Action-specific feature processing in the human cortex: An fMRI study

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ABSTRACT

Sensorimotor integration involves feedforward and reentrant processing of sensory input. Grasp-related motor activity precedes and is thought to influence visual object processing. Yet, while the importance of reentrant feedback is well established in perception, the top-down modulations for action and the neural circuits involved in this process have received less attention. Do action-specific intentions influence the processing of visual information in the human cortex? Using a cue-separation fMRI paradigm, we found that action-specific instruction processing (manual alignment vs. grasp) became apparent only after the visual presentation of oriented stimuli, and occurred as early as in the primary visual cortex and extended to the dorsal visual stream, motor and premotor areas. Further, dorsal stream area aIPS, known to be involved in object manipulation, and the primary visual cortex showed task-related functional connectivity with frontal, parietal and temporal areas, consistent with the idea that reentrant feedback from dorsal and ventral visual stream areas modifies visual inputs to prepare for action. Importantly, both the task-dependent modulations and connections were linked specifically to the object presentation phase of the task, suggesting a role in processing the action goal. Our results show that intended manual actions have an early, pervasive, and differential influence on the cortical processing of vision.

1. Introduction

Most neuroimaging studies of visual-motor integration have focused on the question of how vision is used to plan movements in a feedforward fashion (Fabbri et al., 2016; Verhagen et al., 2012; for reviews see: Gallivan and Culham, 2015; Vesia and Crawford, 2012). Despite the importance of feedforward processes, feedback is required to combine low-level features, such as line orientation, with high-level concepts, such as affordances (Michalowski et al., 2022). Indeed, the intended action itself often determines which visual details are relevant for the feedforward transformation (Craighero et al., 1999). For instance, while some object features like size, shape, and orientation are important for grasping, pointing only requires knowledge of the object location (Van Elk et al., 2010). Further, the same object feature, such as orientation, might be processed differently depending on the nature of the action (Gutteling et al., 2011), e.g., grasping an object versus matching the

orientation of an object by aligning the hand. Indeed, these two movements require a different degree of adjustment of hand, fingers, and wrist posture. Therefore, the motor system might benefit from controlling the sensory inputs in a task-specific manner, presumably through reentrant feedback (Gilbert and Li, 2013). Consistent with this, recent evidence shows that the activity pattern in the early visual cortex (EVC) is differentially modulated by action plans (Gallivan et al., 2019; Monaco et al., 2020; Velji-Ibrahim et al., 2022). However, it remains unclear how task instruction interacts with visual inputs and what functional connectivity is involved.

The influence of action on perception is well established. For example, placing the hand near a stimulus can influence blindsight (Schendel and Robertson, 2004; Brown et al., 2008), extinction (di Pellegrino and Frassinetti, 2000), reaction times (Reed et al., 2006), visual search (Abrams et al., 2008), and enhance visual memory recall (Heuer et al., 2016a) as well as orientation selectivity in macaque's V2

neurons (Perry et al., 2015). Further, neurons in macaque's anterior intraparietal sulcus (AIP), an area known to be involved in grasping, show enhanced responses to action instruction when a stimulus is presented before as opposed to after the action cue (Baumann et al., 2009). Gutteling and collegues (2011) have shown that such motor enhancements can be specific to action-relevant features. For instance, orientation perception is more accurate when one intends to grasp an object as opposed to simply point towards it. Importantly, this effect is attenuated by stimulation of the anterior intraparietal sulcus (aIPS), known to have a role in the control of grasp also in humans (Culham et al., 2003; Gutteling et al., 2013; Monaco et al., 2019), suggesting that the aIPS is involved in the reentrant filtering of visual orientation. Some of this reentrant filtering might occur at the level of occipital cortex. For example, the lateral occipital complex (LOC) is more active during delayed grasping than reaching movements in the dark (Singhal et al., 2013), presumably because of the additional sensory processing required to shape the hand for grasping an object. However, little more is known about how the details of motor planning influence visual feature processing, how early this occurs in the visual system, and which reentrant feedback pathways are involved.

A recent study by Velji-Ibrahim et al. (2022) has investigated the representation of action plans using fMRI by having participants perform manual alignment movements as opposed to nonspecific movements that did not require interaction with the object. The authors found that the early visual cortex, in addition to frontal and parietal areas, shows significant decoding accuracy for the dissociation between object orientations in the Align but not nonspecific movements. In the current study, both tasks (grasp vs. manual alignment) require an interaction with the object but involve different muscles and therefore different movement plans. Would this difference be enough to elicit a difference in the extent of brain activation during the presentation of the object and subsequent action plan?

It might not be surprising to find action-specific stimulus processing in dorsal visual stream action areas (Goodale and Milner, 1992; Culham et al., 2003), but there is growing evidence that reentrant feedback from motor systems influences visual processing at an earlier level. For example, reentrant pathways from fronto-parietal areas to the visual system might explain attentional enhancements near the movement goal (Moore and Fallah, 2001; Moore and Armstrong, 2003; Heuer et al., 2016b; Perry and Fallah, 2017) and perceptual detection tasks (Gutteling et al., 2011). Therefore, it is also possible that action plans modify early sensory input to predict the sensory consequences of the impending action. In addition, according to the theory of reverberating circuits (Hebb, 1949), these connections would persist well after the visual stimulus (the origin for feedforward visual signals) has disappeared. These factors could explain reactivation of the visual cortex during target-directed movements in the dark (Singhal et al., 2013; Chen et al., 2014; Cappadocia et al., 2017; Blohm et al., 2019; Monaco et al., 2019), and representation of action intention in the early visual cortex (Gutteling et al., 2015; Gallivan et al., 2019; Monaco et al., 2020). However, these decoding experiments did not test functional connectivity generated by motor signals, or if/when/how they interact with the sensory inputs to visual cortex. If these motor signals result from reentrant feedback for the purpose of shaping visual inputs, one would expect them to show 1) functional connectivity with parieto-frontal motor areas, and 2) specific interactions with the relevant stimulus-related visual inputs. Here, we tested these hypotheses with functional Magnetic Resonance Imaging (fMRI) by using a cue-separation task in which participants performed one of two actions (manual alignment and grasp) towards a rod in two possible orientations. While the location and orientation of the rod were the same for the two actions, the same orientation required different kinematics for manual alignment vs. grasping movements. To examine the influence of specific action instructions on the cortical processing of visual information, we temporally separated action cues and stimulus presentation, with the action being specified *before* the stimulus. Specifically, we instructed subjects to either grasp or align their hand with the oriented object, then showed them the orientation of the object, and finally provided a 'go' signal that cued participants to perform the action. We examined if the cortical response following the visual stimulus was modulated by action instruction, and whether the same modulation was already present during the action instruction phase. In addition, we used Psychophysiological Interaction (PPI) analysis (Friston et al., 1997; McLaren et al., 2012; O'Reilly et al., 2012) to identify potential neural pathways for action-related modulation of sensory information. Our results confirm that during action planning, the supplementary motor cortex, aIPS, and V1 are modulated in a task instruction-dependent manner. In addition, aIPS and V1 show that these task-dependent modulations are reflected in functional connections with parietal and frontal regions, and only occur when the features of the stimulus to be acted upon have been specified.

2. Material and methods

2.1. Overview of experiment and hypotheses

Fourteen human participants lay on the bed of the MRI and used their right (dominant) hand to perform delayed grasp or hand-alignment actions towards a real 3D rod oriented obliquely or horizontally and placed on an apparatus located above their pelvis (Fig. 1A and B). Our experimental paradigm (Fig. 1C) exploited a cue-separation task based on previously published neurophysiological (Baumann et al., 2009) and neuroimaging studies (Beurze et al., 2009; Cappadocia et al., 2017). In each trial, participants received an Auditory Action-cue, followed by an 8-s delay (Instruction phase) and then briefly viewed the oriented rod, the Visual Orientation-cue, followed by another 8-s delay (Object phase). Participants maintained gaze fixation throughout the trial in an otherwise completely dark space. At the end of the Object phase, an auditory "go" Execution-cue instructed the participants to perform the movement toward the rod (Action execution). We used a slow event related design and randomly interleaved task (Grasp, Align) and stimulus orientation (Horizontal, Oblique) across trials. The Align condition required participants to adjust the hand and wrist posture according to the orientation of the rod, while in the Grasp condition participants adjusted the fingers on the rod in a whole-hand grasp and, to a lesser extent, the hand and wrist posture. Therefore, Align and Grasp movements required different muscle control (proximal vs. distal), as well as different degrees of adjustment (Fig. 1B). Proximal muscle control was higher in the Align than Grasp condition, while distal muscle control was higher in the Grasp than Align condition. This paradigm was designed to test whether the task instruction (Align vs. Grasp) modulated the subsequent activation elicited by the visual presentation of the stimulus during the Object phase.

We hypothesized that cortical regions that integrate visual and action-specific input would show differences in visual processing of the stimulus for one action as compared to the other. In fact, different affordances for the two action types would require different object processing. This would be reflected in differential activation for the two action plans in the Object as compared to Instruction phase and Action execution, which would result in a 2 × 3 interaction with factors Task (Grasp, Align) and Phase (Instruction phase, Object phase, Action execution). The differential activation would become evident only after the action instruction and the object have become apparent and the related information can be integrated in a motor plan.

2.2. Participants

Fourteen participants (3 males and 11 females, age range: 24–42 years, average 32 years) participated in this study and were financially compensated for their time. All participants were right-handed and had normal or corrected-to-normal visual acuity. They gave their consent prior to the experiment. This study was approved by the York University
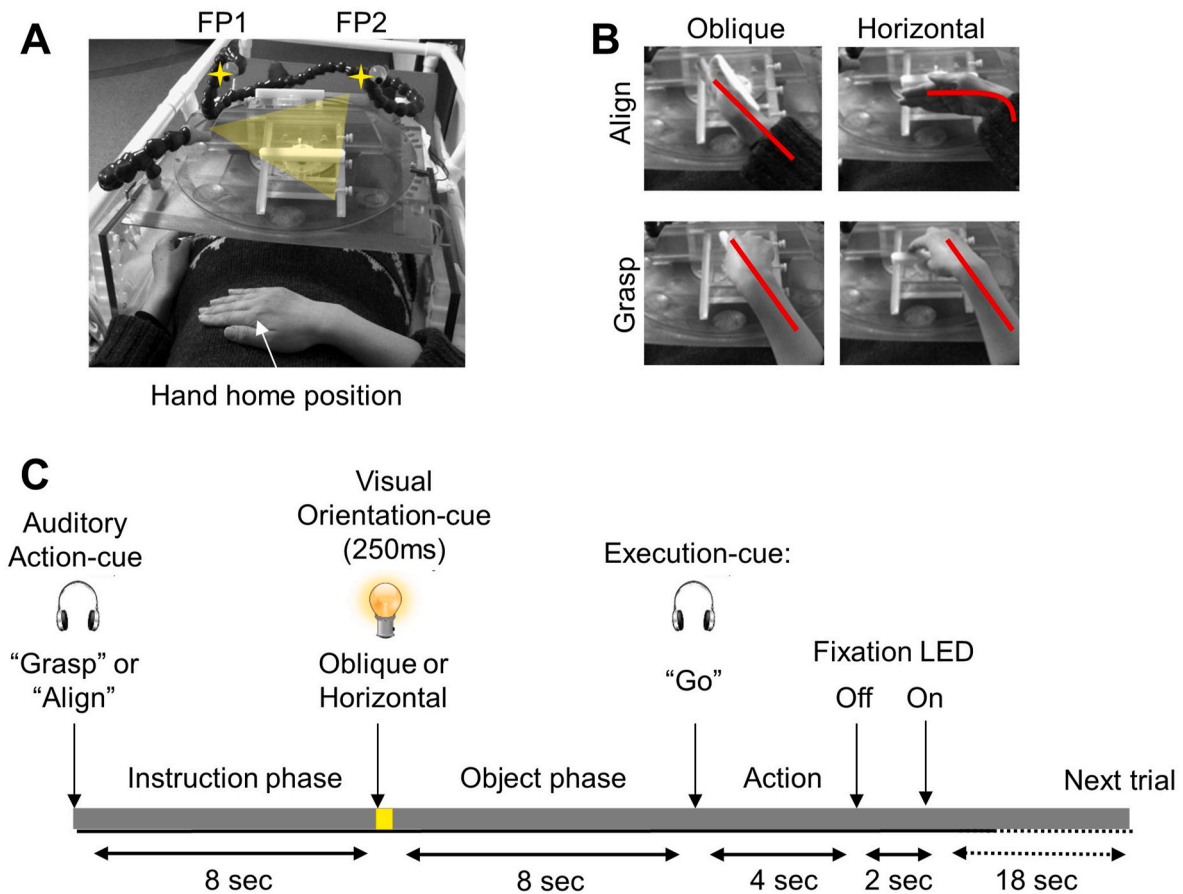
Fig. 1. Illustration of setup and task. A. Participants were required to gaze at one of two fixation points (FP 1 and 2, marked with a star) for the duration of each trial. The target object consisted of a white rod and was placed centrally below the fixation points. **B.** The task consisted of grasping the rod or aligning the hand according to the orientation of the rod (Oblique or Horizontal). **C.** Illustration of the experimental timing. Each trial started with the auditory cue ("Grasp" or "Align") about the action that had to be performed at the end of the trial. After an 8-s delay, the rod was illuminated for 250 ms in one of two possible orientations (Oblique or Horizontal). After another 8-s delay, a "go" cue instructed participants to perform the action towards the rod. After 4 s the fixation cue was turned off for 2 s then re-appeared in the same or different location. The next trial started 18 s later.

Human Participants Review Subcommittee.

2.3. Apparatus and stimuli

Stimuli were presented to the participants on the inclined surface of a platform placed above the participant's pelvis. For details about the set up see (Monaco et al., 2014). Each participant lay supine in the scanner with the head tilted allowing a direct view of the stimulus. Participants wore headphones to hear auditory instructions about the task that they were to perform at the end of the trial.

The platform was reached by the participant (from inside the bore) to perform the task and by the experimenter (from outside the bore) to change the stimulus orientation between trials. The platform was made of Plexiglas and was fixed to the bore through hooked feet. The location of the platform could be adjusted to ensure that both the participant and the experimenter could reach it comfortably. The head of the participant was tilted by 20° to allow comfortable viewing of the stimuli. The inclination of the platform could also be adjusted to improve the view and the reachability of the object for each participant. A rectangular surface was angled atop the turntable to improve the visibility of the object and its location could be adjusted for each participant (Fig. 1A). A fitted rotating wheel (radius = ~4 cm) was embedded on the surface of the platform. The rod was secured to the rotating wheel through fitted pins. Lateral stoppers on the platform served as markers for the experimenter to adjust the orientation of the rod in the dark for the upcoming trial. The orientation of the rod was adjusted to ensure that each

participant could reach it comfortably avoiding awkward hand and wrist postures. A cloth was mounted on the ceiling of the magnet bore to occlude the participant's view of the experimenter.

The stimulus consisted of a rod (10 cm × 1 cm x 1 cm) made from Plexiglass and painted white to increase the contrast with the workspace (Fig. 1A). The angular size of the rod was approximately 8° and was presented at approximately 8–10° of eccentricity in the lower visual periphery. Participants practiced the task and familiarized themselves with the objects for about 5 min prior the experiment.

Except for the brief illuminated presentation of the object, subjects were in near-complete darkness throughout the duration of the trial (only a small dim light was provided by fixation). During the intertrial interval (ITI), and after the participant had performed the task, the orientation of the rod was quickly changed by the experimenter or left in the same orientation for the next trial.

Optic fibers were used to provide a fixation point, to illuminate the workspace, and to cue the experimenter regarding stimuli on upcoming trials. The participant maintained the fixation on one of the two points of light positioned above the object, so that all objects were presented in the left or right participant's lower visual field. A bright light (illuminator) was used to briefly illuminate the object at the onset of each event of a trial. The illuminator was placed above the participant's head and shone light onto the object. Another source of light was based at the end of the platform, visible to the experimenter, but not to the participant, to instruct the experimenter about the orientation of the rod on upcoming trials. The lights and audios were controlled by a program in MATLAB

(The MathWorks, Inc., Natick, MA, USA) on a laptop PC that received a signal from the MRI scanner at the start of each trial. The window in the scanner room was blocked and the room lights remained off such that, with the exception of the dim fixation point which remained on for the duration of a trial, nothing else in the workspace was visible to the participant when the illuminator was off. An infrared camera (MRC Systems GmbH) recorded the performance of each participant for offline investigation of the errors, which were excluded from further analysis. The errors were defined as mistakes in the performance of the participants during the task, such as initiating a movement during the delays, performing a grasp in an align condition or vice versa. Less than 1.5% of total trials were discarded from the analyses due to participants' errors.

2.4. Timing and experimental conditions

We used a slow event-related design to prevent contamination of the blood oxygen level-dependent (BOLD) response by any potential artifacts generated by the hand movement. Trials onsets were spaced every 40 s with an ITI of 16 s to allow the hemodynamic signal to return to baseline between trials. Each trial started with the Auditory Action-cue that consisted of a recorded voice that said "Grasp" or "Align" and instructed the participant about the task to be performed at the end of the trial (Fig. 1C). The auditory cue was followed by a delay of 8 s (Instruction phase), after which the stimulus, Visual Orientation-cue, was illuminated for 250 ms showing the rod in one of the two orientations. The visual cue consisted of the brief illumination of the 3D rod presented in one of two possible orientations: horizontal (approximately 0° angle) or oblique (approximately −45° angle). The visual cue was followed by another delay of 8 s (Object phase), after which an auditory go cue instructed the participant to perform either grasp or align action (Action execution) that had been instructed at the beginning of the trial. After 3 s from the go signal, a "Beep" sound cued the participant to return the hand to the home position. One second later, the fixation light was turned off for 2 s during which participants were instructed to gaze freely. The same or different fixation light was then turned on and participants fixated the LED in the dark.

Note that the delays following the Auditory Action-cue and the Visual Orientation-cue allowed us to examine the brain activation in the phases that followed auditory action instruction and visual input while also allowing us to separate the sensory processing from the motor response.

For each run, consisting of 8 trials, the fixation points and orientations of the stimuli were equally balanced for Align and Grasp conditions, and the order of the conditions was randomized in each run. A baseline of 16 s was added at the beginning and at the end of each run yielding a run time of approximately 6 min per run. Each participant performed 6 runs, for a total of 24 trials for each Task (Grasp and Align). A session for one participant included set-up time (~45 min), six functional runs and one anatomical scan, and took approximately 90 min to be completed.

2.5. Imaging parameters

All imaging was performed at York University (Toronto, ON, Canada) using a 3-T whole-body MRI system (Siemens Magnetom TIM Trio, Erlangen, Germany). The posterior half of a 12-channel receive-only head coil (6 channels) at the back of the head was used in conjunction with a 4-channel flex coil over the anterior part of the head (see Monaco et al., 2014). The anterior part of the 12-channel coil was removed to allow the participant to see the stimuli directly and comfortably but at a cost of anterior signal loss, hence the addition of the 4-channel flex coil. The posterior half of the 12-channel coil was tilted at an angle of 20° to allow the direct viewing of the stimuli. We used an optimized T2-weighted single-shot gradient echo echo-planar imaging (211-mm field of view [FOV] with 64 × 64 matrix size, yielding a resolution of 3.3-mm isovoxel; 3.3-mm slice thickness with no gap; repetition time

[TR] = 2 s; echo time [TE] = 30 ms; flip angle [FA] = 90°). Each volume comprised 38 slices angled at approximately 30° from axial (i.e., approximately parallel to the calcarine sulcus) to sample occipital, parietal, posterior temporal, and posterior/superior frontal cortices. The slices were collected in ascending and interleaved order. During each experimental session, a T1-weighted anatomical reference volume was acquired along the repeated orientation as the functional images using a 3D acquisition sequence (256 × 240 × 192 FOV with the repeated matrix size yielding a resolution of 1-mm isovoxel, inversion time, TI = 900 ms, TR = 2300 ms, TE = 5.23 ms, FA = 9°). The coil configuration used allowed coverage of most part of the brain, except for the ventral part of the cerebellum.

2.6. Preprocessing

Data were analyzed using the Brain Voyager QX software (Brain Innovation 2.8, Maastricht, The Netherlands). The first 2 vol of each fMRI scan were discarded to allow for T1 equilibration. Functional data were preprocessed with spatial smoothing (full-width at half-maximum = 8 mm) and temporal smoothing to remove frequencies below 2 cycles per run. Slice-time correction with a cubic spline interpolation algorithm was also performed. Functional data from each run were screened for motion or magnet artifacts with cine-loop animation to detect eventual abrupt movements of the head. In addition, we ensured that no obvious motion artifacts (e.g., rims of activation) were present in the activation maps from individual participants. Each functional run was motion corrected using a trilinear/sinc interpolation algorithm, such that each volume was aligned to the volume of the functional scan closest to the anatomical scan. The motion correction parameters of each run were also checked: three runs from one subject showed abrupt head motion over 1 mm and were discarded from further analyses. Functional data were superimposed on anatomical brain images, aligned on the anterior commissure–posterior commissure line, and transformed into Talairach space (Talairach and Tournoux, 1988).

2.6.1. General linear model

To investigate which brain areas are involved in our task, we conducted voxelwise analyses on group data with a random effect (RFX) general linear model (GLM). The GLM included a predictor for each event of the trial: Instruction phase, Object phase, and Action execution. Each predictor was derived from a rectangular wave function convolved with a standard hemodynamic response function (HRF; Brain Voyager QX's default double-gamma HRF). In particular, we used predictors covering the following time windows: 8 s (or 4 vol) for the Instruction and Object phase, and 4 s (or 2 vol) for the Action execution. Each of these phases included two predictors (Align and Grasp) for a total of six predictors of interest. In addition, we included a predictor of 4 s (or 2 vol) to account for the free gazing when the fixation light was turned off and on after the execution of the action. The following 16 s, during which participants fixated the fixation cross, were considered as baseline, together with the 16 s at the beginning and at the end of each run. Therefore, in total the RFX GLM included seven predictors for each participant in addition to the 6 motion correction parameters. Contrasts were performed on the %-transformed beta weights (β).

2.7. Voxelwise interaction

Our hypothesis was aimed to test if the cortical activity associated with sensory processing is modulated by action instruction. If so, the activation during the Object phase, following the Visual Orientation-cue, would be influenced by the task that was instructed at the beginning of the trial (Grasp or Align). This would be reflected in higher activation for one task over the other during the Object but not Instruction phase. In other words, this effect would elicit a significant Task by Phase interaction in a 2 × 3 ANOVA with 2 tasks (Grasp and Align) and three phases (Instruction phase, Object phase, and Action). We

investigated the effect of such interaction at voxelwise level by using BrainVoyager's ANCOVA random effect analysis. For areas that showed a significant interaction, we extracted the β weights and performed t-tests to explore the reason that gave rise to the interaction. Specifically, we compared Align vs. Grasp during Instruction phase, Object phase, and Action execution.

It is important to emphasize that during the Object phase, participants: 1) were not performing any action yet and 2) had received the auditory instruction about the action (Grasp or Align) 8 s earlier. Although during this phase participants briefly viewed one of the two oriented objects, our hypothesis is not based directly on the visual information (i.e. object orientation), but on the action to be performed on the viewed object 8 s later.

Before testing our hypotheses, we explored the network of areas showing a general response during Instruction and Object phase, and Action execution [(Align + Grasp) > Baseline]. As expected, a wide network of areas ranging from occipital to parietal and frontal cortex were involved in all three phases of the task. The EVC (including the posterior part of the Calcarine sulcus and the Cuneus) was also involved in all three phases even though visual input was briefly provided only in the Object phase.

For each activation map, we performed the cluster threshold correction (Forman et al., 1995) using the Brain Voyager's cluster-level statistical threshold estimator plug-in (Goebel et al., 2006). This algorithm uses Monte Carlo simulations (1000 iterations) to estimate the probability of a number of contiguous voxels being active purely due to chance while taking into consideration the average smoothness of the statistical map. Because map smoothness varies with the contrast, different contrasts have different cluster thresholds. In cases in which the activation foci did not survive cluster threshold correction at an alpha-correction level of 0.001, we indicated the regions with a triangle in Figs. 3 and 4.

The rationale for having two fixations is as follows: we wanted to examine whether the action-specific processing of the object would be lateralized to the hemisphere contralateral to object presentation. In particular, we expected to see stronger effects for Align vs. Grasp (or vice versa) in the left hemisphere when participants fixated the fixation LED placed on the left (and the object was in the right visual field), and stronger effects in the right hemisphere when participants fixated the fixation LED on the right (and the object was in the left visual field). Since this was not the case, we collapsed the data for Left and Right stimulus location relative to gaze.

Complementary Voxelwise analyses aimed at testing the key hypothesis are shown in the Supplemental material.

2.8. Psychophysiological interaction analysis (PPI)

We used the psychophysiological interaction method (Friston et al., 1997; McLaren et al., 2012; O'Reilly et al., 2012) to estimate the task-specific changes in effective connectivity between our seed regions and the rest of the cortex. The PPI identifies brain regions whose functional connectivity is task-dependent and results from an interaction between the psychological component (the task) and the physiological component (the time course) of the seed region. In particular, we examined which brain areas show task-specific correlations with aIPS and V1. With this aim, we created a PPI model for each area, run, and participant. The PPI model included: 1) the physiological component corresponding to the z-normalized timecourse extracted from the seed region, 2) the psychological component corresponding to the task model (boxcar predictors convolved with a standard hemodynamic response function), and 3) the psychophysiological interaction component, corresponding to the z-normalized timecourse multiplied, volume by volume, with the task model. The boxcar predictors of the psychological component were set to +1 for the Align task, −1 for the Grasp task, and zero for baseline. The psychological and physiological components were added as co-variates to our model to account for confounds related to 1)

an effect of task, regardless of the physiological component, and 2) a correlation with the seed ROI timecourse, regardless of the task and shared task input. We selected our seed region based on the contrast of Align vs. Grasp in the Object phase. The motion correction parameters from each participant were added as co-variates of no interest. The individual GLM design matrix files were used for a random effects model analysis (Friston et al., 1999). The GLM was based on the same predictors and timings used for the univariate analysis. The statistical threshold criterion was set to p < 0.05 for all presented contrasts, and the connectivity map was corrected for multiple comparisons using the Monte Carlo simulation approach (Forman et al., 1995).

3. Results

We have divided the results into three parts. First, we overviewed the areas involved in Align and Grasp tasks during Instruction, Object and Action phases. We then showed the Task by Phase interaction during the Object phase. Lastly, we presented the PPI results where aIPS and V1 have been used as the seed region.

3.1. General observations: preparatory set, planning, and motor execution

As an overview, our tasks (Align and Grasp) elicited above baseline activation in cortical areas involved in visual processing for action during Instruction and Object phase, as well as Action execution (Fig. 2). These included well known reach and grasp areas such as the superior parietal-occipital cortex (SPOC), anterior intraparietal cortex (aIPS), dorsal premotor cortex (dPM) and the pre-supplementary motor area (preSMA). It is noteworthy that non-motor areas, such as occipital areas involved in early vision (such as the Calcarine sulcus; Cal) and temporal areas (such as posterior part of the inferior temporal sulcus; pITS) known to be involved in higher level functions, were also activated during Instruction and Action execution phase despite the absence of visual stimulation. Re-activation of the early visual cortex during actions in the dark has already been shown in earlier neuroimaging studies (Singhal et al., 2013; Monaco et al., 2017). The auditory instruction might have elicited activation in the early visual cortex through functional connections. Indeed, in some species the auditory cortex has direct connections to primary visual cortex (Budinger et al., 2006; Campi et al., 2010). At this level of analysis many of these cortical areas were active throughout the duration of the task, including the first Instruction phase

Table 1

Talairach coordinates and number of voxels of areas showing a Task by Phase interaction.

Brain areas	Talairach coordinates			Number of voxels
	X	Y	Z	
LH preSMA	−2	9	48	600
RH preSMA	6	6	50	902
LH dPM	−16	−19	65	379
RH dPM	17	−17	59	485
LH SMA	−4	−5	58	572
RH SMA	13	−17	57	562
LH M1	−39	−20	54	990
RH M1	36	−20	58	767
LH S1	−44	−30	54	875
RH S1	41	−28	58	721
LH aIPS	−51	−29	41	802
RH aIPS	34	−38	31	502
LH mpCS	−20	−43	56	793
RH mpCS	14	−46	56	941
LH pIPS	−25	−77	19	559
RH pIPS	21	−67	31	653
LH SPOC	−17	−75	29	699
RH SPOC	19	−68	33	205
LH V1	−6	−88	−8	218

Note: areas refer to the results in the activation map in Fig. 4.

(Fig. 2A), the second Object phase (Fig. 2B), and the final motor response (Fig. 2C). This suggests that as soon as participants were instructed about the nature of the forthcoming action (Align or Grasp), preparatory activity (sometimes called 'preparatory set') commenced in

these cortical areas. According to our experimental design, this preparatory activity would then combine with visual information about object orientation to allow the creation of a specific motor plan in the Object phase, which precedes motor execution. This is the focus of the
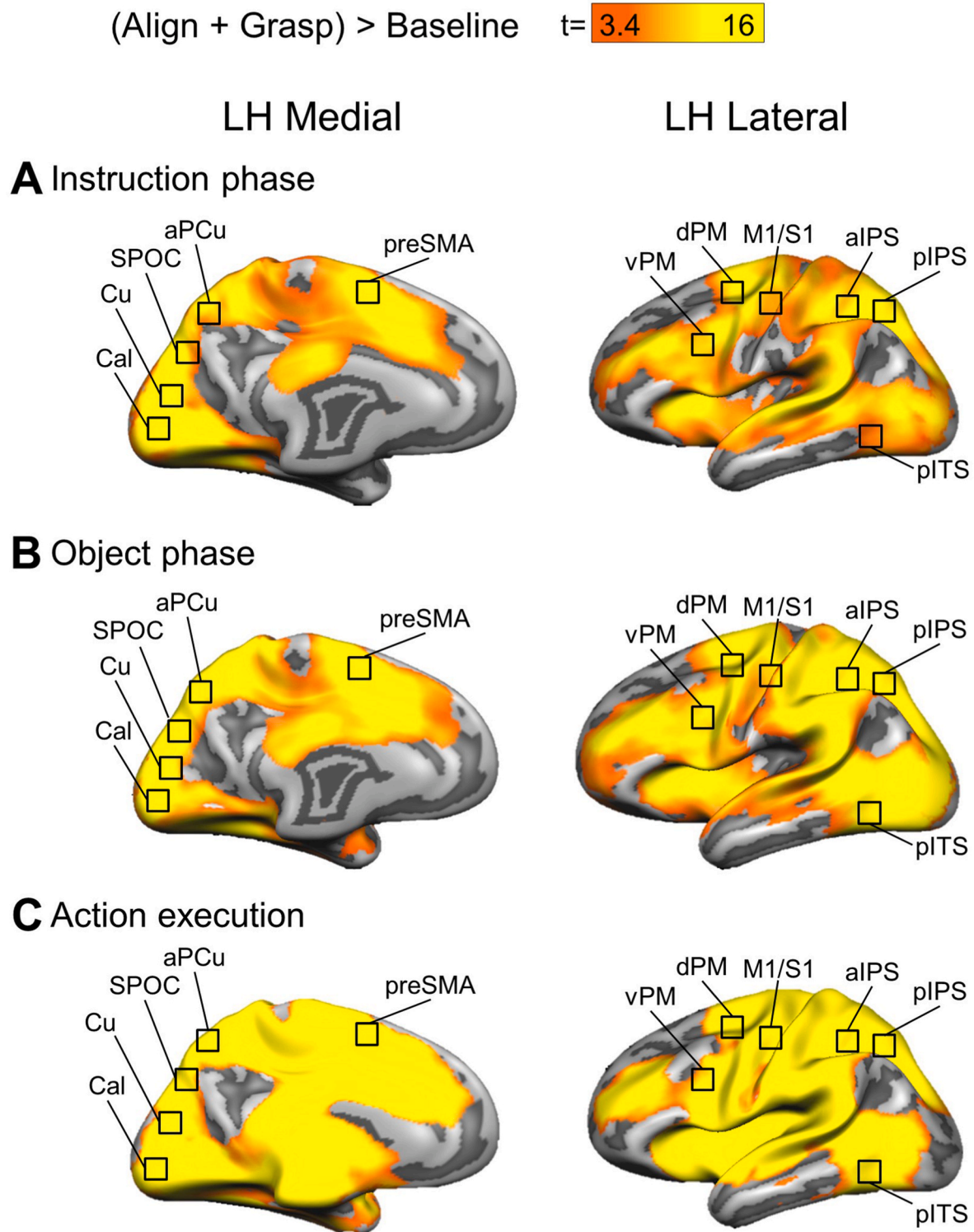

Fig. 2. General activity for Align and Grasp conditions during the three phases of the trial in the medial and lateral view of the left hemisphere. Statistical parametric maps are overlaid on the average cortical surface derived from the cortex-based alignment performed on 11 of the 14 participants. The anatomical scans from 3 participants were discarded because the poor quality of the T1 images lead to sub-optimal surface reconstruction of the cortical sheet. The surface from the average of 11 subjects has the advantage to show less bias in the anatomy of the major sulci as compared to the surface of one participant only. We verified that activation from volumetric maps appeared on the corresponding region of the cortical surface. The statistical parametric maps show areas with above-baseline activation for Align and Grasp conditions during: **A.** Instruction phase, **B.** Object phase, and **C.** the Action execution.

remainder of our analysis, i.e., how specific action instructions and preparatory activity from the Auditory Action-Cue influence cortical visual processing for the purpose of motor planning in the Object phase (8 s later) (Fig. 2).

3.1.1. Task by phase interaction

We performed a voxelwise analysis aimed at testing our hypothesis. The activation map resulting from the Task by Phase interaction is illustrated in Fig. 3. The Talairach coordinates and number of voxels for each area are indicated in Table 1. Our hypothesis predicts that areas that differentially process visual information as a function of previous task instruction would show differential activation for the two action types in the Object phase. This effect would result in a significant Task by Phase interaction, with differential Task activation in the Object but not Instruction phase. Note that in the Object phase the visual

information was related to the object orientation, while task instruction was delivered in the previous phase (8 s earlier). Fig. 3 provides the activation map corresponding to the Task by Phase interaction, which yielded activation in bilateral dorsal premotor (PM) cortex, presupplementary and supplementary motor (preSMA and SMA) areas, primary motor (M1) and somatosensory (S1) cortices, anterior intraparietal sulcus (aIPS), medial post-central sulcus (mpCS), posterior intraparietal sulcus (pIPS), superior parieto-occipital sulcus (SPOC), as well as left primary visual cortex (V1). We ran t-tests on the β weights of each area simply to confirm that the reason that gave rise to the interaction was indeed aligned with our hypothesis. As such, we compared Align vs. Grasp in the Instruction phase, Object phase and Action execution. Statistical values are shown in Table 2 (Fig. 3).

Although overall activation appeared to be fairly consistent across the three trial phases (Fig. 2), the details of cortical processing were
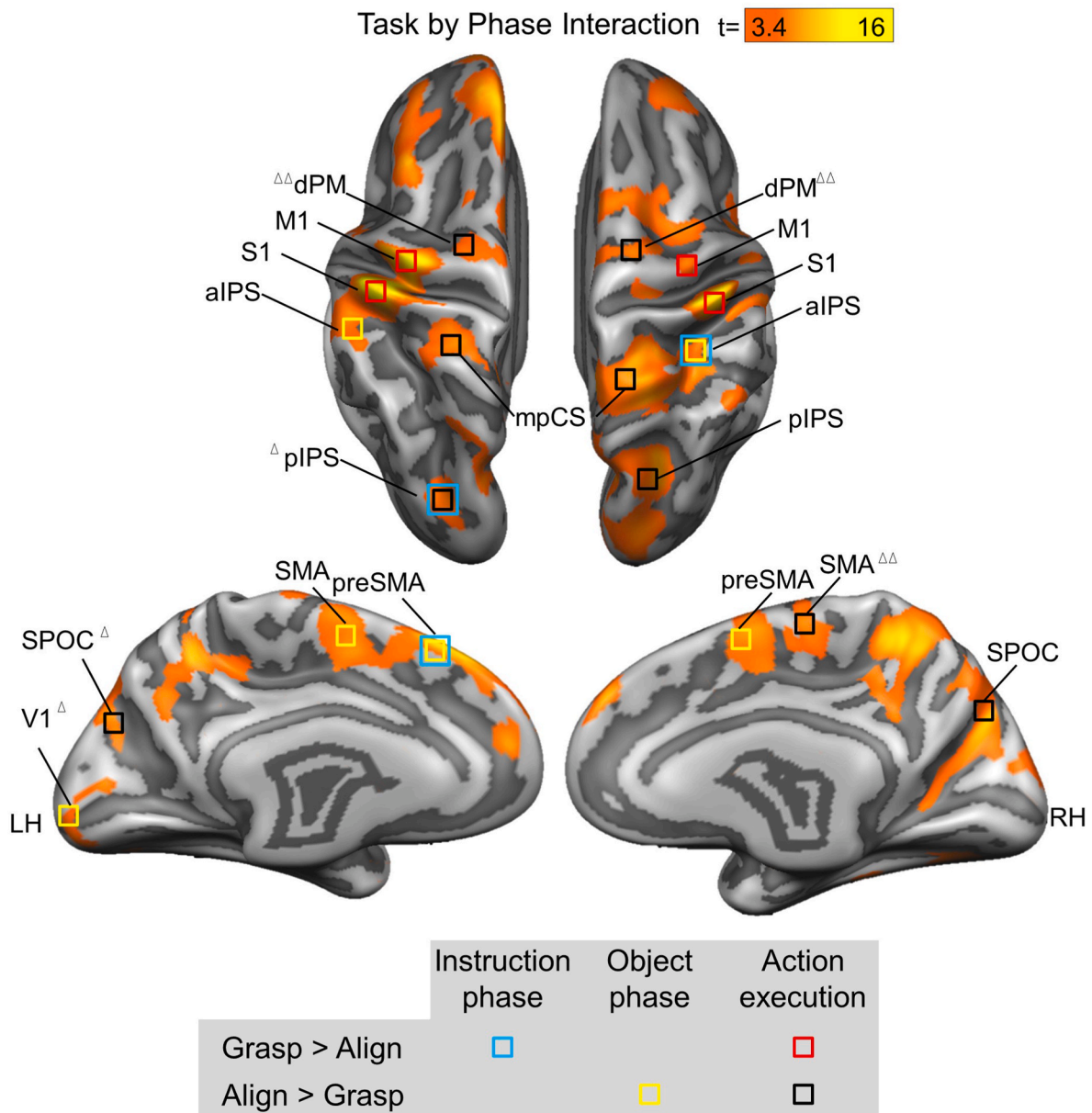

Fig. 3. Influence of action intention on sensory processing. Statistical parametric map obtained with the RFX GLM for the Task by Phase interaction. Areas marked in yellow and black show higher activation for Align than Grasp in the Object phase and Action execution, respectively. Conversely, areas marked in light blue and red show higher activation for Grasp than Align in the Instruction phase and Action execution, respectively. The triangles indicate areas that did not survive cluster threshold correction at an alpha-correction level of 0.01 ($^\triangle$) and 0.001 ($^{\triangle\triangle}$). The presentation of these areas allows for results that did not make the cluster threshold correction to be inspected.

Table 2
Statistical values for Task by Phase interaction.

	Align vs. Grasp		
	Instruction phase	Object phase	Action execution
LH preSMA	**t₁₃ = 2.5, p = 0.03**	**t₁₃ = 3.1, p = 0.008**	t₁₃ = 0.6, p = 0.5
RH preSMA	t₁₃ = 1.7, p = 0.1	**t₁₃ = 3.7, p = 0.002**	t₁₃ = 0.5, p = 0.6
LH dPM	t₁₃ = 0.9, p = 0.3	t₁₃ = 1.8, p = 0.1	**t₁₃ = 2.4, p = 0.03**
RH dPM	t₁₃ = 0.7, p = 0.5	t₁₃ = 1.4, p = 0.2	**t₁₃ = 2.2, p = 0.049**
LH SMA	t₁₃ = 0.2, p = 0.8	**t₁₃ = 2.6, p = 0.02**	t₁₃ = 1.8, p = 0.1
RH SMA	t₁₃ = 1, p = 0.3	t₁₃ = 1.2, p = 0.2	**t₁₃ = 2.3, p = 0.04**
LH M1	t₁₃ = 0.2, p = 0.8	t₁₃ = 0.5, p = 0.6	**t₁₃ = 4.5, p < 0.001**
RH M1	t₁₃ = 1, p = 0.3	t₁₃ = 0.5, p = 0.6	**t₁₃ = 3.3, p = 0.005**
LH S1	t₁₃ = 0.6, p = 0.35	t₁₃ = 0.6, p = 0.5	**t₁₃ = 3.4, p = 0.005**
RH S1	t₁₃ = 1.9, p = 0.08	t₁₃ = 0.3, p = 0.7	**t₁₃ = 3.5, p = 0.004**
LH aIPS	t₁₃ = 0.8, p = 0.4	**t₁₃ = 2.5, p = 0.02**	t₁₃ = 1.5, p = 0.1
RH aIPS	t₁₃ = 2.3, p = 0.04	**t₁₃ = 2.4, p = 0.03**	t₁₃ = 1, p = 0.3
LH mpCS	t₁₃ = 1.1, p = 0.3	t₁₃ = 2.1, p = 0.05	**t₁₃ = 4.4, p < 0.001**
RH mpCS	t₁₃ = 1.8, p = 0.08	t₁₃ = 1.5, p = 0.2	**t₁₃ = 3.2, p = 0.007**
LH pIPS	**t₁₃ = 3.1, p = 0.008**	t₁₃ = 0.4, p = 0.6	**t₁₃ = 3.7, p = 0.003**
RH pIPS	t₁₃ = 1.8, p = 0.09	t₁₃ = 1.2, p = 0.3	**t₁₃ = 3.1, p = 0.009**
LH SPOC	t₁₃ = 0.7, p = 0.5	t₁₃ = 1, p = 0.3	**t₁₃ = 2.6, p = 0.02**
RH SPOC	t₁₃ = 1.7, p = 0.1	t₁₃ = 1.4, p = 0.2	**t₁₃ = 3.1, p = 0.008**
LH V1	t₁₃ = 0.2, p = 0.8	**t₁₃ = 2.6, p = 0.02**	t₁₃ = 1.8, p = 0.1

Note: significant results (p < 0.05) are in indicated in bold.

different in each phase. Our results show that while most of the areas involved in the interaction showed differential Task activation in one of the three phases, a few areas showed differential Task activation in opposite directions in two phases. Specifically, we found higher activation for Align than Grasp during Object but not Instruction phase or Action execution in bilateral preSMA and aIPS, as well as in SMA and V1 in the left hemisphere (these areas are marked in yellow in Fig. 3). The results in these areas are consistent with our hypothesis. The left lateralization of the interaction in SMA and V1 could be explained by the fact that participants used their right hand to perform the actions and would indicate that the neural responses within these regions may reflect a functional advantage during memory-guided actions for the hand used during the action. This could be tested by having participants perform actions with the left and right hand. The areas that showed higher activation for Align than Grasp during Action execution but not in Instruction or Object phase are bilateral PM area, mpCS, SPOC and right SMA, and pIPS (these areas are marked in black in Fig. 3). In addition, M1 and S1 showed higher activation for Grasp than Align during the Action execution but not Instruction or Object phase (these areas are marked in red in Fig. 3). Further right aIPS and left preSMA showed higher activation for Grasp than Align during the Instruction phase as well as the opposite pattern (higher activation for Align than Grasp) in the Object phase. Similarly, the left pIPS showed higher activation for Grasp than Align in the Instruction phase and the opposite pattern in Action execution.

In order to determine whether the occipital area corresponds to V1, V2 or V3, we used a published probabilistic atlas (Wang et al., 2015) that provides a dataset with the full probability maps of topographically organized regions in the human visual system (www.princeton. edu/~napl/vtpm.htm). In particular, the atlas provides the probabilistic maps generated from a large population of individual subjects (N = 53) tested with standard retinotopic mapping procedures and allows defining the likelihood of a given coordinate being associated with a given functional region for results obtained from any independent dataset once transformed into the same standard space. Therefore, we converted our Talairach coordinates in MNI space and used the atlas to examine whether the coordinates fall within V1, V2, V3, etc. As shown in Fig. 4, our occipital area falls within the boundaries of V1 in the left hemisphere (Fig. 4).

3.1.1.1. Psychophysiological interaction analysis. The results described

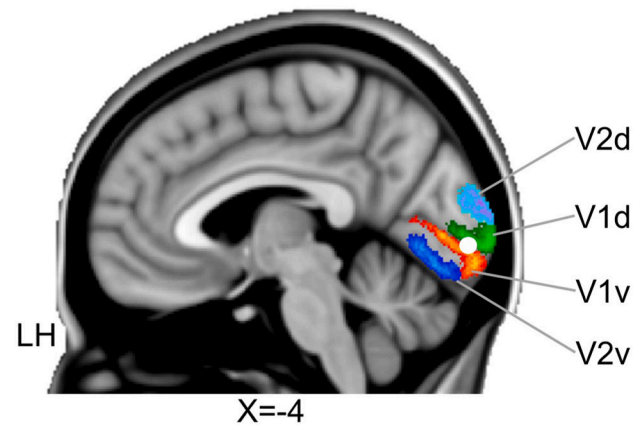## Probabilistic Maps of Visual Topography

Fig. 4. Retinotopic visual areas. The activation maps were taken from a published and freely available probabilistic atlas (Wang et al., 2015). The white circle shows the MNI coordinates of the occipital areas found with the Task by Phase interaction in our experiment.

above, in particular the action-specific modulation in aIPS and V1 during the Object phase, suggest that action-specific visual enhancements might be mediated by reentrant pathways from motor areas. To test this hypothesis, we performed Psychophysiological Interaction analysis focusing on the connectivity of aIPS and V1 as the seed regions. First, we chose aIPS because this areas is well-known to be involved in action planning and object manipulation (Culham et al., 2003; Gallivan et al., 2011), and shows an anterior-to-posterior gradient between action and visual responses (Singhal et al., 2013). As such, aIPS could be involved in mediating re-entrant signals to lower-level areas. Second, we chose V1 because it should carry the earliest visual signals at the cortical level, and this would allow us to test the most extreme case of our hypothesis on reentrant pathways from higher-level areas (that have previously processed action instruction) to primary sensory areas. Specifically, we investigated which areas show enhanced connectivity with the left aIPS and V1 during the Object phase for Align as compared to Grasp conditions. While aIPS did not show any significant connection for this contrast, the PPI results for V1 are illustrated in Fig. 5, and show bilateral preSMA, M1/S1 as well as the posterior ITS (pITS) and V1 in the left hemisphere. The M1/S1 region was found in the fundus of the Central Sulcus. Thus, V1 showed functional connectivity both with motor/somatosensory areas and the ventral visual stream during the Object phase. This analysis cannot show the directionality of influence, but note that the contrast of the PPI analysis is based on action type (Align vs. Grasp) and not visual stimulus (Oblique vs. Vertical), so the enhanced connections between V1 and other cortical areas could not be driven by purely feedforward sensory signals from V1. Although the left aIPS did not show differential functional connections for Align vs. Grasp in the Object phase, there were stronger connections during the Object phase as compared to baseline, and regardless of the planned action, with the middle and posterior regions of the intraparietal sulcus (mIPS and pIPS) bilaterally, M1/S1 and the middle STS (mSTS) in the left hemisphere.

4. Discussion

Our results provide two findings. First, during the planning of manual action, specific task instructions influence activity in several lower and higher visual areas only after the target features become available. We observed instruction-specific (Align vs. Grasp) modulations in a constellation of cortical areas spanning parietal and frontal cortices, including areas involved in hand actions like aIPS and
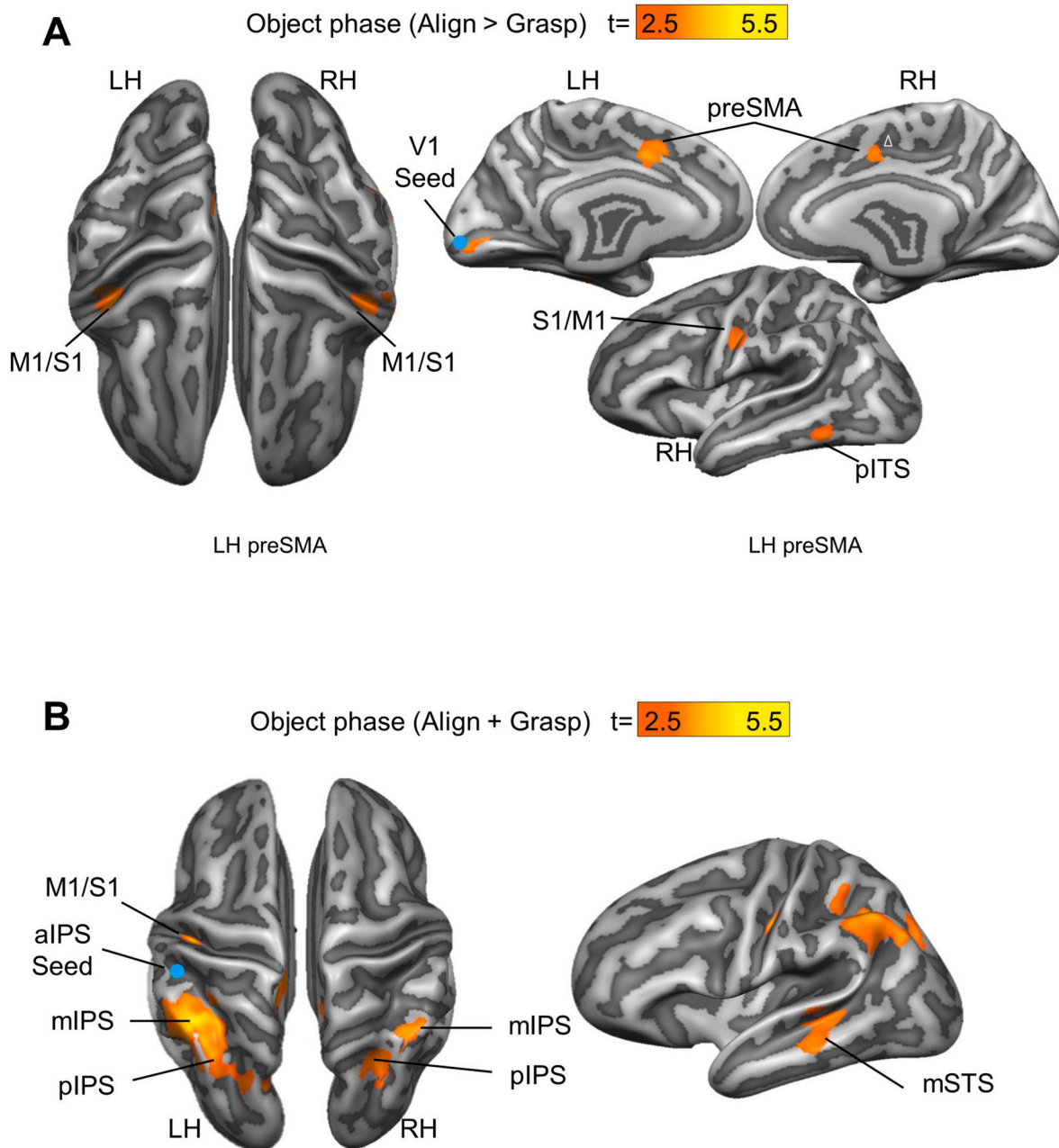
Fig. 5. Task-related functional network of areas involved in the modulation of sensory processing driven by object presentation. Statistical parametric maps showing the psychophysiological interaction results using V1 (**A**) and aIPS (**B**) in the left hemisphere as the seed regions. The map in **An** indicates areas that show stronger functional connections with the seed region for Align vs. Grasp movement plans during the Object phase. The map in **B** indicates areas that show stronger functional connections with the seed region for Align and Grasp movement plans during the Object phase as compared to baseline. The light blue circles correspond to the peak voxel of the seed ROIs.

supplementary motor areas, as well as a weak involvement of V1 (Fig. 3, areas marked in yellow). Although the results in V1 are not as strong as in other areas, they are consistent with emerging evidence showing that action intentions are represented in the early visual cortex seconds before participants perform a movement (Gutteling et al., 2015; Gallivan et al., 2019; Monaco et al., 2020; Velji-Ibrahim et al., 2022), and that the amplitude of neural oscillations in V1 is predicted by the activity in M1 before movement onset (Benedetto et al., 2020). Importantly, these

effects only emerged after the full set of information required to execute the movement became available and were specific to the presentation of the stimulus and the planning period before the "go" signal for action. Conversely, the go signal also evoked task-specific motor activation (Fig. 3, areas marked in red and black), but in a group of cortical areas that were not modulated during planning. Second, during the Object phase V1 showed stronger functional connectivity with motor areas (preSMA, M1/S1), as well as higher level visual cortex in the ventral

stream (pITS) for the Align than Grasp condition. Indeed, the Align but not the Grasp task required participants to adjust the posture of the hand and wrist according to the orientation of the rod. Note that these activations and task-specific functional connections occurred well after task instruction, suggesting a memory-dependent mechanism (Heuer et al., 2016b) . Further, area aIPS showed stronger functional connections with frontal, parietal and temporal areas during the object phase as compared to baseline, regardless of the action being planned.

Our results reinforce evidence that action intention modulates the response to sensory processing in the early visual cortex and extend previous findings about the role of this area during execution. Indeed, Previous investigations have reported that action intention can be decoded from the activity pattern in the EVC while participants have online visual information about the target object and its features (Gallivan et al., 2019; Monaco et al., 2020), and have shown re-activation of the EVC *during* the execution of actions in the dark towards unfamiliar
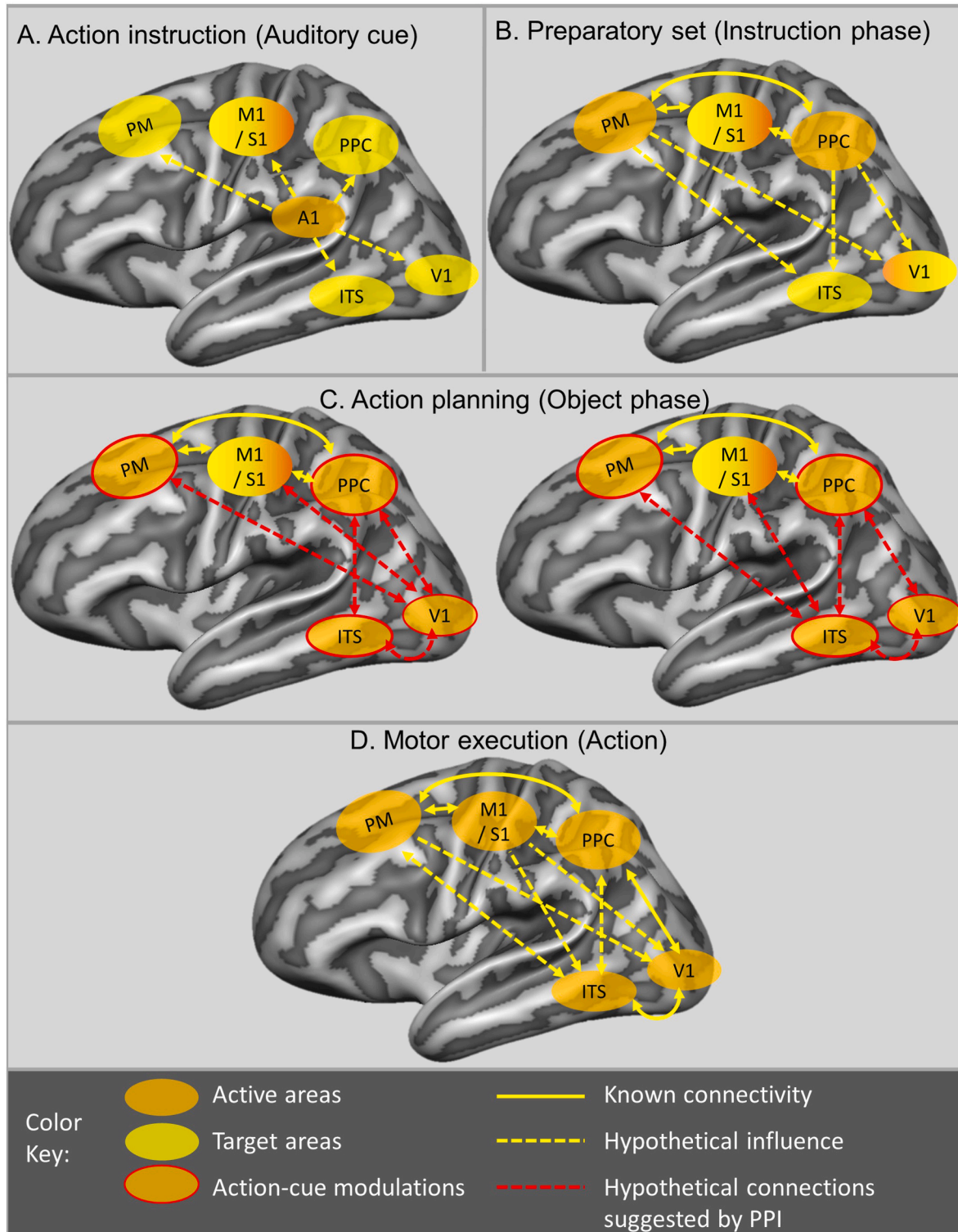

Fig. 6. Schematic representation of functional networks involved in different stages of the experiment.

shapes (Singhal et al., 2013; Monaco et al., 2017). Our results confirm and extend these findings by showing that: 1) action-specific modulation in the primary visual cortex during action planning is triggered by the presentation of the target object, and 2) this processing is propagated and elaborated throughout the dorsal and ventral visual stream. Thus, our results provide further evidence that the role of the early visual cortex includes not only visual processing and memory, but also action-specific planning.

We note that, since PPI analysis does not provide directionality, our data by themselves do not prove that any of the areas shown in Fig. 5 are involved in reentrant processing.

4.1. Possible mechanisms for the influence of action instruction

We provide a framework for understanding the likely neural events that occurred during our experiment, embedding the current findings within the literature (Fig. 6). In order to organize this discussion, the task has been broken down into four phases, beginning with action instruction (Fig. 6A) and its influence on preparatory set (Fig. 6B). Clearly, the auditory instruction (Grasp and Align) initiated the preparatory activity that we observed during Instruction phase (Fig. 2A). This included widespread activation in well-known prefrontal and parietal-frontal areas primed for action, as well as extensive occipital-temporal activation, presumably primed for the expected visual stimulus. One can safely assume that the instruction was processed by auditory cortex (Fig. 6A), which in some species has direct connections to primary visual cortex (Budinger et al., 2006; Campi et al., 2010). The instruction-dependent influence, most likely mediated by the language-processing areas (Broca's area and Wernicke's area) and executive control mechanisms, might have acted as a 'trigger'. The premotor cortex is thought to play a role in 'preparatory set' (pre-cued activation of neurons in anticipation of action), possibly initiating the reentrant propagation of signals through motor-to-sensory areas. This likely included general priming of feature-specific processing mechanisms (Martinez-Trujillo and Treue, 2004; Heuer et al., 2016a), in this case intention-related orientation selectivity (Perry and Fallah, 2017). We observed a Task-specific response during the Instruction phase (Fig. 3, areas marked in light blue), however the direction of this effect was opposite to the one observed during the Object phase. It is likely that the visual information about the object allowed updating the plan for the manual response in order to program a suitable action.

4.1.1. Instruction-dependent integration of the visual signal into the motor plan

Once the visual stimulus was shown it became possible for our participants to plan a specific movement with a specific orientation (Fig. 6C). This would involve the feedforward propagation of highly precise retinal input with the less precise and broader information conveyed to V1 through cortical feedback (Muckli et al., 2013; Chong et al., 2016; Petro and Muckli, 2016). The second type of information participates in building an internal model that allows the brain to make predictions and anticipate the outcome of a movement generated by the self.

During the Object phase, we observed motor planning selective responses in visual areas (V1) and reach and grasp planning areas (aIPS, PM, SMA, preSMA), marked in red in Fig. 6C. Since this specificity was not observed until the second phase, it appears that neither instruction nor vision alone were sufficient to produce this pattern. Rather, it appears that preparatory set and visual stimulation were combined to produce action specific planning responses. Our psychophysiological interaction analysis suggests that the early modulations observed in primary visual cortex could be mediated by connections from preSMA and S1/M1, which is known to encode specific grasp before an actual movement (Gallivan et al., 2011) and have interconnections with V1 (Miller and Vogt, 1984) (Fig. 6C, left panel). Another possible interpretation depicted in Fig. 6C (right panel) is that V1 activation is

modulated by premotor and motor areas via ventral stream areas through reciprocal connections that allow ventral stream areas to influence processing in motor areas as well as in early visual cortex. This would be consistent with findings showing that the extrastriate body area (EBA) is involved in action planning and motor control (Astafiev et al., 2004; Kühn et al., 2011; Lingnau and Downing, 2015; Zimmermann et al., 2016) and has connections with dorsal stream areas (Beer et al., 2013; Orgs et al., 2015; Simos et al., 2017; Zimmermann et al., 2018). Dorsal stream areas may in turn affect lower visual areas through feedback connections to facilitate predictive coding by obtaining more detailed information of the object to be grasped. These connections might affect activity levels in line with action complexity and demands on visual processing. Since PPI and fMRI in general do not allow distinguishing between direct and indirect connections, our results do not allow making conclusions about the possible connections involved in action-related processing of V1 activity during action planning. It is likely that both scenarios participate in the process through reciprocal connections to and from lower and higher visual areas, as well as parietal and motor cortex. The effective connectivity between V1 and motor areas observed here might also sub-serve visual and somatosensory-motor associations in subjective experience. For example, during manipulation we often visualize both the hand and object.

It is possible that the top-down influence that we detected in occipital cortex is generated by subthreshold post-synaptic activity (Logothetis, 2003), possibly intended for the attentional modulation of visual input (Moore and Armstrong, 2003). This interpretation would be consistent with evidence for BOLD activation, but not action potentials, in early visual areas during working memory tasks (Harrison et al., 2009; Leavitt et al., 2017). However, as one proceeds to the higher levels of parietal and premotor cortex there is ample evidence for delay-related action potential activity (neurophysiology: Snyder et al., 1997; fMRI: Gallivan et al., 2011), so one would expect to see task-dependent modulations of action potentials in the areas we identified. Another possible explanation of the effect observed in V1 is that the more complex action (Aligning the hand to the bar) may have required more time to plan than the grasping movement, causing the information to be retained in memory for a longer duration, and thus affecting both amplitude differences between action types, as well as connectivity between V1 and other regions involved in planning. Working memory serves a role not only in visual tasks, but also in action planning (van Ede, 2020), with neural mechanisms that might require a reentrant loop for the integration of visual memory of the oriented bar into the action plan. Attention might have also played a role by increasing activation for the action plan that requires more engagement. Indeed, task-related activity levels are affected by global attentional load (Chan et al., 2015). While this would not directly be related to specific object properties, it would still be induced by action intention and the upcoming interaction with the object.

Our results show that instruction-dependent modulations were neither related to general action preparation nor action execution, but rather were specific to processing visual input for the purpose of an action plan. Likewise, our finding of functional connectivity between visual and motor areas suggests that this process is sub-served by reentrant connectivity. Therefore, it appears that action intention, likely initiated in the frontal cortex, shapes the way that vision is processed for action execution. However, when it comes time to act, our results show this profile of action selectivity shifts to a different set of cortical areas, as described in the next section.

While visual, occipito-temporal, parietal, somatosensory, motor and premotor cortices respond to action and orientation cues, reciprocal connections between all these areas are likely to occur during the planning phase preceding the movement to determine predictive coding activity in V1. In particular, we suggest that: **A.** the Auditory Action-cue primes motor preparation and upcoming object processing, **B.** Motor preparation primes the visual system for processing action-related object

properties, **C.** Task-Dependent Integration of Visual Stimulus into motor plan (two possible scenarios are shown in left and right panel), and **D.** Integrated network contributes to the execution of the movement.

4.1.1.1. Action execution. During Action Execution (Fig. 3) we found higher activation for Align than Grasp actions in areas known to have a crucial role in orienting the hand during actions, such as SPOC, pIPS, SPL and PM cortex. Specifically, the superior parietal-occipital cortex of humans (SPOC), the putative homologue of macaques' V6/V6A, is involved in orienting the hand during grasping movements (humans: Monaco et al., 2011, macaques: Fattori et al., 2009). In addition, SPOC has been shown to be crucial for the control of hand posture during grasping actions as lesions to this area in macaques lead to profound impairments in orientating the wrist and hand posture during grasping movements (Faugier-Grimaud et al., 1978; Battaglini et al., 2002). Similarly, the human premotor cortex shows an involvement in hand posture (Monaco et al., 2011), and stimulation to this area disrupts adjustments in wrist orientation (Taubert et al., 2010).

The primary somatosensory and motor area (S1 and M1) were the only areas that showed higher response for Grasp than Align during movement execution. This is likely due to the larger somatosensory feedback and finer motor output associated with grasping movements. In particular, two factors might have contributed to these results. First, during grasp but not align movements, the participants touched the object with the five digits eliciting a rich somatosensory stimulation. Second, there was a higher degree of online motor control of the five fingers in grasping but not aligning movements during action execution. Indeed, for the grasp but not the align movement, the position of the digits could be adjusted after movement initiation and once the fingers touched the object. In contrast, to properly align the hand to the orientation of the rod, the hand posture had to be defined prior to initiating the movement. Therefore, online movement adjustments were required to a lesser extent for Align than Grasp movement.

Despite the well-known role of aIPS in grasping actions, we did not observe higher activation for grasp than align movements in area aIPS during the execution of the action. This might seem at odds with the well-known role of area aIPS in grasping movements. One possible explanation is that the coarse whole hand grasp used in our experiment falls within the range of grasping movements that elicit the lowest activation in aIPS among the different types of grips. Indeed, the activity in human aIPS is modulated by the amount of precision required by a movement. Specifically, grasping movements that require higher precision elicit higher activation than coarse grasping movements in the aIPS (Cavina-Pratesi et al., 2018). The involvement of the aIPS in orienting the hand posture is not surprising, as shown by neurophysiological studies indicating a role of the aIPS in hand orientation (Murata et al., 2000; Baumann et al., 2009). These factors might have led to the lack of higher responses for grasp than align in area aIPS. An alternative and non-mutually exclusive explanation is that manual alignment actions might be as demanding on motor control as grasping actions. In fact, Align actions needed to be continuously maintained (and updated) to optimize performance, and unlike Grasp actions could not rely on settled endpoints on the stimulus.

To this point we have focused on the dorsal visual stream of visuomotor control, but the pITS – a ventral stream area implicated in object recognition — showed general preparatory activity (Fig. 2) and increased functional connectivity with V1 for Align than Grasp conditions during the Object phase (Fig. 5). In light of the known role of ventral stream areas in perception, we suggest that functional connections between dorsal and ventral stream areas during action planning could have a role in influencing both conscious perception and movement outcome.

4.1.1.2. Concluding remarks. Our results show that the intent for specific actions can influence visual processing as early as the early visual

cortex, extending through temporal, parietal, and frontal cortex, and this seems to originate from functional connectivity between motor and sensory areas. This suggests that action plans shape how the brain both perceives and uses what the eyes see. Overall, our results are consistent with the notions that motor systems modulate attention to relevant sensory details and/or modulate sensory inputs to predict for the consequences of impending actions (Gilbert and Li, 2013; Yon et al., 2018; Monaco et al., 2019, 2020).

CRediT authorship contribution statement

Simona Monaco: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - original draft, Writing - review & editing. **Nicholas Menghi:** Formal analysis, Writing - review & editing. **J Douglas Crawford:** Funding acquisition, Project administration, Resources, Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare there are no conflicts of interest.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.neuropsychologia.2023.108773.

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