Title: Action intention modulates the representation of object features in early visual cortex

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Abstract

The role of the early visual cortex (EVC) has been extensively studied for visual recognition but to a lesser degree to determine how action planning influences perceptual representations of objects. We used functional MRI and pattern classification methods to determine if during action planning, object features (orientation and location) could be decoded in an action-dependent way and if so, whether this was due to functional connectivity between visual and higher-level cortical areas. Sixteen participants used their right dominant hand to perform movements (Align or Open Hand) towards one of two oriented objects that were simultaneously presented and placed on either side of a fixation cross. While both movements required aiming toward target location, only Align movements required participants to precisely adjust hand orientation. Therefore, we hypothesized that if the representation of object features in the EVC is modulated by the upcoming action, we could use the pre-movement activity pattern to dissociate between object locations in both tasks, and orientations in the Align task only. We found above chance decoding accuracy between the two objects for both tasks in the calcarine sulcus corresponding to the peripheral location of the objects in the visual cortex, suggesting a task-independent (i.e. location) modulation. In contrast, we found significant decoding accuracy between the two objects for Align but not Open Hand movements in the occipital pole corresponding to central vision, and dorsal stream areas, suggesting a task-dependent (i.e. orientation) modulation. Psychophysiological interaction analysis indicated stronger functional connectivity during the planning phase of Align than Open Hand movements between EVC and sensory-motor areas in the dorsal and ventral visual stream, as well as areas that lie at the interface between the two streams. These results demonstrate that task-specific

preparatory signals modulate activity not only in areas typically known to be involved in perception for action, but also in the EVC. Further, our findings suggest that object features that are relevant for successful action performance are represented in the part of the visual cortex that is best suited to process visual features in great details, such as the foveal cortex, even if the objects are viewed in the periphery.

Keywords: action planning, object features, early visual cortex, functional magnetic resonance imaging (fMRI), functional connectivity

1. Introduction

To execute actions in daily life successfully, our brain needs to obtain accurate information about the orientation, location, shape and size of a target object. Picking up a pen, for example, would be more successful when one is focused on its orientation rather than its color. Considerable research has investigated the role of frontoparietal reaching and grasping networks in successfully executing actions (for reviews see: Gallivan & Culham, 2015; Vesia & Crawford, 2012). However, perception is enhanced by the mere intention to grasp (Gutteling et al., 2011). This suggests that feedback connections between frontal and parietal areas involved in action preparation modulate the activity in visual areas (Gutteling et al., 2013), mediating the enhancement of feature perception during action planning and allowing for the sharing of action-relevant information between visual and somatomotor areas. The outstanding question is how early in the visual system is this modulation detected.

The involvement of early visual areas during action execution comes from evidence showing that the EVC is reactivated at the time of delayed actions despite the absence of visual information (Monaco, Gallivan, Figley, Singhal, & Culham, 2017; Singhal et al., 2013). The re-recruitment of the EVC during action execution might enhance the processing and retrieval of object features for subsequent object manipulations. However, the somatosensory and motor feedback elicited during the execution of a movement might also be responsible for these responses in the visual cortex despite the absence of online visual information. Evidence from electrophysiology has shown preparatory activity in visual areas shortly before action execution (van Elk, van Schie, Neggers, Bekkering, & Sakata, 2010), and fMRI shows above baseline activity when reaching actions were prepared but not yet executed in occipital areas such as lingual gyrus, as well as inferior and superior occipital gyri (Cappadocia et al. 2016). Overall,

these findings suggest that visual areas might be involved in more than just low-level feature processing for action planning.

The goals of this study were to determine: how early in the visual cortex representation of object orientation and location is modulated by hand actions during action planning, and which functional connections between the EVC and action-related brain areas might produce these modulations. To test this, we used a paradigm in which participants performed one of two actions towards one of two objects that differed in location and orientation and were concurrently presented. While object location was relevant for both motor tasks, object orientation was relevant only in one of the two tasks. To uncover influences of action preparation on processing of object features in early visual areas we used multi-voxel pattern analysis (MVPA) and psychophysiological interaction (PPI) analysis on the planning phase preceding the action. We hypothesized that during movement preparation 1) EVC areas that play a specific role in orientation processing (versus location processing alone) would be modulated in a task-specific fashion during action planning, and 2) EVC would show functional connectivity with higher level motor areas that might provide the feedback necessary to engage these early responses.

2. Methods

Our main question was aimed to investigate whether action intention modulated the activity pattern in the EVC elicited by visual perception of two simultaneously presented objects. To this aim, we examined the activity pattern in the calcarine sulcus, corresponding to the peripheral location of the objects. As for perception, information about the category of objects viewed in the periphery can also be decoded in central vision, indicating that position-invariant information about objects is fed back to the foveal retinotopic cortex and correlates with behavioral performance (Williams et al., 2008). To test whether action-relevant features of objects presented in the periphery are also distinguishable in the foveal cortex, we localized the part of the retinotopic map corresponding to central vision in the occipital pole. If the representation of an object is shaped by the intended action, we would see enhanced dissociation between the two oriented objects when participants were planning an action that had to be adjusted to the orientation of the object (Align) as compared to a movement for which object orientation was irrelevant (Open Hand). In addition, we examined the activity pattern in areas of ventral and dorsal visual stream known to have a representation of action intention.

2.1. Sessions

The experimental and retinotopic mapping sessions took place on two different days. The experimental session lasted approximately 2 hours, including screening and set-up time, while the retinotopic mapping session took approximately 30 minutes to be completed.

2.2. Participants

Twenty-six right-handed volunteers (14 females) participated in this study. The age range of participants was 20-45, with an average age of 30.4 years. Sixteen participants volunteered for the experimental runs and 14 participants took part in the independent localizer runs for

retinotopic mapping. Four of these participants took part in both sessions. All participants had normal or corrected-to-normal vision and none of the participants had any known neurological deficit. All participants provided informed consent and approval was obtained from the ethics committee for experiments involving human participants at the University of Trento.

2.3. Experimental Setup: Apparatus and Stimuli

The experimental set up is illustrated in Figure 1A. Participants lay on the bed of a 4-Tesla MRI scanner and performed actions towards one of two real objects. Both objects were affixed to strips of Velcro attached to a platform that was covered with the complementary side of Velcro. The platform was placed over the pelvis of the participant. This device enabled subjects to perform hand actions (Align and Open Hand movements) towards two wooden objects mounted on the platform. The two objects were placed on either side of a fixation cross. The object on the left was oriented at about -45° and will be referred to as counterclockwise-left (CCW-Left) while the one on the right was oriented approximately at 45° and will be referred to as clockwise-right (CW-Right) (Figure 1A, left panel). The head of the participant was slightly tilted (~30°) to allow direct viewing of the stimuli presented on the platform. The platform was perpendicular to gaze and approximately 65 cm from the eyes. To limit motion artifacts, the right upper arm was supported with foam and gently restrained. Reaches were thus performed by movements of the right forearm and hand. A button box was placed around the participants' abdomen and served as the starting point for each trial. Hand actions were monitored with a Sony HDR-UX1E digital video camera. The lights were on throughout the experiment and the hand was visible to participants. Participants wore headphones to hear auditory instructions and cues.

Figure 1

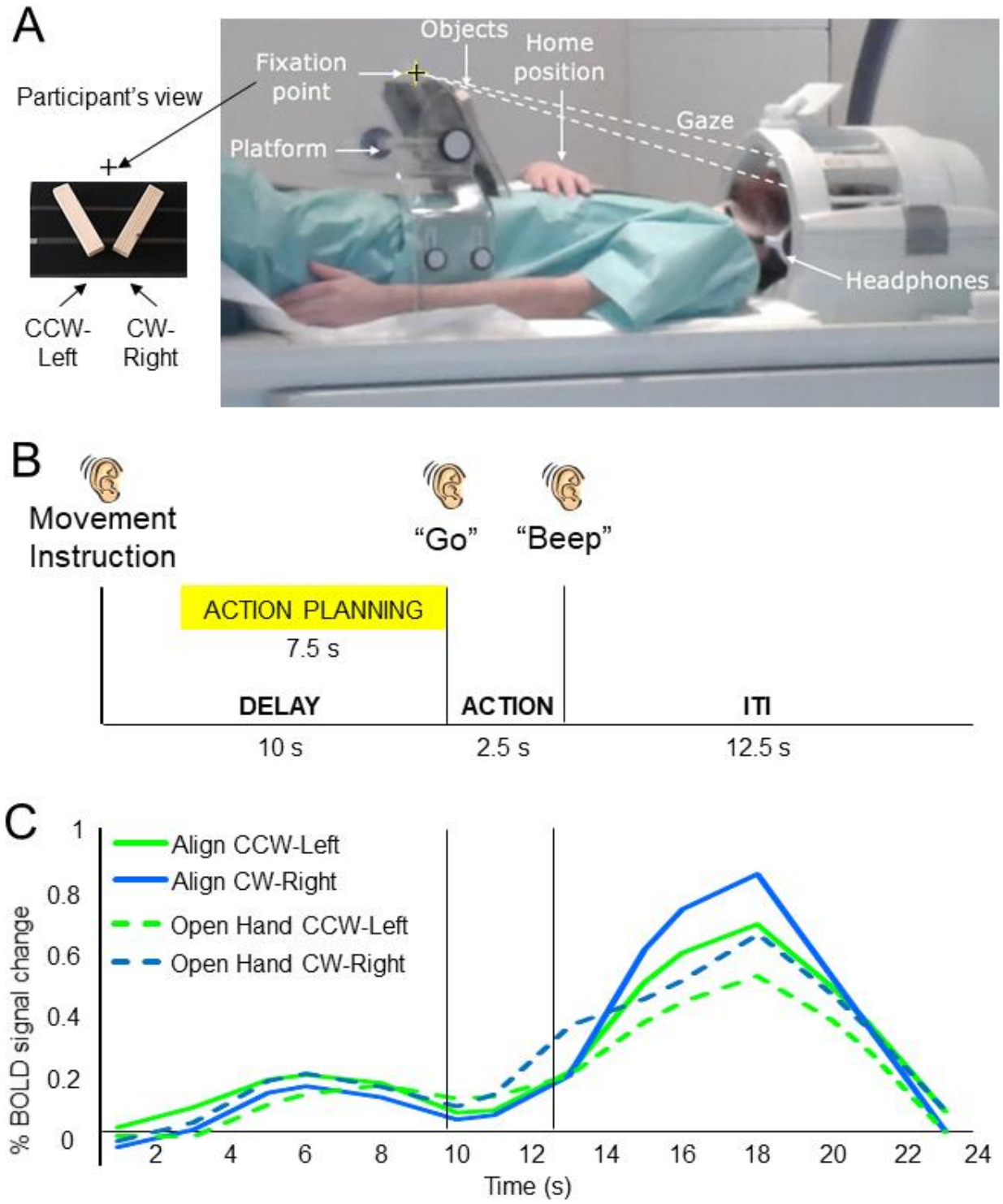
A
Participant's view
CCW-
Left
CW-
Right
Fixation
point
Objects
Home
position
Gaze
Platform
Headphones
B
Movement
Instruction
"Go"
"Beep"
ACTION PLANNING
7.5 s
DELAY
ACTION
ITI
10 s
2.5 s
12.5 s
C
Align CCW-Left
Align CW-Right
Open Hand CCW-Left
Open Hand CW-Right
% BOLD signal change
Time (s)
0
0.2
0.4
0.6
0.8
1
2
4
6
8
10
12
14
16
18
20
22
24

Figure 1.

Image of the experimental setup and timing of experimental runs. (A) The setup required participants to gaze at the fixation point, marked with a cross, while preforming the task. Shown on the left side is the participant's view of the platform with the two oriented objects. (B) At the beginning of each trial, an auditory cue indicated the condition type to the participant ("Align Left", "Align Right", "Open Hand Left" and "Open Hand Right"). There was a delay of 10 seconds during which participants did not perform any action until they heard a "go" cue upon which they performed the movement that they had been instructed at the beginning of the same trial. The end of the trial was cued by a "beep" sound, which prompted participants to return the hand to the home position. We used a 12.5 second intertrial interval. We focused our analysis on the 7.5 sec preceding action execution, during the delay phase. (C) Group-averaged % BOLD signal change extracted from the calcarine sulcus in the left hemisphere for Align and Open Hand CCW-Left and CW-Right. The timing of events in C correspond to events in B.

2.4. Experimental Paradigm

We used functional magnetic resonance imaging (fMRI) to measure the blood-oxygenation-level dependent (BOLD) signal (Ogawa et al., 1992) in a slow event-related delayed-action paradigm. As shown in Figure 1B, each trial began with an auditory cue that indicated the condition type to the participant. There were 4 conditions: Align CCW-Left, Align CW-Right, Open Hand CCW-Left and Open Hand CW-Right. Then there was a delay of 10 seconds during which participants did not perform any action until they heard a go cue. When hearing the go cue, participants had 2.5 seconds to perform the movement that they had been instructed at the beginning of the same trial. A beep sound cued the participant to return the hand to the home position on the button box where it rested until the next trial began. The inter trial interval (ITI) lasted 12.5 seconds. The delayed timing of the experiment allowed us to isolate the pre-movement activity during planning phase before the execution of the movement.

Participants were instructed to fixate their eyes on the fixation cross throughout the experiment. The objects were always visible to the participants. Align movements consisted of reaching to the CCW-Left or CW-Right object and adjusting the hand precisely over it. The Open Hand movements consisted of moving the hand above the instructed object with an open palm. Therefore, while both movements were directed to one of the two object locations, only Align movements also required adjusting the hand according to the orientation of the object. Each participant was trained and tested in a short practice session (10-15 minutes) prior to the fMRI experiment. The hand was monitored with a camera to confirm that participants were performing the correct tasks during the fMRI experiment.

As shown in Figure 2, we had a 2 x 2 factorial design, with factors of Movement (Align or Open Hand) and Object Orientation and Location (CCW-Left or CW-Right), which lead to 4 conditions: Align CCW-Left, Align CW-Right, Open Hand CCW-Left and Open Hand CW-

Right. Each run included 7 trials per experimental condition, for a total of 28 trials per run. Each trial type was presented in counterbalanced order for a run time of ~12.5 minutes. Participants completed 5 functional runs for a total of 140 trials per subject (35 trials per condition).

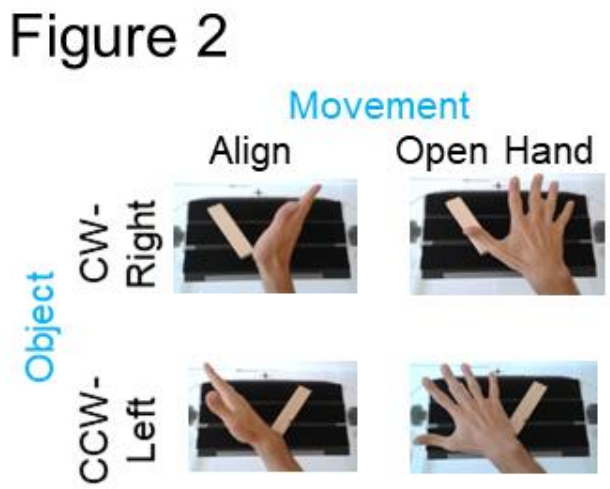

Figure 2

Experimental design. Participants performed four actions towards the instructed oriented object. Movements consisted of Align or Open Hand towards the CCW-Left or CW-Right object. As shown here, Align required the precise adjusting of a participant's hand over the object while Open Hand movements were coarse.

2.5. Imaging Parameters

This study was conducted at the University of Trento's Center for Mind/Brain Sciences (CIMeC) in Mattarello, Italy using a 4T Bruker MedSpec whole body MRI system (Bruker BioSpin, Ettlingen, Germany), equipped with Siemens Magnetom Sonata gradients (200 T/m/s slew rate, 40 mT/m maximum strength; Siemens Medical Solutions, Erlangen, Germany) and an eight-channel head coil. Functional data was acquired using T2*-weighted segmented gradient echo-planar imaging sequence (repetition time [TR] = 2500 ms; echo time [TE] = 33 ms; flip angle [FA] = 78° for experimental runs, 73° for eccentricity mapping; field of view [FOV] = 192 × 192 mm, matrix size = 64 × 64 leading to an in-slice resolution of 3 × 3 mm; slice thickness = 3 mm, 0.45mm gap). Each volume was comprised of 35 slices for experimental runs, 33 slices for eccentricity mapping which were collected in interleaved order. During each experimental session, a T1-weighted anatomical reference volume was acquired using a MPRAGE sequence (TR = 2700 ms; TE = 7°; inversion time TI = 1,020 ms; FA = 7°; FOV = 256 x 224 x 176, 1 mm isotropic resolution).

2.6. Preprocessing

Data was analyzed using Brain Voyager QX software version 2.8.4 (Brain Innovation, Maastricht, Netherlands). The first 3 volumes of each functional scan were discarded to avoid T1 saturation effects. For each run, slice scan time correction (cubic spline), temporal filtering (removing frequencies <2 cycles/run), and 3D motion correction (trilinear/sinc) were performed. To complete 3D motion correction, each volume of a run was aligned to the volume of the functional scan that was closest in time to the anatomical scan. Seven runs showing abrupt head movements greater than 1mm were discarded from the analyses. The data was transformed into Talairach space (Talairach & Tournoux, 1988).

2.7. General Linear Model (GLM)

We analyzed the data from the experimental runs using a group random-effects (RFX) general linear model (GLM) that included 1 predictor for each of the 4 conditions (Align CCW-Left, Align CW-Right, Open Hand CCW-Left, Open Hand CW-Right) and 3 phases (Instruction, Delay and Action) resulting in a total of 12 predictors of interest. In addition, we included 6 motion correction parameters as predictors of no interest. Each predictor was derived from a rectangular-wave function (1 volume or 2.5 s for the movement instruction, 3 volumes or 7.5 s for the delay phase and 1 volume or 2.5 s for the action phase) convolved with a standard hemodynamic response function (HRF; Brain Voyager QX's default double-gamma HRF). The GLM was performed on %-transformed beta weights (β). The predictors of interest were: 1) Instruction Align CCW-Left, 2) Instruction Align CW-Right, 3) Instruction Open Hand CCW-Left, 4) Instruction Open Hand CW-Right, 5) PlanAlign CCW-Left , 6) PlanAlign CW-Right , 7) PlanOpen Hand CCW-Left , 8) PlanOpen Hand CW-Right , 9) Action Align CCW-Left, 10) Action Align CW-Right, 11) Action Open Hand CCW-Left, 12) Action Open Hand CW-Right.

2.8. Voxelwise Analysis

To determine whether there were areas that showed a univariate difference between the processing of the two objects during the planning phase of Align and Open Hand tasks, we performed the following contrasts: (Plan Align CCW-Left > Plan Align CW-Right), and (Plan Open Hand CCW-Left > Plan Open Hand CW-Right).

Activation maps for group voxelwise results were overlaid on the average inflated brains of all participants by cortex based alignment. To correct for multiple comparisons, we performed cluster threshold correction for each activation map using Brain Voyager's cluster-level statistical threshold estimator plug-in (Goebel et al., 2006; Forman et al., 1995). This algorithm

applied 1000 iterations of Monte Carlo simulations to estimate the number of neighboring false positive voxels which were active purely due to chance. Areas that did not survive this correction were excluded from the analyses.

2.9. Multi-Voxel Pattern Analysis (MVPA)

2.9.1. Linear Discriminant Analysis (LDA) single-trial classification

MVPA was performed to determine if actions modulate the activity pattern in our ROIs through the decoding of object location and orientation during the planning phase preceding the two actions. In particular, in areas that show movement-dependent representation of object orientation during action planning (with little or no location processing), we expected significant decoding accuracy for the dissociation of CCW-Left versus CW-Right in Align but not Open Hand conditions (Figure 3A). On the other hand, in areas that show movement-independent representation of object location, we would expect above chance decoding for Align and Open Hand conditions (Figure 3B). In areas that have no representation of object features for action, we would expect decoding accuracy at chance level for the dissociation between the two objects for either movement (Figure 3C).

We used a combination of in-house software (using MATLAB) and the CoSMo MVPA Toolbox for MATLAB (http://cosmomvpa.org), with an LDA classifier (http://cosmomvpa.org/matlab/cosmo_classify_lda.html#cosmo-classify-lda). For each participant, we estimated a GLM on unsmoothed data modeling every trial per condition. The 4 experimental conditions (Align CCW-Left, Align CW-Right, Open Hand CCW-Left, Open Hand CW-Right) by 3 phases of the trial (Instruction, Delay, Action) by 7 repetitions per run by 5 runs, gave rise to a total of 420 repressors of interest per subject. In addition, we modelled movement parameters (3 rotations and 3 translations) as predictors of no interest. We adopted a ‘leave-one-

run-out' cross-validation approach to estimate the accuracy of the LDA classifier.

2.9.2. Classifier inputs

To provide inputs for the LDA classifier, the β weights were extracted from the phase of interest (i.e. Delay or Action phase) for each voxel in the ROI. Each phase included the volumes defined in the predictors for the GLM estimated on unsmoothed data. In particular, the Delay phase consisted of 3 volumes following the Instruction phase, while the Action phase consisted of 1 volume following the Delay phase.

Figure 3

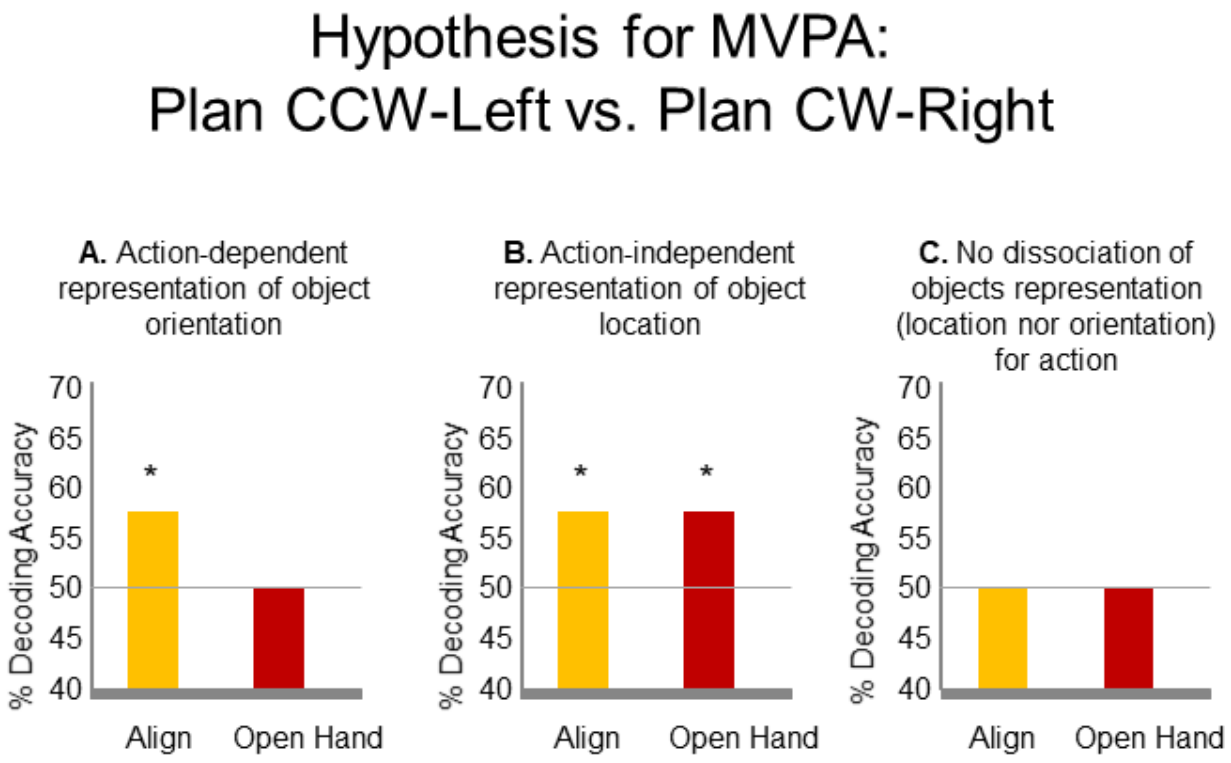

Figure 3.

Predicted percent decoding accuracies based on MVPA for the dissociation between CCW-Left and CW-Right in Align and Open Hand movements during action planning. We hypothesized: (A) Areas showing a action-dependent dissociation of object orientation for Align but not Open Hand tasks; (B) Areas whose activation pattern allow us to decode CCW-Left versus CW-Right in both hand movements; and (C) Areas that do not show enhancement of object features for either movements.

2.10. Statistical analysis

We statistically assessed decoding significance across participants with a one-tailed t-test versus 50% chance decoding. We used one-tailed t-tests because we expected the decoding accuracy to be significantly over but not below chance level.

To further explore whether the decoding accuracy was higher for the dissociation between the two objects in Align than Open Hand movements, we performed one tailed paired sample t-tests between the decoding accuracies in the two movement types. To control for multiple comparisons, a false discovery rate (FDR) correction of $q \leq 0.05$ was applied, based on the number of ROIs and the number of t-tests performed within each time phase (Benjamini & Yekutieli, 2001). We flagged the results that did not survive FDR correction. However, we only discuss FDR-corrected results.

2.11. Retinotopic Mapping

In a separate session, a set of 14 participants underwent eccentricity mapping procedures. Of these participants, 4 also took part in the experiment. The expanding ring, used for eccentricity mapping, increased logarithmically as a function of time in both size and rate of expansion, so as to match the estimated human cortical magnification function (for details, see Swisher, Halko, Merabet, McMains, & Somers, 2007). The smallest and largest ring size corresponded, respectively, to 1° and 10° of diameter. We divided the 10° into 8 equal time bins (of 8 seconds each). The eccentricity mapping localizer was composed of 8 cycles, each lasting 64 seconds. A fixation time was added at the beginning and at the end of the experiment for a total duration of 9 minutes per run. The stimuli were rear-projected with an LCD projector (EPSON EMP 7900 projector; resolution, 1280x1024, 60-Hz refresh rate) onto a screen mounted behind the participants head. The participants viewed the images through a mirror mounted to

the head coil directly above the eyes. For eccentricity stimuli, we convolved a boxcar-shaped predictor for each bin with a standard HRF and performed contrasts using an RFX GLM.

We present results of eccentricity mapping because our arguments are in terms of the eccentric locations rather than the specific visual areas implicated. Moreover, the meridia from polar angle maps are less straightforward to combine across participants and the discrimination of visual areas within the fovea is technically challenging, as the occipital pole corresponds to the foveal confluence of numerous retinotopic visual areas, specifically V1, V2, V3, hV4, LO-1 and LO-2 (Schira et al., 2009; Wandell, Dumoulin, & Brewer, 2007).

2.12. Regions of Interest (ROIs)

The calcarine sulcus and occipital pole were localized to determine whether action-relevant features of objects (orientation and location) can be distinguished from the activity pattern in the part of the retinotopic visual cortex corresponding to the peripheral location of the objects (calcarine sulcus) as well as central vision (occipital pole).

To localize the calcarine sulcus, corresponding to the peripheral location of our stimuli in the EVC (~8° of visual angle), we ran a contrast of: (bins: 678 > 123). Bins from 6 to 8 correspond to eccentricities from 6.7° to 10.1°. Therefore, we selected our ROI based on voxels that showed higher activation for eccentricities between 6.7 and 10.1 than for lower eccentricities (activation shown in green in Figure 4A), and slightly above the calcarine sulcus (consistent with the location of the objects in the lower visual filed). We checked that the activation for the contrast (Plan > Baseline), which corresponded to the phase when participants viewed the stimuli while fixating the fixation cross, overlapped with the selected ROI. We localized the occipital pole, corresponding to central vision, based on the contrast of: (bins: 123 > 678). Bins from 1 to 3 correspond to foveal vision with eccentricities up to 4.5° (Wandell, 1995; Strasburger et al.,

2011). Therefore, we selceted our ROI based on voxels that showed higher activation for eccentricities up to 4.5° than higher eccentricities.

In addition to the ROIs in the EVC, we also identified areas that are typically part of the action network (Figure 4B): superior-parietal occipital cortex (SPOC), anterior intrapariental sulcus (aIPS), posterior intraparietal sulcus (pIPS), lateral occipital cortex (LOC) and dorsal premotor cortex (PMd). We chose these ROIs based on their involvement in adjusting hand orientation in humans (SPOC, PMd, pIPS: Monaco et al., 2011) and macaques (aIPS: Baumann, Fluet, & Scherberger, 2009; V6A/SPOC: Battaglini et al., 2002; Fattori et al., 2009). In addition, LOC is involved in discriminating object orientation (Ganel & Goodale, 2017).

We localized our ROIs near their expected anatomical locations by looking for the landmark that are typical for each area: the superior end of the parietal occipital sulcus for SPOC; junction of intraparietal and postcentral sulci for aIPS; posterior end of the intraparietal sulcus for pIPS; T-junction of superior frontal and precentral sulci for dPM; and junction of inferior temporal sulcus and lateral occipital sulcus for LOC.

A sphere with a radius of 9 mm was centered on the voxel with peak activation for each ROI. Therefore, each ROI consisted of 3071 voxels. Since these areas are also involved in action execution (Culham et al. 2003; Chen et al. 2014), we ensured that the anatomical localization of each localized area overlapped with the activation from the contrast : (All Actions > Baseline).

Figure 4

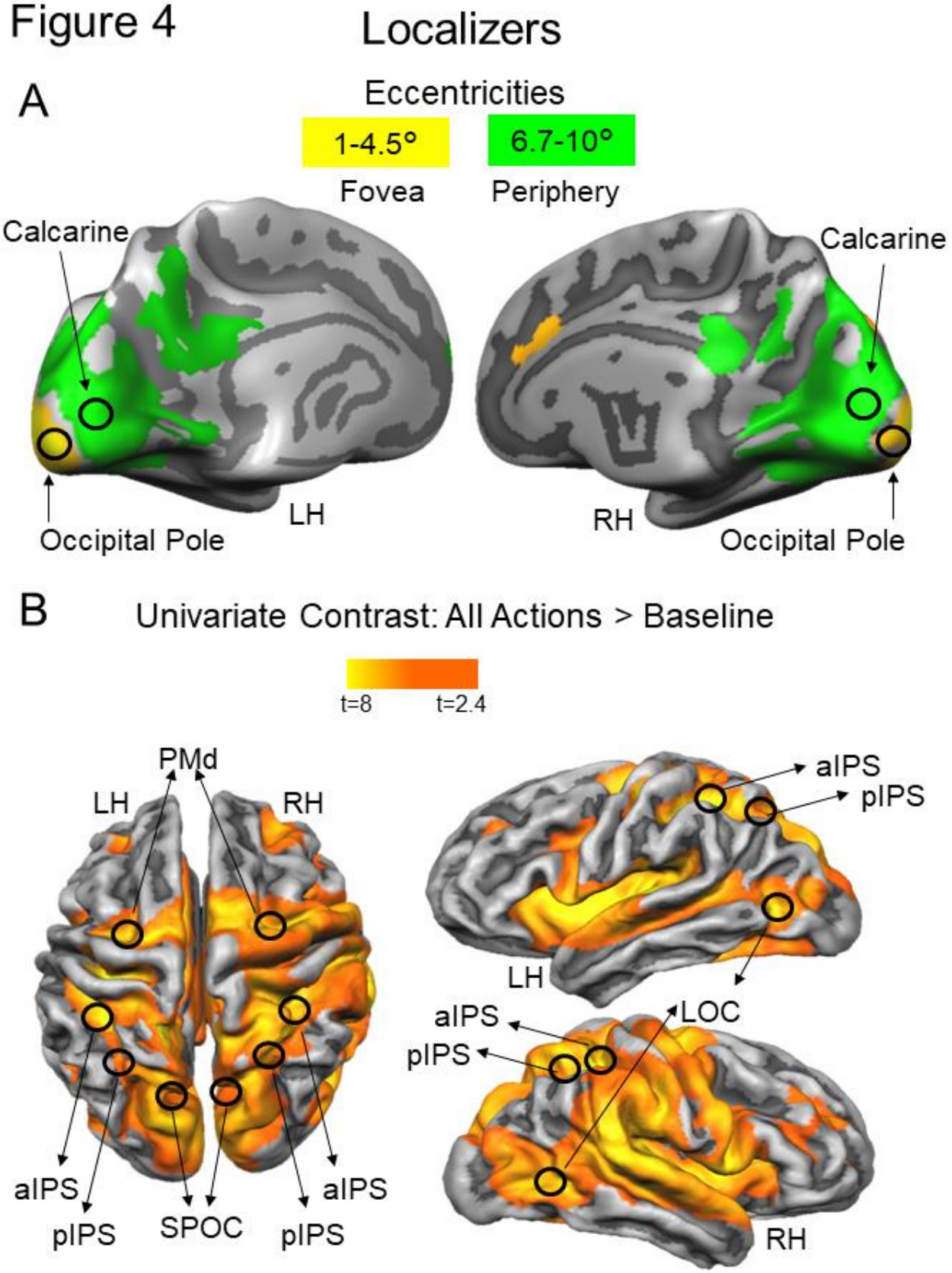
Localizers
A
Eccentricities
1-4.5°
6.7-10°
Fovea
Periphery
Calcarine
Calcarine
LH
RH
Occipital Pole
Occipital Pole
B
Univariate Contrast: All Actions > Baseline
t=8
t=2.4
PMd
LH
RH
aIPS
pIPS
SPOC
aIPS
pIPS
aIPS
pIPS
LH
aIPS
LOC
pIPS
RH

Figure 4.

Activation maps in the EVC and areas of the action network. (A) EVC activation maps for eccentricities from 1 to 10° of visual angles in the occipital pole and calcarine sulcus. Overlap between two activation maps showing: 1) areas with higher activation for 6.7-10° than 1-4.5° (green) and areas with higher activation for eccentricities 1-4.5° than 6.7-10° (yellow). Eccentricity mapping was completed to independently localize the calcarine sulcus (which corresponds to the objects' placement in the visual field) and the occipital pole (which corresponds to the foveal cortex). Eccentricity mapping was completed separately from the experiment on a set of 14 participants. (B) Activation maps for the localization of ROIs in dorsal and ventral stream obtained with the univariate contrast: All Actions > Baseline. Voxelwise statistical maps were obtained with the Random Effects GLM of experimental runs. The activation maps are overlaid on the average cortical surface. Abbreviations: SPOC = superior parietal occipital cortex; pIPS = posterior intraparietal sulcus; aIPS = anterior intraparietal sulcus; PMd = dorsal premotor area; LOC = lateral occipital cortex.

2.13. Psychophysiological Interaction (PPI) Analysis

We measured task-specific changes in functional connectivity using psychophysiological interaction (PPI) analysis (Friston et al. 1997; McLaren et al. 2012; O'Reilly et al. 2012). PPI identifies brain regions whose functional connectivity is modified by the task beyond correlations based on physiology ("physiological component") and task-modulated activity ("psychological component"). We determined connectivity between seed regions (calcarine sulcus in left and right hemisphere) and the rest of the brain during the Delay phase. For each participant, the PPI model for each run included: i) the physiological component of z-normalized time-courses extracted from the seed region, ii) the psychological component, corresponding to the task model where predictors were convolved with a standard hemodynamic response function, and iii) the "psychophysiological interaction component", resulting from a volume by volume multiplication of the z-normalized time course with the task model. The predictors of the psychological component were set to +1 for the Align CW-Right and Align CCW-Left conditions for the Planning phase, -1 for Open Hand CW-Right and Open Hand CCW-Left conditions for the Planning phase, and zero for baseline and other phases of the trial (Instruction and Action). The individual GLM design matrix files were used for a random effects model analysis (Friston et al. 1999).

3. Results

Localizers and Univariate Results

The Talairach coordinates of each ROI are specified in Table 1. Activation maps and activation levels for each ROI are shown in Figure 4. We used retinotopic mapping to localize the parts of the visual cortex corresponding to the peripheral representations of the objects as well as central vision on a set of 14 participants. As shown in Figure 4A, the calcarine sulcus showed higher activation for eccentricities corresponding to the peripheral (6.7-10°) than central vision (1-4.5°). In contrast, the occipital pole showed higher activation for eccentricities corresponding to foveal than peripheral vision. We used the univariate contrast (All Actions > Baseline) to localize areas that are part of the action network (Figure 4B).

Univariate voxelwise analyses did not reveal any active voxel for the contrasts: (Plan Align CCW-Left > Plan Align CW-Right) nor (Plan Open Hand CCW-Left > Plan Open Hand CW-Right). This is expected given that participants were lying still and viewed both objects in the lower periphery simultaneously. Therefore, at this point of the task there was no difference in sensory or motor signals in the two conditions that could have elicited higher activation in one case than the other. Figure 1C shows a time course from the left calcarine which is representative of other EVC areas and areas of the action network. We then performed MVPA to examine differences in the pattern of activity.

Table 1. Talairach coordinates for each ROI.

	Talairach coordinates		
ROI	**x**	**y**	**z**
LH Calcarine sulcus	-6	-82	-1
RH Calcarine sulcus	6	-82	0
LH Occipital pole	-9	-91	-12
RH Occipital pole	12	-90	-6
LH SPOC	-16	-81	32
RH SPOC	15	-79	37
LH pIPS	-30	-47	44
RH pIPS	30	-47	44
LH aIPS	-43	-37	39
RH aIPS	42	-41	41
LH PMd	-27	-16	54
RH PMd	27	-16	57
LH LOC	-43	-66	-6
RH LOC	39	-66	-4

Note: LH: left hemisphere; RH: right hemisphere.

Talairach coordinates refer to the peak activation of the functional cluster.

3.1. MVPA

Statistical values for each comparison are specified in Table 2. Figures 4 and 5 show the percent decoding accuracy in each ROI for pairwise comparisons of object orientation/ location during the planning and execution phase within Align and Open Hand movements. Specifically, within the Align and Open Hand trials we trained and tested the classifier on the dissociation between Plan CCW-Left and Plan CW-Right, as well as Action CCW-Left and Action CW-Right.

3.1.1. Early Visual Cortex

During the planning phase (Figure 5), we found significant decoding of CCW-Left versus CW-Right for both Align and Open Hand movements in the left and right calcarine sulcus. This result indicates an action-independent representation of object features (i.e. location), as both tasks required information about object location. Interestingly, the occipital pole showed above chance decoding accuracy for CCW-Left versus CW-Right in Align but not Open Hand tasks in the left and right hemisphere, indicating an action-dependent representation of object orientation. This suggests that the occipital pole is sensitive to sensory or motor feedback in planning an action that requires orientation processing. This is surprising given that participants did not look directly at the objects as they were fixating above the objects during the task.

In the execution phase, we found significant decoding of CCW-Left versus CW-Right for both Align and Open Hand Movements in the calcarine sulcus as well as the occipital pole in the left and right hemisphere. This would be expected since participants saw their own hand moving in the lower periphery during the action.

3.1.2. Dorsal and Ventral Visual Stream Areas

As shown in Figure 6, during the planning phase, bilateral SPOC and left pIPS showed an action-dependent dissociation of object orientation. In fact, we could decode object orientation during the Align but not Open Hand condition. In addition, left pIPS showed higher dissociation of object orientation in Align than Open hand movements. In contrast, there was no dissociation for CCW-Left versus CW-Right during the planning phase for Align nor Open Hand movements in the right pIPS, bilateral aIPS, bilateral PMd and bilateral LOC.

In the execution phase, we found significant decoding of CCW-Left versus CW-Right for both Align and Open Hand movements in SPOC bilaterally and left PMd. Additionally, we could dissociate CCW-Left versus CW-Right for Align but not Open Hand movements in the left pIPS, bilateral aIPS and bilateral LOC. In our experiment this suggests that the activity pattern in these areas was predominantly modulated by sensory-motor feedback for adjusting hand orientation rather than hand location during action execution.

We also explored whether we could predict action intention (Align versus Open Hand) within object location (CCW-Left and CW-Right) in visual areas and areas of the action network. For the ROIs in the EVC, in the planning phase there was no significant decoding accuracy for Align versus Open Hand movements for CCW-Left as well as CW-Right object locations. This was also the case for most areas of the action network.

Table 2. Statistical values for MVPA.

Area	**Plan CCW-Left vs. Plan CW (p values)**		**Action CCW-Left vs. Action CW (p values)**	
	Align	Open Hand	Align	Open Hand
LH Calcarine	**0.001**	**0.008**	**0.001**	**0.001**
RH Calcarine	**0.008**	**0.002**	**0.001**	**0.001**
LH Occipital pole	**0.005**	0.06	**0.001**	**0.001**
RH Occipital pole	**0.005**	0.05	0.02	**0.004**
LH SPOC	0.02	0.23	**0.003**	**0.02**
RH SPOC	**0.007**	0.07	**0.01**	**0.001**
LH pIPS	**0.001**	0.41	**0.002**	0.20
RH pIPS	0.32	0.37	0.06	0.11
LH aIPS	0.07	0.03	0.02	0.24
RH aIPS	0.14	0.42	**0.01**	0.36
LH PMd	0.04	0.38	**0.004**	**0.009**
RH PMd	0.13	0.16	0.04	0.02
LH LOC	0.12	0.42	**0.001**	0.24
RH LOC	0.25	0.30	**0.001**	0.04

Note: LH: left hemisphere; RH: right hemisphere.

Values in bold are significant at corrected p. Values underlined are significant at uncorrected p.

Figure 5

MVPA Results: CCW-Left vs. CW-Right

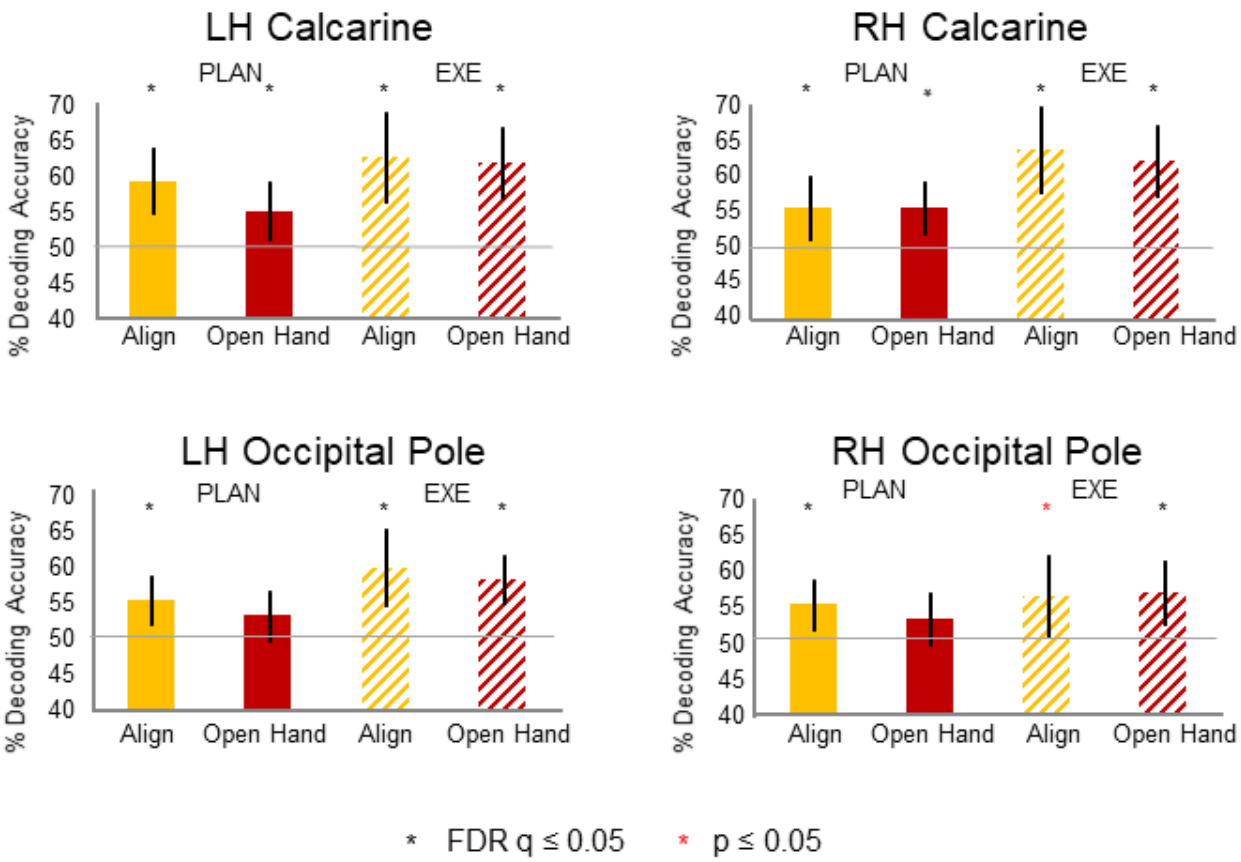

Figure 5.

MVPA results for early visual cortex areas. Bar graphs indicate the MVPA results for the calcarine sulcus and occipital pole. Percent decoding accuracy is shown for the Phase (Plan, Execution) and the Task (Align, Open Hand). The black star indicates statistical differences at corrected p value. The red star indicates differences that are significant at uncorrected p value. Error bars indicate 95% confidence intervals.

Figure 6

MVPA Results: CCW-Left vs. CW-Right

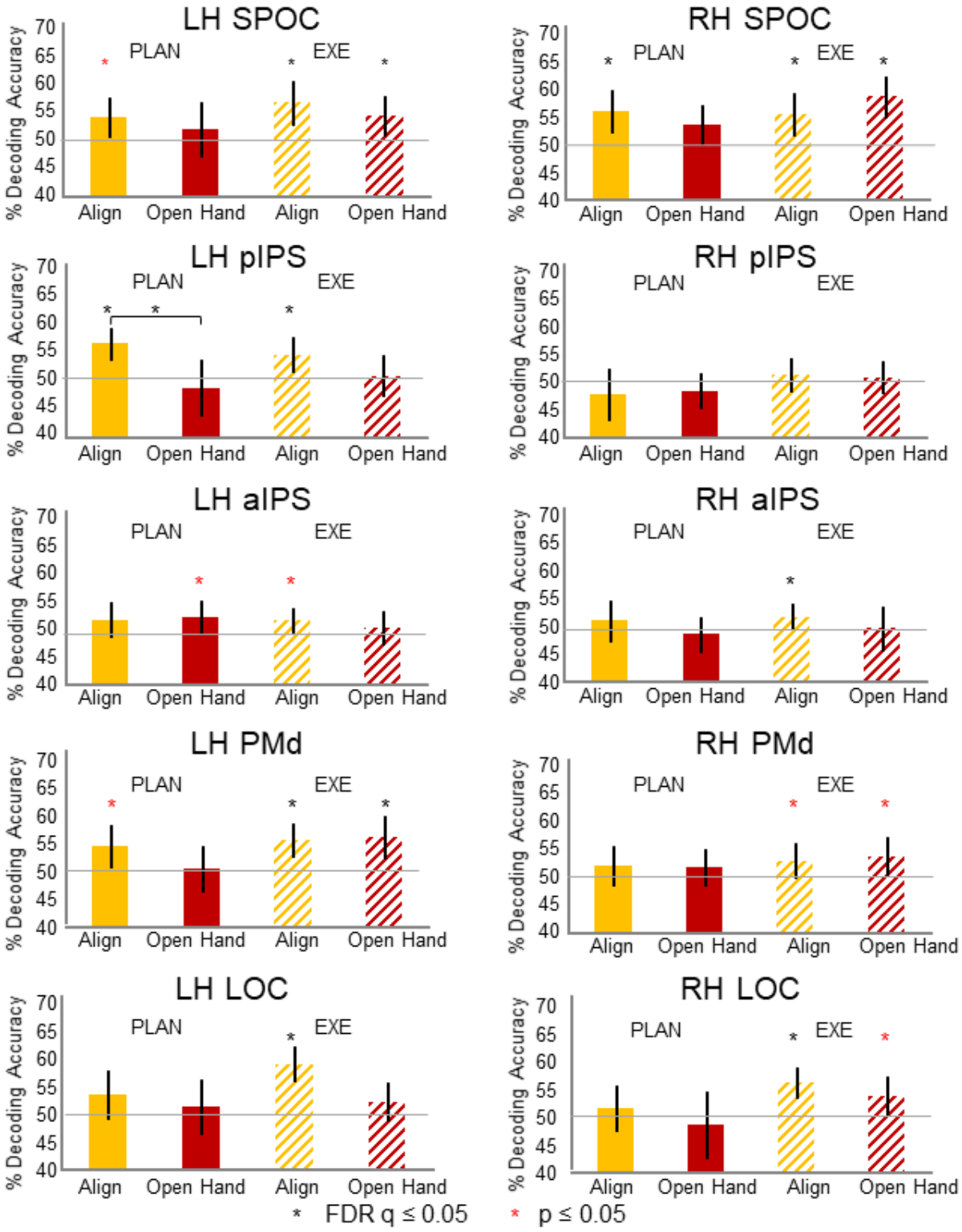

Figure 6.

MVPA results for ROIs in dorsal and ventral stream. Legends are as in Figure 5. Abbreviations: SPOC = superior parietal occipital cortex; pIPS = posterior intraparietal sulcus; aIPS = anterior intraparietal sulcus; PMd = dorsal premotor area; LOC = lateral occipital cortex.

3.2. PPI Analysis

We used PPI to test whether connectivity between early visual areas and other cortical regions is modulated in a task-dependent manner by the planned movement. We used the calcarine sulcus as the seed region since it corresponds to the peripheral cortex where objects were placed.

As shown in Figure 7, we found that the left calcarine sulcus showed stronger connections for planning the Align than Open Hand movement with numerous areas including those implicated in sensory and motor tasks, such as bilateral pIPS, PMd, left supplemental motor area (SMA), primary motor and somatosensory cortices (M1/S1), ventral premotor cortex (PMv), superior temporal gyrus (STG), right aIPS and supramarginal gyrus (SMG). Interestingly, we found connections to areas interfacing the dorsal and ventral stream. In particular, there were stronger functional connections for Align than Open Hand movements with left middle temporal gyrus (MTG), superior temporal sulcus (STS), as well as with occipital areas including the right parieto-occipital sulcus (POS), calcarine sulcus, left anterior cingulate and frontal operculum (FOp).

The right calcarine sulcus showed stronger connections for planning Align than Open Hand movements with bilateral SMA, PMd, STG, left M1/S1, aIPS, FOp, right precentral gyrus, and inferior frontal sulcus (IFS). Taken together, the PPI results reinforce the idea that early visual areas are more strongly connected to somatomotor areas for planning an Align versus Open Hand movement.

Figure 7

PPI: Plan Align > Plan Open Hand

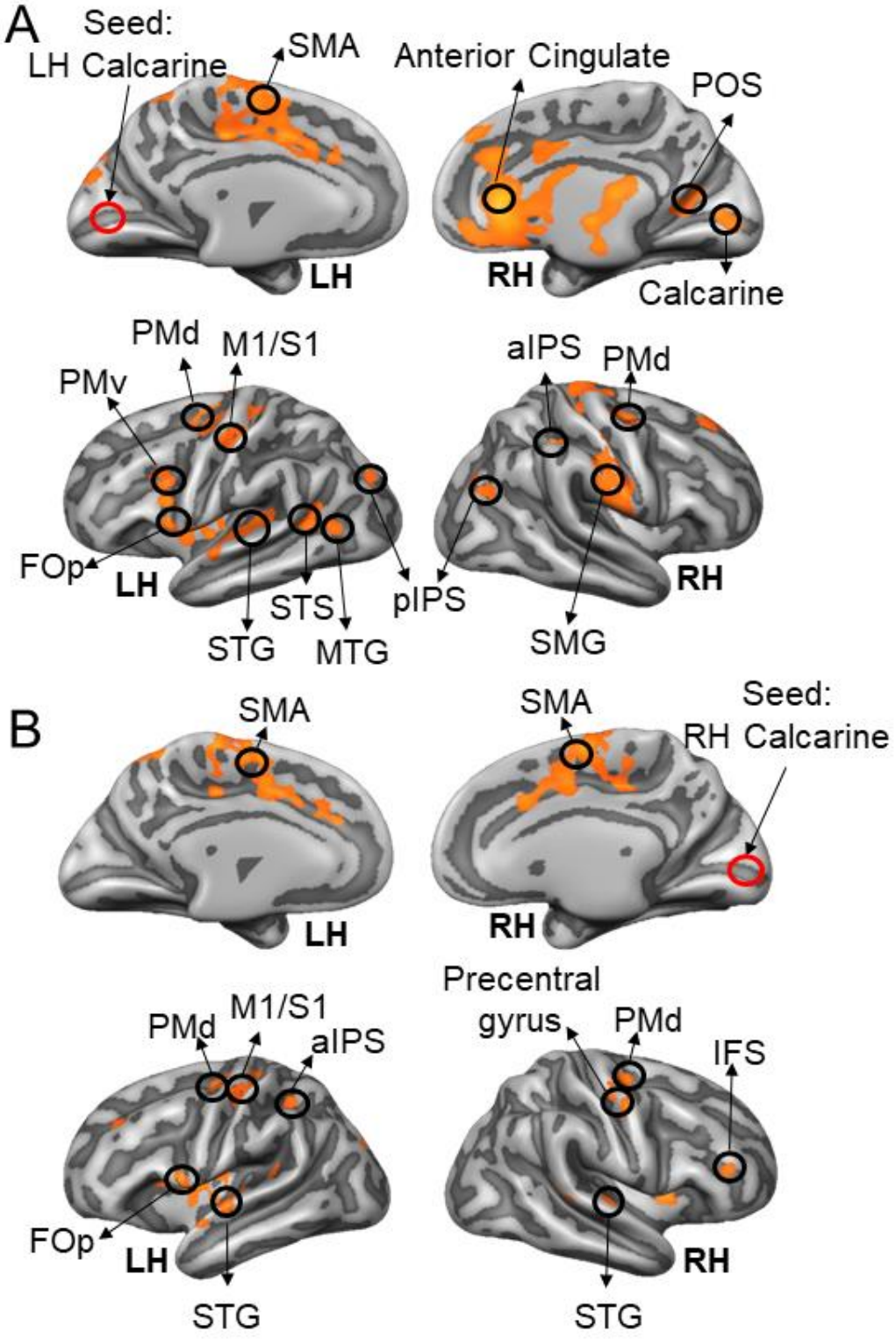

Figure 7.

Functional network of areas more strongly connected to the calcarine sulcus during the planning phase of Align than Delay Open Hand. Statistical parametric maps showing the psychophysiological interaction results using the calcarine sulcus in the LH (A) and RH (B) as seed regions. Abbreviations: PMv = ventral premotor area; PMd = dorsal premotor area; SMA = supplementary motor area; M1/S1 = primary motor cortex/ primary somatosensory cortex; pIPS = posterior intraparietal sulcus; aIPS = anterior intraparietal sulcus; MTG = middle temporal gyrus; STS = superior temporal sulcus; LOC = lateral occipital cortex; SMG = supramarginal gyrus; STG = superior temporal gyrus; IFS = inferior frontal sulcus; FOp = frontal operculum.

4. Discussion

We examined whether the cortical representation of object orientation and location was modulated by the planned action. In the calcarine sulcus, corresponding to the retinotopic location of the objects in the visual cortex, we could reliably use the activity pattern to dissociate the two object locations regardless of the upcoming action. Strikingly, in the occipital pole, SPOC and left pIPS, we could dissociate the two objects using pre-movement activity in Align but not Open Hand tasks. This suggests that in these areas, upcoming actions enhance the representation of object properties that are relevant for the particular action. Moreover, PPI shows that the calcarine sulcus is more strongly connected with somatomotor areas as well as areas that lie at the interface between the dorsal and ventral stream during the planning phase for Align than Open Hand movements. These findings indicate that cross-talks between the EVC and dorsal/ventral stream areas are present at an early stage of motor preparation, before performing the movement. Taken together, these results provide a whole-brain, network-level framework for understanding how action-relevant object features are cortically represented during action planning.

4.1. The Representation of Orientation is Shaped by Action Intention

Our results provide evidence of connections between higher-level areas involved in motor control and the EVC during the planning phase preceding an action. Behavioral and neuroimaging research have revealed that the processing of action-relevant features can be enhanced during movement preparation and relies on areas including the visual cortex (Bekkering & Neggers, 2002; van Elk et al., 2010; Gutteling et al., 2015). Interestingly, we could dissociate CCW-Left versus CW-Right as a function of the upcoming action in the occipital pole which corresponds to central vision. This is surprising given that the objects were placed below

the fixation point (peripheral vision). In particular, MVPA revealed that during action planning, the calcarine sulcus, which corresponds to the objects' placement in the visual field, showed significant decoding regardless of action type, while in the occipital pole, which corresponds to the foveal cortex, there was a task-dependent representation of the object with above chance decoding accuracy only in the Align but not the Open Hand task. The foveal cortex has been shown to contain visual information even about objects presented in the visual periphery and this phenomenon has been found to correlate with task performance and to be critical for extra-foveal perception (Williams et al., 2008; Chambers et al., 2013). Our results extend previous findings by showing that this neural mechanism applies also to action planning. Indeed, we show that during planning, the enhancement of relevant visual information, such as orientation, differs in an action-dependent way. The Align action required an adjustment of the hand to the orientation of the object, modulating the representation of object orientation in the occipital pole. Conversely, a coarse movement, such as opening the hand above the object, did not influence the representation of object orientation. This is likely because that information is not critical to successfully plan and execute the action.

We found a significant decoding accuracy for orientation during action planning in bilateral SPOC and left pIPS for Align but not Open Hand movements. Studies in both humans and monkeys have reported that SPOC plays a key role in processing wrist movements for hand orientation (Battaglini et al., 2002; Fattori et al., 2010; Monaco et al., 2011; Vesia & Crawford, 2012). Moreover, pIPS encodes 3D visual features of objects for hand actions (Sakata et al., 1998) and is involved in the adjustment of orientation of the hand and wrist (Monaco et al., 2011).

For aPIS, there was no dissociation for orientation during the planning phase of Align or

Open Hand movements. Previous studies have shown that during movement execution, aIPS shows more activation for grasp than other hand movements, such as reaching, and it is highly involved in the preshaping of the fingers (Cavina-Pratesi et al., 2010; Culham et al., 2003; Monaco et al., 2017). The fact that in our experiment participants were performing actions that did not require hand preshaping and object interaction, might have led to less recruitment of area aIPS during the planning phase. However, during action execution, aIPS showed significant decoding accuracy for orientation in Align but not Open Hand movements, in line with neurophysiology studies indicating enhanced neuronal activity in this area when orienting the wrist during a grasping movement (Murata et al., 2000; Baumann et al., 2009). Similarly, area PMd showed above chance object representation during the execution of the action, in line with studies indicating that the activity in this area is modulated during hand actions (Raos, 2005).

4.2. Psychophysiological Interactions: Functional Connectivity During Action Planning

It is possible that actions differentially modulate the representation of objects in EVC areas because of differential functional connectivity. Neurophysiology and human imaging studies have shown connections from frontoparietal areas providing feedback to early visual areas (Moore, & Fallah, 2004; Ruff et al., 2006, 2008). In line with these findings, our PPI analysis revealed stronger connections for planning Align versus Open Hand movements between the calcarine sulcus and somatomotor areas such as aIPS, pIPS, SMA, M1/S1, PMd, PMv, SMG and precentral gyrus. These results suggest that the EVC might be modulated in a top-down manner by the dorsal stream areas. In addition, areas such as MTG, STS and STG may form a hub between the dorsal stream and EVC allowing the integration of somatomotor and perceptual anticipation of a movement. Again, our results might be explained by the fact that Align movements require more adjustments than coarse Open Hand movements.

Previous studies have shown task-dependent functional connections between LOC and S1 passive tactile stimulation of the hand, as well as between the occipital pole with S1 and dorsal stream areas while participants' haptically explored objects in the dark (Tal, Geva, & Amedi, 2016; Monaco et al., 2017). We demonstrate that a task-dependent functional connectivity exists even before action execution, and without any tactile stimulation. Our study sheds light into a mechanism illustrating that cross-talks between EVC and other areas exist not only during sensory feedback but also during action preparation, and this network might allow for anticipating the consequences of the upcoming actions.

4.3. Functional Significance for Behavior

We filter feature information from redundant stimuli in the world around us to successfully plan actions. The feedback connections illustrated in this study may help with sensory gating. Moreover, the planning of actions elicits motor, somatosensory and proprioceptive anticipations that, allow for error detection and motor learning. For example, Perry, Sergio, Crawford, and Fallah (2015) showed that the receptive fields of V2 neurons displayed enhanced orientation selectivity due to the presence of a nearby hand. Behavioral and neural evidence has shown that attention is directed to the location of a planned movement (Bekkering & Neggers, 2002; Moore & Fallah, 2004). Since there is a tight linkage between attention and intention, researchers have suggested that these processes are subserved by the same neural mechanisms (Cattaneo & Rizzolatti, 2009; Rizzolatti, Riggio, Dascola, & Umilta, 1987). The dissociation of attention from action planning (intention) have been attempted. It has been suggested that if the neuronal responses that form prior to movement were due to spatial attention alone, they should fail to discriminate effector type such as eye versus limb or right versus left limb (Gallivan et al., 2013). Similarly, if our results had been driven by a higher

attentional load in Align than Open Hand tasks, we should have been able to dissociate Align versus Open Hand movements within object location. Since this was not the case, we suggest that attention alone might not drive the observed modulation.

4.4. Eye Movements Unlikely to Explain Retinotopic Effects

It is unlikely that our results showing foveal representation of the two objects during planning for Align but not Open Hand movements are due to task-related eye movements. Although we did not record eye movements during this experiment, Gallivan and colleagues (2013) conducted a behavioral study using univariate and multivariate analyses to examine fixation when participants planned actions towards an object presented in the lower visual field. Participants, including naive ones, could reliably fixate on a point for long intervals during each phase of a trial (Gallivan et al., 2013).

4.5. Disentangling Object Features Driving Modulation of Activity Pattern

For areas that show a dissociation during the planning phase between CCW-Left versus CW-Right for Align as well as Open Hand movements (i.e., the calcarine sulcus) we suggest that these areas predominantly receive location-relevant feedback. However, we cannot disambiguate whether object location or orientation drives the modulation. Indeed, both these properties might contribute to successful decoding. However, in areas that show a dissociation between the two objects for Align but not Open Hand such as the occipital pole, SPOC and left pIPS, it is likely that object orientation allows for decoding, as it is relevant for Align movements but not coarse Open Hand movements.

4.6. The Representation of Action Type During Planning

Unlike previous studies showing a dissociation between grasp and reach in dorsal and ventral stream areas during planning (Gallivan et al., 2011, 2013), we did not find a dissociation between action types within object orientation/location during the planning phase preceding actions. This difference might be related to different movements used in the two studies. Indeed, grasping and reaching might differ more from each other than Align and Open Hand movements do. For instance, grasping requires the movement of the fingers for subsequent manipulation of the objects while Align and Open Hand movements do not involve direct object interaction.

4.7. Conclusion

To conclude, we found that the visual cortex corresponding to central vision and dorsal stream areas SPOC and pIPS have an action-dependent representation of object orientation, as the pre-movement activity pattern in these areas could be reliably used to decode object features for aiming movements that required adjusting the hand according to the orientation as well as the location of the object, but not for movements that only had to be adjusted to object location. This finding in the occipital pole is interesting considering that the objects were presented in the visual periphery. In addition, functional connectivity analyses showed strong task-specific functional connections between the EVC and somatomotor areas during the planning phase preceding the action.

These results suggest a role of the EVC in predictive coding of actions based on internal models that take into account visual and somatosensory anticipations of upcoming movements, as well as object features that are relevant for subsequent actions. This mechanism might be mediated by bidirectional functional connections between dorsal stream areas, known to be involved in action planning, and the EVC, known to process the visual features of objects.

Feedback connections from the dorsal stream areas might tune the signal in the EVC to enhance the representation of action-relevant object features.

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