not interpret effects showing that one brain area (e.g. FFA) shows different values than another brain area (e.g. EBA).

Results

Behavioral results

Behavioral analyses confirmed that participants performed the task correctly. This analysis was limited to hand responses because face responses were not recorded. Participants responded with the correct hand response following the hand target signaling a left or right button press on average 96.6% (range: 87.3–100%) of the trials, and they rarely did not respond to these trials (mean: 0.5%; range: 0.0–6.3%). They correctly withheld a hand response after a hand target signaling no action during 99.5% (range: 96.3–100%) of the trials. Finally, hand responses to face action targets were rare (mean: 2.1%; range: 0.0–11.1%). These effects did not differ between the \$\$\$ action = face group and the \$\$\$ action = hand group ($ps > 0.178$).

Neural precision in visual cortex reveals perceptual outcome encoding

In our first analysis, we investigated the precision of neural representations in category-specific visual areas FFA and EBA during the preparation of face versus hand actions. Action preparation is hypothesized to activate the perceptual representations of associated outcomes (Kühn et al., 2011). An ANOVA on the angular dispersion values in the EBA and FFA regions of interest revealed an interaction between the action modality and ROI, in the hypothesized direction, $F(1,28) = 9.8$, $p = 0.004$, $MSE = 0.0001$. As Fig. 2 shows, neural patterns were more consistent (lower angular dispersion) during the cued action that was congruent with the ROI in comparison to the cued action that was incongruent with the ROI (compare Fig. 1C, left panel). This effect was not significantly different between the two action-reward mapping groups, as the three-way interaction between action, ROI and group was not significant, $F(1,28) = 0.9$, $p = 0.343$, $MSE = 0.0001$.

Neural precision in visual cortex reveals reward modulation

In the same ANOVA, a main effect of action also revealed that the preparation of actions associated with high (versus low) reward led to reduced angular dispersion (increased precision) collapsed across ROI, $F(1,28) = 5.3$, $p = 0.029$, $MSE = 0.0003$. However, an interaction between action and action-reward mapping revealed that the effect of reward was not equally strong in both groups, $F(1,28) = 9.9$, $p = 0.004$, $MSE = 0.0005$. Subsequent ANOVAs run for both participant groups separately, revealed that the effect of reward was significant in the group that had learned to associate face actions with high reward (Fig. 2, middle panel; bottom), $F(1,14) = 21.7$, $p < 0.001$, $MSE = 0.0005$, but was absent in the group of participants that had learned to associate hand action with high reward (Fig. 2, middle panel; top), $F(1,14) = 0.4$, $p = 0.547$, $MSE = 0.0004$.

Individual differences in outcome-related neural precision predict speed of action execution

In order to provide converging evidence for the idea that the observed precision in perceptual representation of action outcomes might reflect a functional mechanism that is directly related to the efficiency of action execution, we correlated the individual size of the interaction effect between action and ROI on mean angular dispersion with the participants' mean speed of responding during the action execution phase. The individual size of the action \times ROI interaction was calculated by subtracting both congruent ROI-action combinations from both incongruent ROI-action combinations, as follows: ($\$ROI^{\$action} + \$\$ROI^{\$action}$) - ($\$ROI^{\$action} + \$\$ROI^{\$action}$). Although the effect should not be different for the type of action executed, we could only include the speed of hand actions in this analysis because face action onset was not recorded. Initial screening of the behavioral data

Across-trial angular dispersion in visual regions

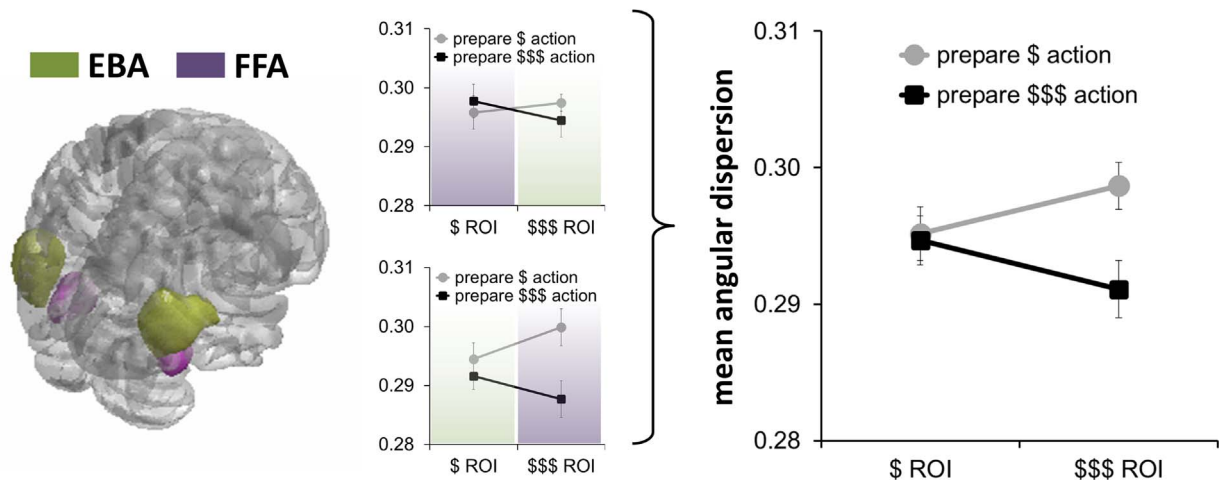


Fig. 2. Across-trial angular dispersion in the EBA and FFA regions of interest hypothesized to represent perceptual codes of hand and face actions respectively. The middle panel shows the data from the two action-reward mapping group: Top graph: \$\$\$ action = hand, bottom graph: \$\$\$ action = face. Error bars indicate standard error of the mean.

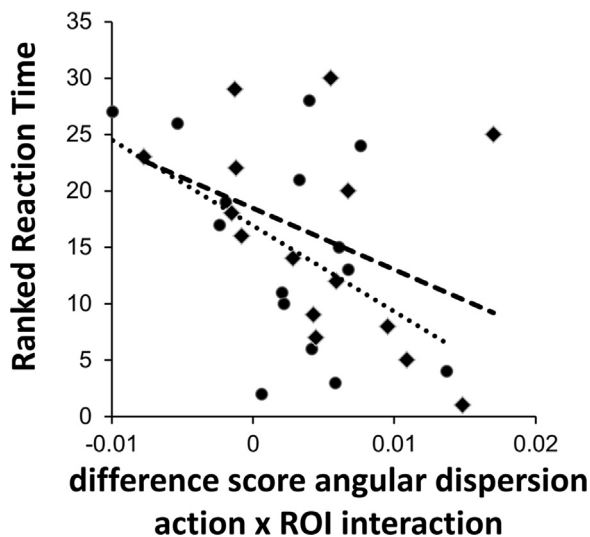


Fig. 3. Area-specific modulation of angular dispersion in the EBA and FFA during action preparation predicts subsequent speeded hand responses after target presentation (correlation across participants). Marker type indicates the action-reward mapping group: diamonds: \$\$\$ action = hand, circles: \$ action = hand.

revealed an extreme outlier (more than 3 interquartile ranges above the 75th percentile) in the mean correct reaction time, so we used a rank-transformed measure in our correlation analysis which confirmed our hypothesis (see Fig. 3): ROI-specific representational precision predicted speeded action during the execution phase, $r(28) = -0.425$, $p = 0.019$; Spearman's $\rho(28) = -0.403$, $p = 0.027$.

Neural precision in motor cortex reveals outcome and reward effects opposite to effects in visual areas

We also examined how action representations in the motor cortex differed when actions coded by a given, congruent ROI were being prepared, versus when actions coded by the alternative, incongruent, ROI were being prepared. As Fig. 4 (right panel) shows, the pattern of results observed in motor cortex (hand motor cortex and face motor cortex) was opposite to the results observed in perceptual ROIs (compare Fig. 2, right panel). An ANOVA confirmed that there was an interaction between ROI and action prepared, $F(1,28) = 4.8$,

$p = 0.037$, $MSE = 0.0006$. A similarly opposite main effect of reward was observed, $F(1,28) = 15.6$, $p < 0.001$, $MSE = 0.0005$. This effect again depended on action-reward mapping, $F(1,28) = 9.9$, $p = 0.004$, $MSE = 0.0005$, and was only significant in the group that associated face actions with high reward, $F(1,14) = 21.7$, $p < 0.001$, $MSE = 0.0005$ versus $F(1,14) = 0.4$, $p = 0.547$, $MSE = 0.0004$. In addition, we observed a significant interaction between action-reward mapping and ROI, $F(1,28) = 39.5$, $p < 0.001$, $MSE = 0.0005$, suggesting overall increased angular dispersion (less precision) in the hand motor cortex than in the face motor cortex (see Fig. 4, middle panel; green versus purple shaded conditions). However, as explained earlier we cannot interpret this effect as it compares different brain regions.

We speculated that the reduced precision in motor cortex observed when planning potential motor actions could be due to the participant vacillating between the two responses, in such a way as that the fluctuation between non-overlapping motor representations between trials drove precision down. As Fig. 5 shows, this account would predict an opposite pattern of results if angular dispersion is analyzed separately for the left and right hand motor cortex. The results of these analyses are shown in Figs. 4B and 4C. Surprisingly, precision was still reduced for the congruent ROI when participants considered hand actions. An ANOVA with the extra factor laterality (left versus right HMC) revealed effects in the same direction as the earlier bilateral analysis: We observed an interaction between ROI and action prepared, $F(1,28) = 4.5$, $p = 0.044$, $MSE = 0.0013$, and a main effect of reward, $F(1,28) = 11.7$, $p = 0.002$, $MSE = 0.0011$, that interacted with action-reward mapping, $F(1,28) = 9.7$, $p = 0.004$, $MSE = 0.0011$. Again, we also observed effects of brain region, including a significant interaction between action-reward mapping and ROI, $F(1,28) = 90.5$, $p < 0.001$, $MSE = 0.0011$, a significant interaction between laterality, action-reward mapping and ROI, $F(1,28) = 6.4$, $p = 0.017$, $MSE = 0.0003$, and a main effect of laterality, $F(1,28) = 6.4$, $p = 0.017$, $MSE = 0.0003$. These latter effects are not interpreted for reasons explained earlier.

Neural precision in cue-related areas increased by reward

In a final analysis on angular dispersion, we asked whether neural encoding of the cue that signaled the face and hand action was modulated by the reward value of the associated actions. We presented pictures of houses as action-modality cues, therefore we could analyze the precision of neural representations in the parahippocampal place area (PPA), an area typically activated by images of scenes, including

Across-trial angular dispersion in motor regions

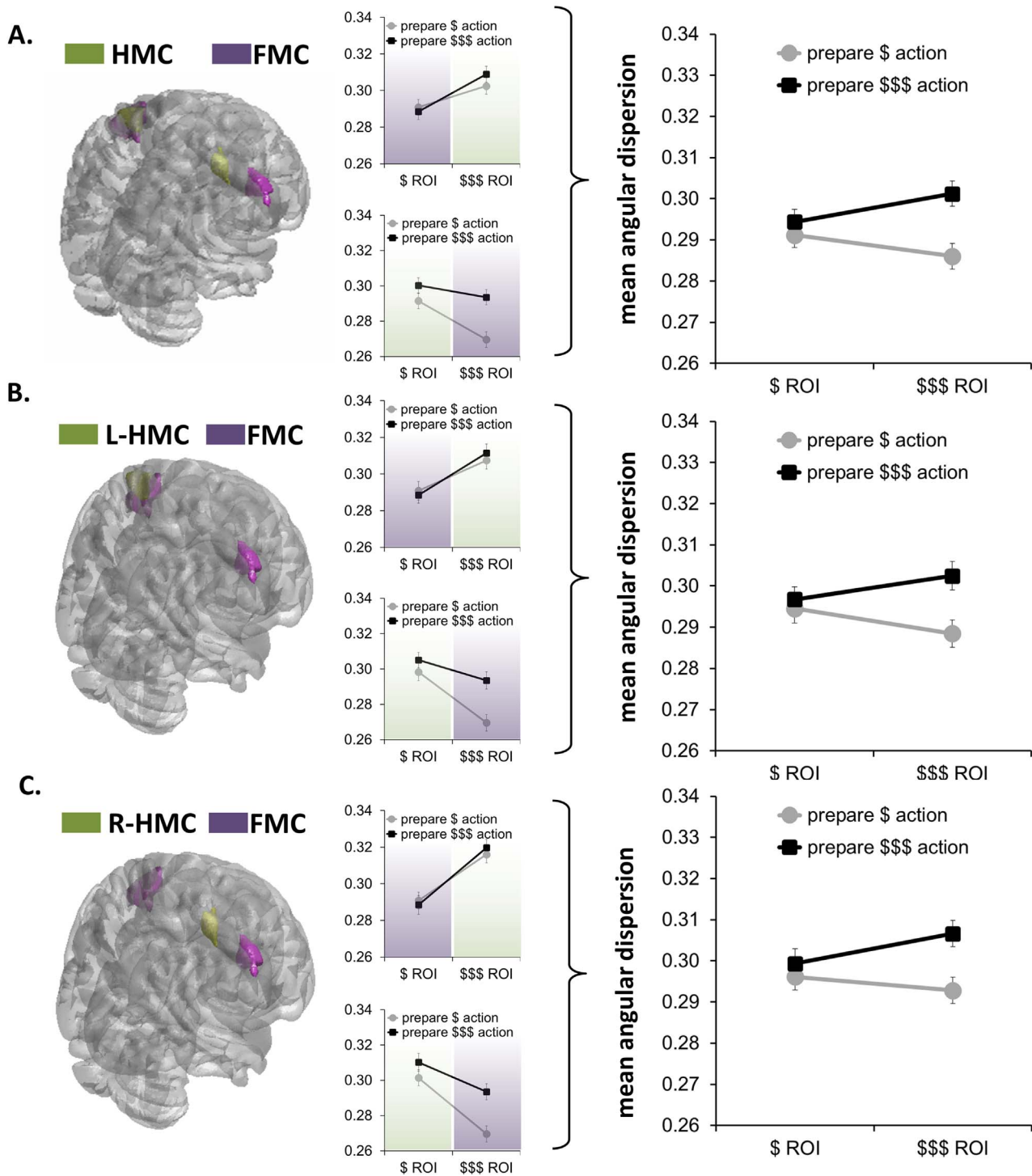
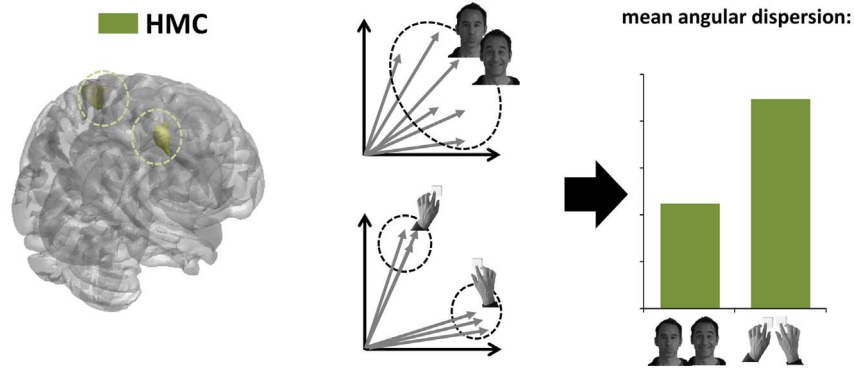


Fig. 4. Across-trial angular dispersion in the HMC and FMC regions of interest hypothesized to represent motor codes of hand and face actions respectively. The middle panel shows the data from the two action-reward mapping group: top graph: \$\$\$ action = hand, bottom graph: \$\$\$ action = face. Error bars indicate standard error of the mean. **A** Shows results from the analyses that compared bilateral HMC and FMC regions. **B and C** show results from the analyses that compare bilateral FMC with left HMC and right HMC, respectively.

houses (Epstein and Kanwisher, 1998). In addition, because the different blocks were associated with different levels of incentive saliency, the block factor might interact with reward. Fig. 6 presents the results of this analyses. An ANOVA with the factors action, block, and action-reward mapping, revealed a main effect of prepared action, $F(1,28) = 4.2, p = 0.049, MSE = 0.0002$, showing decreased angular

dispersion when participants prepare a high reward compared with a low reward action. The effect did not depend on the action-reward mapping used, $F(1,28) = 0.6, p = 0.427, MSE = 0.0002$. In addition, there was a trend for a main effect of block, $F(2,56) = 3.3, p = 0.061, MSE = 0.0003$, but no interaction with action, $F(2,56) = 0.6, p = 0.524, MSE = 0.0001$.

A. Predicted angular dispersion in bilateral Hand Motor Cortex



B. Predicted angular dispersion in unilateral (right) Hand Motor Cortex

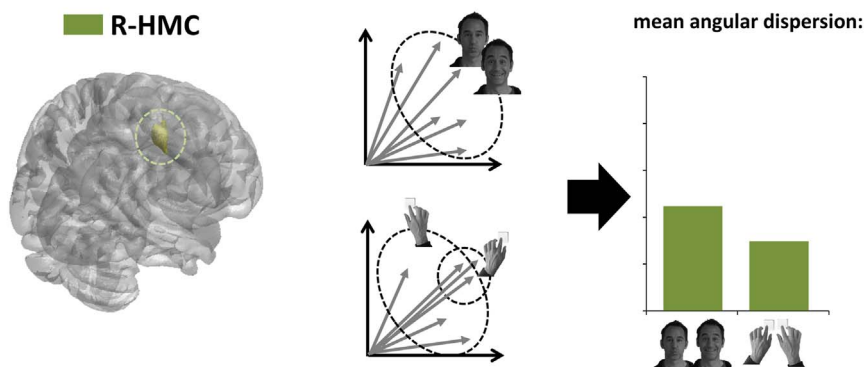


Fig. 5. A. Illustration of the possible interpretation of the increased angular dispersion observed in the action-congruent ROIs for the hand motor cortex. The middle graph shows how different trials are projected in multidimensional space (two-dimensional for display purposes), separately for preparing a face (top) and a hand (bottom) action. Given the topological organization of the motor cortex, preparing a hand action will involve non-overlapping (lateralized) representations in bilateral hand motor cortex. When participants prepare a hand action, they might vacillate between the representations of the two hands in different trials. This will result in increased angular dispersion in bilateral hand motor cortex relative to face action trials that produce noisy representations. **B.** Example of expected results in unilateral hand motor cortex to test the vacillation account. Angular dispersion is expected to be reduced when preparing hand actions (versus face actions) because it will lead to reduced angular dispersion in those trials that involve the representation of the contralateral hand. Combining these trials with the noisy representations during the trials that involve the ipsilateral hand results in a mean decrease in angular dispersion.

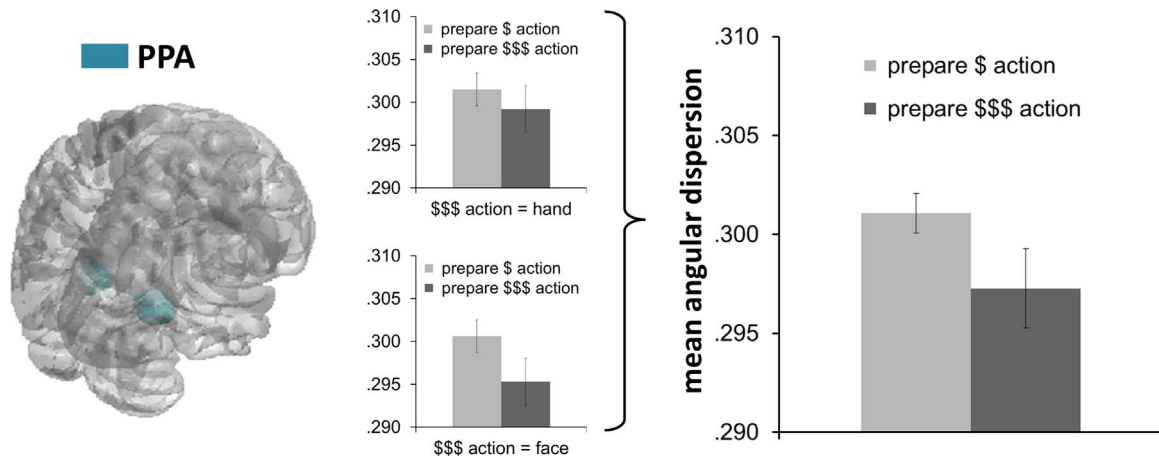


Fig. 6. Across-trial angular dispersion in the PPA region of interest hypothesized to represent cue-related processing. The middle panel shows the data from the two action-reward mapping group: top graph: \$\$\$ action = hand, bottom graph: \$\$\$ action = face. Error bars indicate standard error of the mean.

Brain activation during reward anticipation and feedback confirmed stronger reward effects for face-action group

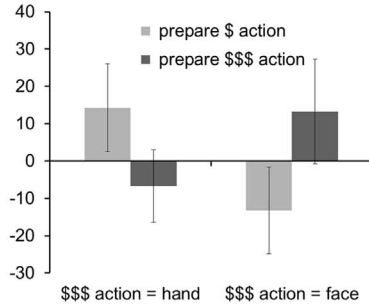
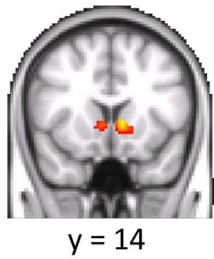
The results from the MVPA analyses on the visual ROIs described above revealed that reward increased neural precision, but that this effect was only significant for the group of participants that associated face actions with higher reward than hand actions. This suggests that

our reward manipulation was only successful for half of the participants. If this is true, the typical profile of brain activation observed in the context of the anticipation and receipt of reward might also be exclusively observed in the participants that showed an effect on the visual ROIs. In order to provide converging evidence for this hypothesis, we ran a conventional univariate event-related analysis and compared the BOLD response during the anticipation and feedback

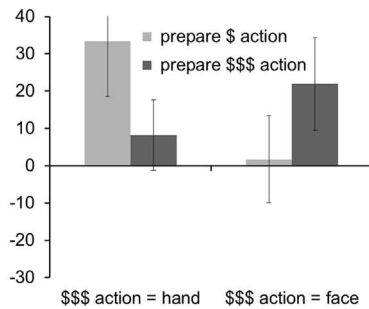
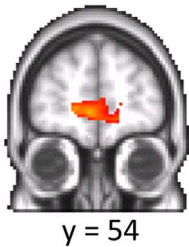
A. BOLD during reward anticipation:

B. BOLD during reward receipt:

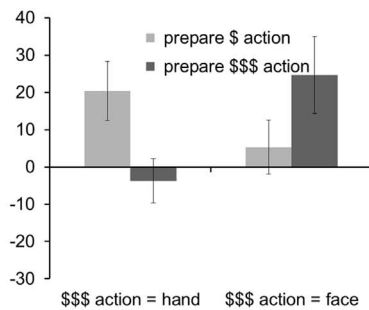
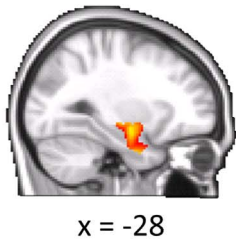
ventral striatum:



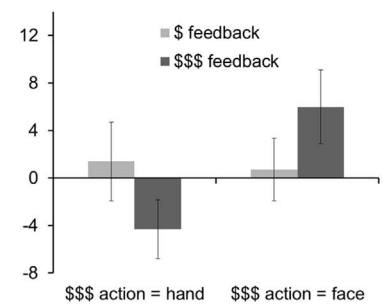
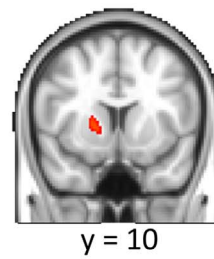
ventromedial PFC:



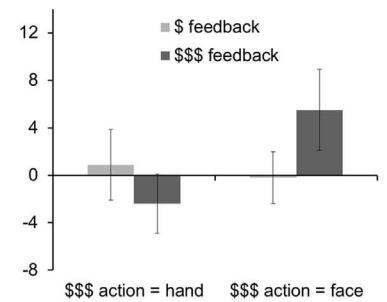
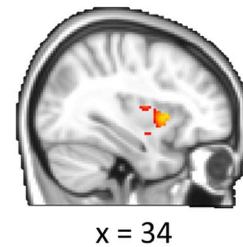
amygdala:



pallidum:



putamen:



amygdala:

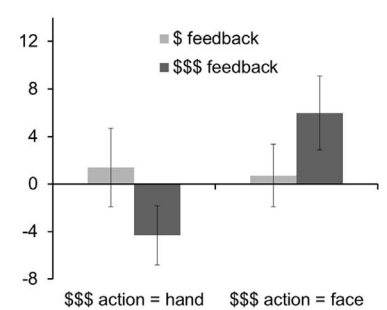
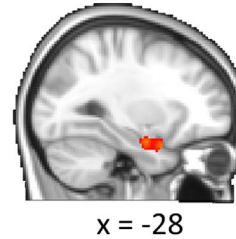


Fig. 7. BOLD response during the reward anticipation phase (A) and the reward receipt phase (B) for the contrast that shows increased reward-related brain activation for the \$\$\$ action = face group than for the \$\$\$ action = hand group. Figure shows small volume corrected (SVC) clusters in the basal ganglia, frontal medial cortex, and amygdala surviving a height threshold of $z > 2.3$ and a cluster probability of $p < 0.05$. Bar graphs show extracted brain activity for illustrative purposes. Error bars indicate standard error of the mean.

phase of the experiment. An initial analysis that collapsed over both groups confirmed that reward anticipation and reward receipt did not yield brain activation in the neural reward circuit at our statistical threshold. Therefore, in a subsequent analysis we contrasted the reward effect for the group of participants that associated face actions with high reward to the reward effect for the group of participants that associated hand actions with high reward and we probed brain activation to the following contrasts: $(\text{$$$ action} > \text{\$ action})^{\text{$$$ action} = \text{face}} > (\text{$$$ action} > \text{\$ action})^{\text{$$$ action} = \text{hand}}$ for the preparation phase, and $(\text{$$$ feedback} > \text{\$ feedback})^{\text{$$$ action} = \text{face}} > (\text{$$$ feedback} > \text{\$ feedback})^{\text{$$$ action} = \text{hand}}$ for the feedback phase.

Analyses using these contrasts focused on the reward network of the brain (Haber and Knutson, 2010). As shown in Fig. 7A, during the anticipation of reward, the interaction contrast $(\text{$$$ action} > \text{\$ action})^{\text{$$$ action} = \text{face}} > (\text{$$$ action} > \text{\$ action})^{\text{$$$ action} = \text{hand}}$ revealed brain activation in the ventral striatum ($x = -8, y = 14, z = 2$ mm; $p = 0.014$; extent = 189 voxels; and $x = 6, y = 16, z = 0$ mm; $p = 0.042$; extent = 82 voxels), ventromedial PFC ($x = 4, y = 58, z = -4$ mm; $p = 0.002$; extent = 683 voxels) and amygdala ($x = -22, y = -2, z = -32$ mm; $p = 0.008$; extent = 745 voxels; and $x = 18, y = -14, z = -8$ mm; $p = 0.015$; extent = 519 voxels). However, the full cross-over

interaction profile observed in the brain activity extracted from these ROIs suggests that during anticipation these regions were not selectively increased for the group of participants that associated face actions with high reward. Instead, the pattern of results are more consistent with the interpretation of a main effect of action modality. In other words, the anticipation of face actions (outer bars in Fig. 7A) leads to increased brain activation in comparison to the anticipation of hand actions (inner bars in Fig. 7A). Given that the face actions were more difficult to perform than the hand actions, it is possible that the brain ROIs revealed by this analysis reflect increased motivation or effort associated with the preparation of those actions.

Analyses that focused on the interaction contrast $(\text{$$$ feedback} > \text{\$ feedback})^{\text{$$$ action} = \text{face}} > (\text{$$$ feedback} > \text{\$ feedback})^{\text{$$$ action} = \text{hand}}$ during the receipt of reward are more consistent with our proposal that reward had a stronger impact in the face-high-reward group. As is shown in Fig. 7B, during the receipt of high reward, activity in the pallidum and putamen ($x = 34, y = 12, z = 4$ mm; $p = 0.043$; extent = 267 voxels; and $x = 16, y = -10, z = 4$ mm; $p = 0.047$; extent = 257 voxels) and amygdala ($x = 30, y = 6, z = -22$ mm; $p = 0.010$; extent = 719 voxels; and $x = -14, y = -2, z = -10$ mm; $p = 0.026$; extent = 364 voxels) was high in the face-high-reward group, whereas it was low for

Table 2

Supplementary univariate analyses on visual and motor areas (brain activation in arbitrary units).

Action-reward group	Cued action	Motor areas (EBA/FFA)		Sensory areas (EBA/FFA)		Peak sensory areas (EBA/FFA)	
		\$ area	\$\$\$ area	\$ area	\$\$\$ area	\$ area	\$\$\$ area
\$\$\$ action = hand	prepare \$ action	79.0	24.6	63.8	65.4	149.8	142.3
	prepare \$\$ action	71.5	28.7	28.8	41.3	111.8	104.8
\$\$\$ action = face	prepare \$ action	49.6	62.3	43.0	20.6	111.8	112.7
	prepare \$\$ action	55.8	115.7	80.2	34.9	141.8	145.0

the hand-high-reward group. A reversal of this effect was not observed during the low reward conditions. Taken together, this pattern of results suggest that the neural effects of reward receipt were stronger for the face-high-reward group.

Supplementary analyses: univariate analyses on visual and motor areas

For reasons of completeness, we also briefly report the conventional univariate analysis on brain activity in visual and motor ROIs during action preparation, as originally reported by Kühn et al. (2011) in a similar paradigm without a reward manipulation. See Table 2 for details.

The analysis on the mean BOLD response in the motor ROIs revealed an action \times ROI interaction, $F(1,28) = 4.3$, $p = 0.047$, $MSE = 4501.0$, replicating findings reported earlier by Kühn et al. (2011). There was also a general increase in BOLD activation when the action was associated with high reward, $F(1,28) = 4.5$, $p = 0.042$, $MSE = 3931.0$, although this effect depended on action-reward mapping, $F(1,28) = 5.7$, $p = 0.024$, $MSE = 3931.0$, and was only significant in the face-high reward group, $F(1,14) = 10.4$, $p = 0.006$, $MSE = 3841.0$ versus $F(1,14) = 0.1$, $p = 0.861$, $MSE = 4021.0$. Finally, a reward \times action-reward mapping interaction, $F(1,28) = 33.0$, $p < 0.001$, $MSE = 4906.1$, revealed that the FMC was overall more activated than the HMC. However, as explained earlier we cannot interpret this effect because it compares different brain regions.

The analysis of the mean BOLD response in the visual ROIs did not reveal the action \times ROI interaction reported earlier by Kühn and colleagues, $F(1,28) = 0.5$, $p = 0.483$, $MSE = 1599.2$. There was a trend for an effect of action-reward mapping on this interaction, $F(1,28) = 4.0$, $p = 0.054$, $MSE = 1599.2$, but subsequent ANOVAs did not support the interaction for separate groups, $F(1,14) = 1.5$, $p = 0.240$, $MSE = 891.0$ and $F(1,14) = 2.6$, $p = 0.132$, $MSE = 2307.5$. There was also an interaction between block and action-reward mapping, $F(2,56) = 4.1$, $p = 0.023$, $MSE = 7728.5$, suggesting that overall brain activation was different in the three blocks in the face-high reward group only, $F(2,28) = 5.1$, $p = 0.015$, $MSE = 5904.6$ versus $F(2,28) = 1.5$, $p = 0.249$, $MSE = 10351.8$.

Finally, we repeated the analysis on the visual ROIs by extracting spheres around the peak voxel (see Methods) from the face and hand localizer scan and running the ANOVA on these individual peaks in the EBA and FFA, thus following exactly the same procedure as described by Kühn et al. (2011). These results were very similar to the univariate analyses reported above on the EBA and FFA ROIs, and did not reveal an action \times ROI interaction, $F(1,21) = 0.1$, $p = 0.884$, $MSE = 1550.9$.

Discussion

In the present study we tested the prediction derived from ideomotor theory (Harleß, 1861; Hommel et al., 2001; James, 1890; Lotze, 1852) that implementing an action goal entails the consistent neural representation of expected action outcomes in visual areas of the brain. We found that when participants prepared a hand or face action, patterns of activity in the EBA and FFA, respectively, were more consistent than when participants prepared an action in the opposite modality. Moreover, the size of this effect on action-congruent precision was predictive of the subsequent speed of executing an action across individuals. In addition, reward was shown to increase the precision of the perceptual representations associated with relevant action outcomes. Finally, motor codes in the hand motor cortex and face motor cortex revealed effects that were similar to the visual areas but opposite in direction.

The results revealed by our multivariate measure of representational precision confirm and extend earlier studies that have used univariate brain activation approaches to show that areas encoding the perceptual consequences of actions are activated during the preparation and execution of actions (Kühn et al., 2011, 2010; Kühn and Brass, 2010; Ruge et al., 2010). The increased precision of perceptual representations revealed in our study is likely supported by bidirectional links between action and outcome representations, as has been shown in studies that have primed perceptual outcomes to bias behavioral choices (Elsner and Hommel, 2004, 2001) and motor cortex responses (Elsner et al., 2002; Melcher et al., 2013, 2008; Pfister et al., 2014). Extending other studies on activation patterns in the EBA and FFA (Astafiev et al., 2004; van Nuenen et al., 2012; Zimmermann et al., 2012), our findings show that the precision of those patterns also plays a role in action control. From this perspective, our results dovetail with other studies that have shown that the EBA and FFA are not only important for the perception of visual stimuli such as body parts and faces (Downing et al., 2001; Kanwisher et al., 1997; Pitcher et al., 2008; Taylor et al., 2007; Urgesi et al., 2004; van Koningsbruggen et al., 2013) but that these areas also play a role when preparing for related actions (Kühn et al., 2011; see also Zimmermann et al., 2016). One may argue that the involvement of the visual cortex is more obvious in perceiving faces of others than one's own face, which in the absence of mirrors and other reflections relies on proprioception. However, activating one's own face can still involve FFA via strong (Heyes, 2001), presumably prenatal (Meltzoff and Moore, 1997, 1977) intermodal connections between kinesthetic, motor, and visual brain regions. Our findings also align with studies that have implicated the same areas in visual imagination (Johnson et al., 2007; O'Craven and Kanwisher, 2000), although these studies focused on the conscious experience of the participant, whereas the concept of outcome anticipation emphasizes the preparation for events to come. However, at a neural level these two terms refer to the same process. That is, both processes translate into the activation of neuronal codes representing the past and therefore to-be-expected action outcomes.

The abstract coding of the perceptual aspects of actions was accompanied with a concrete coding of the actions in motor cortex, producing opposite effects in neural precision. This result is difficult to interpret. The three key differences between representations in perceptual areas versus motor areas are that there is more overlap in representation in perceptual areas, perceptual areas represent information at a greater level of abstraction than motor areas, and perceptual areas typically represent input whereas motor areas typically represent output. It is worth noting that whereas A.K. Churchland et al. (2011) found that during decision formation, neural activity (in monkeys) is more variable in the lateral intraparietal area, M.M. Churchland and colleagues (Churchland et al., 2006) found that during decision formation neural activity is less variable in premotor cortex. This reversal of effect between perceptual and motor areas is similar but opposite to the pattern we find. However, their results come from cell

recordings in monkeys during accumulation of noisy evidence toward a decision, whereas we report patterns of fMRI activity during which there is no perceptual evidence in favor of either of two options. We speculate that uncertainty about the ultimate action may drive pattern variability upward when patterns are discrete, concrete, and directly drive physical behavior, but we cannot determine which of these factors is most, or solely, important for producing this result.

Another novel aspect of the current study is that we investigated how different levels of reward associated with particular actions alter the associated perceptual and action representations. Although some recent behavioral studies have started to investigate how reward signals can modulate outcome-mediated action control (Allman et al., 2010; Eder et al., 2015; Hogarth and Chase, 2011; Marien et al., 2013; Muhle-Karbe and Krebs, 2012; Watson et al., 2014), there are no studies to date that have investigated the modulation of perceptual outcome representations at a neural level. If outcome-specific representations are increased by reward, as some behavioral studies suggest (Allman et al., 2010; Eder and Dignath, 2015; Muhle-Karbe and Krebs, 2012) but see (Eder et al., 2015; Hogarth and Chase, 2011; van Steenbergen et al., 2017; Watson et al., 2014), this might lead to a modulation of the area-specific representational precision effect in the visual areas.

However, this is not what we observed. Instead, anticipated reward increased representational precision in all perceptual areas, but decreased precision in motor areas. This effect was limited to the group that associated face actions with high reward (see below). A brain-wide boost in neural stability mediated by a neuromodulatory increase in signal-to-noise ratio (Warren et al., 2016, 2015) could explain the consistent effect across perceptual areas, but we had no basis to predict that such an effect would lower precision in motor areas. Our results suggest that patterns of activation in the hand motor cortex are actually less consistent when preparing two hand actions than when preparing two face actions, and vice versa for the face motor cortex. Insofar as this effect is a natural outcome of lingering uncertainty, it is not unreasonable to speculate that increased signal-to-noise ratio would enhance the effect. In fact, this effect may be driven more by precision in the incongruent action condition, than by imprecision in the congruent action condition. That is, patterns of activity in the motor cortex may default to a representation that is less noisy when no action is being prepared than when two actions are being prepared. Findings from electrophysiological research suggest motor cortex demonstrates synchronized oscillations at rest that become desynchronized as a motor action is imagined or prepared (Miller et al., 2007; Pfurtscheller et al., 2006, 1996). The relationship between this phenomenon and the results we observe is admittedly speculative and we acknowledge that more research is needed to determine how the motor cortex represents multiple possible outputs versus no possible outputs.

Our conclusions must be tempered by the fact that the effect of reward on angular dispersion was only significant in the group of participants that associated face actions with high reward. We speculate that because the face actions required in our study were unusual and might have been more difficult to perform than the hand actions (simple button presses), participants might have been more motivated in the group where effortful actions were associated with a corresponding higher (instead of lower) reward. By this account, the impact of reward is reduced in the group of participants that associated the more difficult face actions with relatively low reward. The patterns of activation in the pallidum, putamen, and amygdala – key structures of the traditionally so-called reward circuit (Haber and Knutson, 2010) – are consistent with this explanation. On the other hand, the pattern of results for the reward anticipation phase indicates that the ventral striatum, vmPFC, and amygdala in this context most likely do not reflect the anticipated subjective value per se, but rather the enhanced motivational saliency or difficulty associated with face actions in comparison to hand actions. This result aligns with studies that have

shown similar task demand effects in these brain areas (Boehler et al., 2011; Schouppe et al., 2014). Alternatively, it is also possible that face actions are simply easier to become associated with reward than hand actions, for example due to different neural connectivity with the reward system and/or because faces carry more affective information than hands.

We also investigated whether neural representations of the house cues were differentially modulated by reward value. Reward-predicting stimuli are typically preferentially selected and processed (Berridge and Robinson, 1998; Hickey et al., 2010; Krebs et al., 2010; Robinson and Berridge, 2001; Serences, 2008). We therefore expected that neural representations in the PPA encoding visual scenes would be more precise in response to house cues signaling high-reward. This prediction was borne out in our data. Notably, this effect was independent of the action-reward mapping and block, suggesting that the incentive salience of the cue was coded independently of the subjective value of reward and works independently of the observed modulation of outcome-related perceptual representations.

We did not use a control condition that used a cue associated with no action modality. The implication of this is that we were not able to demonstrate action-specific effects such that, for example, preparing a hand action only decreased angular dispersion in the EBA without affecting activity in the FFA. Another limitation of this study is that we were not able to replicate the univariate effects in peak brain activity in the EBA/FFA as earlier demonstrated using a similar task (Kühn et al., 2011). The failure to observe this effect might be attributed to several differences between our study and theirs. First, instead of the abstract letter cues that were presented in the original study we presented pictures of houses as cues. Pictures of houses also activate the ventral temporal cortex, potentially overshadowing action-specific effects in the EBA and FFA. Second, we introduced a reward manipulation that was not in the previous study. Some studies have shown that reward can undermine intrinsic motivation (Deci et al., 1999; but see also Cameron et al., 2001), and that reward is associated with reduced voluntary task engagement and diminished activation of the neural valuation system (Murayama et al., 2010). Generally undermined motivation might thus have reduced participants' neural anticipation effects in the current study, reducing the odds of observing it in a univariate analysis. Nevertheless, the main results of our study do show that multivariate analyses were highly sensitive to modulation of the visual cortex. Multivariate analyses typically are more sensitive than univariate analyses (Poldrack, 2012), and can reveal neural encoding in brain areas that are not possible to measure with univariate approaches (Etzel et al., 2016).

We also note that because our study included a behavioral measure of performance for the hand actions, but not for the face actions, we could not investigate the action-specific relationship between neural precision and efficiency in execution. One way to improve this design in future studies is to use video recording of face and hand actions, which would enable testing of whether general modulation as observed here can produce modulation of outcome-specific behavioral control as observed in some behavioral studies (Allman et al., 2010; Muhle-Karbe and Krebs, 2012).

From a more methodological perspective, our study demonstrates how angular dispersion of vectors defined by brain activation patterns can be used to investigate the precision of neural representations in different areas of the brain. The findings presented here thus extend the seminal studies that have investigated the precision of neural representations over time in relation to consciousness (Schurger et al., 2015, 2010) and memory (Xue et al., 2010). As such, this body of work demonstrates added value to other multivariate approaches. For example, the seminal work by Haxby et al. (2001) characterizing the way perceptual category information is represented in inferior temporal cortex, the design of classification algorithms focused on whether or not information is represented in particular areas (Haynes and Rees, 2006), and the development of representational similarity analyses (Kriegeskorte et al., 2008a, 2008b).

Conclusions

Using a multivariate measure of representational precision, we showed for the first time how the precision of representations in perceptual and motor areas is modulated by the specific action goal and the associated reward value when participants prepare face or hand actions. Our findings show that increased temporal consistency of neural representations in visual cortex provides an important neural signature of the perceptual expectations involved in goal-directed action.

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