Title: Predictive coding of action intentions in dorsal and ventral visual stream is based on visual anticipations, memory-based information and motor preparation

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Running title: Visual and Blind Grasp

Abstract

The prediction of upcoming movements is based on several types of neural signals that we normally experience on a daily basis and span the visual, somatosensory, motor and cognitive system. We used functional magnetic resonance imaging (fMRI) and multivoxel pattern analysis (MVPA) to test whether the neural signals evoked by visual, memory-based and somato-motor information can be reliably used to predict upcoming actions in areas of the dorsal and ventral visual stream during the preparatory phase preceding the action, while participants were lying still. Nineteen human participants (nine women) performed one of two actions towards an object with their eyes open or closed. Despite the well-known role of ventral stream areas in visual recognition tasks and the specialization of dorsal stream areas in somato-motor processes, we decoded action intention in areas of both streams based on visual, memory-based and somato-motor signals. Interestingly, we could reliably decode action intention in absence of visual information based on neural activity evoked when visual information was available, and vice-versa. Our results show a similar visual, memory and somato-motor representation of action planning in dorsal and ventral visual stream areas that allows predicting action intention across domains, regardless of the availability of visual information.

Keywords

Functional magnetic resonance imaging (fMRI), multivoxel pattern analysis (MVPA), humans, actions, predictive coding, vision

Introduction

Predictions are at the basis of accurate and effective actions. The ability to predict the consequences of a movement allows us to anticipate the future state of our body with respect to the ultimate goal of our action and generate an accurate motor command (Wolpert et al. 1995; Miall and Wolpert 1996). Predictive mechanisms are also crucial to adjust our movements according to rapid changes in the environment and to differentiate the sensory consequences of our own actions from external factors (Blakemore et al. 2000). What information do we use to anticipate actions? Anticipations likely originate from experience. Our everyday-life is rich of actions that elicit visual responses when we see ourselves performing actions, somatosensory responses when we feel our hands moving, and motor responses that generate the action. We can therefore retrieve and use this information to predict how a movement is going to look and feel like.

Recent human neuroimaging work has shown that movement planning affects the activity pattern in areas of the dorsal visual stream (Gallivan et al. 2011; Ariani et al. 2015, 2018) known to be involved in action, as well as the ventral visual stream (Gallivan et al. 2013; Freud et al. 2018), specialized in object perception. However, it still remains poorly understood whether the factors that drive the modulation of the activity pattern in these areas during action planning are related to the visual aspect of the upcoming movement kinematics or to the motor goal signals associated with movement planning. Areas in the dorsal visual stream are likely to have a representation of action planning that can be explained by both motor preparation as well as visual predictions of the impending movement, as the dorsal visual stream is known to be specialized in action (Goodale and

Milner 1992). Moreover, the dorsal stream has strong anatomical connections with somatosensory and premotor areas as well as with the early visual cortex (Luppino et al. 1999, 2003; Passarelli et al. 2011), processes somatosensory and kinesthetic information associated with passive and active arm movements (Sakata et al. 1973; Mountcastle et al. 1975; Seitz et al. 1991; Lacquaniti et al. 1997; Binkofski et al. 2001; Breveglieri et al. 2002), and is involved in visual and tactile exploration of objects (Reed et al. 2005; Dijkerman and de Haan 2007; Konen and Kastner 2008; Marangon et al. 2015). Conversely, the known specialization of areas in the ventral visual stream in perception (Goodale 2014), their strong connections with early visual areas (Baizer et al. 1991; Catani et al. 2003), and their crucial role in the visual identification of shapes (Kourtzi and Kanwisher 2000, 2001; Downing et al. 2001; James et al. 2003), indicate that in these areas, visual anticipations might better explain the representation of action planning as compared to motor preparation.

Although vision for action has been extensively investigated in the past decades (Goodale and Westwood 2004; Grol et al. 2007; Castiello and Begliomini 2008; Rossit et al. 2013; Singhal et al. 2013), much less in known about the neural processing of somatosensory and proprioceptive information during motor preparation and action execution. Yet, these are crucial aspects for skilled motor behavior since they provide us with continuous updates about the state of our movement through online feedback during movement execution. Indeed, movements elicit somatosensory responses that provide us with the awareness of how we move even in absence of visual information. Importantly, the lack of somatosensory and proprioceptive feedback profoundly affects our ability to move. For example, patients who have lost the sense of touch, proprioception, and consequently

the awareness of the spatial position of their limbs, have also lost the ability to move spontaneously until they re-learn to do so by constantly monitoring their movements with vision (Cole 1995, 2016; Hermsdörfer et al. 2008). In addition to their crucial role for generating actions, afferent proprioceptive feedback alone modulates motor representations used for cognitive tasks like motor imagery (Mercier et al. 2008).

Kinesthetic memory acquired throughout our life while performing hand actions, enables us to anticipate how a movement is going to feel like even before we initiate it, through somatosensory predictions about the upcoming action. As such, kinesthetic memory likely plays an important role in planning actions that require interacting with our surrounding, such as grasping objects. Indeed, action planning relies on internal models that are based on knowledge of the current position of our hand in space as well as the next state, and the process of getting to the next state involves anticipations of somatosensory consequences of the movement (Miall and Wolpert 1996). To what extent the activity pattern in dorsal and ventral stream areas during action planning is related to anticipating the visual consequences of upcoming actions as opposed to retrieving memory-based information about action performance and motor preparation?

We answered this question using multivoxel pattern analyses on fMRI data to identify the visual, memory-based and motor preparation components for the anticipation of actions. To this end, we manipulated the presence or absence of visual information while participants performed delayed grasp or open-hand movements towards a centrally-located object. While in visual conditions participants relied on continuous visual feedback of the object (during the planning phase) and the hand approaching the object

(during the execution phase), in absence of visual information participants relied solely on the memory of the object (during the planning phase) and the somatosensory and motor responses (during the execution phase). Therefore, visual and memory-based anticipations of actions in the planning phase would be reflected in above chance decoding accuracy for the two action types in vision and no vision conditions, respectively. The common aspect between Vision and No Vision conditions were the somatosensory, proprioceptive and kinesthetic components elicited by the two actions, as well as the motor preparation component. In fact, this information differed for the two action types (Grasp vs. Open-hand), but not across visual conditions, as the movements and the object were the same regardless of the availability of visual information. We hypothesize that cortical areas that process the anticipations of somatosensory, proprioceptive and motor components of action would show above chance decoding accuracy for the comparison between action types across visual conditions during the planning phase preceding the action. It seems plausible that areas specialized in perception and visual recognition of shapes, in the ventral visual stream, might have a role in anticipating visual predictions of the upcoming movements. Conversely, areas specialized in action, in the dorsal visual stream, might anticipate the proprioceptive and somatosensory consequences of a movement.

Materials and Methods

The goal of our study was to investigate the extent to which we could decode action planning in areas of the dorsal and ventral visual stream based on visual, memory-based and somatosensory information. To this aim, in our experiment participants were asked to perform two types of hand actions (Grasp and Open-hand) with the eyes open or closed towards a centrally-located target object (Figure1A). At the beginning of each trial participants were first cued to the action to be performed and whether they had to have their eyes closed or open. Following a delay period, they executed the action (Figure 1B). The delayed paradigm allowed us to analyze the activity patterns during the delay preceding the action and distinguish it from movement execution. We used multi-voxel pattern analysis (MVPA) to examine whether we could decode the dissociation between the two actions (Grasp vs. Open-hand) in areas of the dorsal and ventral visual stream known to be involved in hand actions, such as grasping. In particular, we used independent functional localizers to identify four ventral visual stream areas: the lateral occipital complex (LO), lateral occipital tactile-visual area (LOtv), extrastriate body area (EBA) and the motion sensitive area (MT). In addition, we used an *ad hoc* univariate contrast with the experimental runs to localize five areas in the dorsal visual stream: the anterior intraparietal sulcus (aIPS), ventral premotor cortex (vPM), dorsal premotor cortex (dPM), superior parietal occipital cortex (SPOC) and primary motor/somatosensory cortex (M1/S1).

Sessions and subjects

The experimental and localizer sessions took place in two different days. The experimental session lasted approximately 2 hours, including screening and set-up time, while the localizer session took approximately 1.5 hours to be completed.

Nineteen volunteers (age range 23-42, 7 men and 9 women) participated in the experimental session. Sixteen participants also took part in the localizer session.

Ethics approval was obtained from the Research Ethics Board at the University of Trento. Participants provided informed written consent prior the experiment. They were right handed and had normal or corrected to normal vision.

Action paradigm

We used high-field (4-Tesla) 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 1A, participants performed delayed hand actions using their right dominant hand towards a three-dimensional (3D) target stimulus which was viewed directly without mirrors (Culham et al., 2003). Each trial started with an auditory cue that instructed participants about: i) whether they had to keep the eyes closed or open for the upcoming trial ("Visual" or "Blind") and ii) the task to be performed at the end of the trial ("Grasp" or "Hand"). The cue was followed by a delay of 10 s after which a Go cue prompted participants to perform the action. The next trial started after 12.5 s of intertrial interval (ITI) (Figure 1B). Grasping movements consisted of reaching-to-grasp the object with a whole hand grip while Open-hand

movements required participants to open the hand and move it above the object and touch the object with the palm of the hand but without interacting with the object. Therefore, somatosensory feedback from the object was present in both movement types. In Visual trials, participants were asked to fixate a black dot on the object, therefore the object was in central vision.

The two by two factorial design, with factors of Task (Grasp, Open-hand) and Visual Feedback (Vision, No Vision) led to four conditions: Vision Grasp, Vision Open-hand, No Vision Grasp and No Vision Open-hand (Figure 2, upper panel). We performed our analyses on the Plan and Execution phase. Critically, while in Vision trials participants viewed the object throughout the three phases (instruction, delay and action), in No Vision trials the object was not visible. Visual and memory-based processes, as well as somatosensory anticipations of the upcoming movement would be reflected in above chance decoding accuracy in the planning phase for the dissociation between Grasp and Open-hand movements in Vision, No Vision and across visual conditions, respectively. In particular, while Vision and No Vision conditions might also include a somatosensory component, the cross decoding between visual conditions allowed us to isolate somatosensory anticipations, which are shared in both visual conditions (Figure 2, lower left panel: delay phase). Similarly, visual feedback during the action, memory-based processes as well as somatosensory feedback elicited by the movement itself would be reflected in above chance decoding accuracy for the dissociation between movement types during the execution phase in Vision, No Vision and across visual conditions, respectively. Specifically, while Vision and No Vision conditions include somatosensory feedback during action execution, the cross decoding enabled us to isolate somatosensory

feedback and motor commands that elicit responses for both action types regardless of the visual information (Figure 2, lower right panel: action phase).

A video camera placed in the magnet room recorded the eyes of the participants as well as their actions for off-line investigation of the errors. The errors were mistakes in the performance of the task (e.g., eyes open in a No Vision trial, initiating a movement in the delay phase or performing a grasp in an Open-hand condition) and were excluded from further analyses. The 1.8 % of total trials were discarded from the analyses because of subject errors.

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 ~12,30 min. Participants completed five functional runs for a total of 140 trials per subject (35 trials per condition).

Apparatus

Goal-directed actions were performed towards a 3-D stimulus located on a platform secured to the bore bed. The platform was made of Plexiglas and its location could be adjusted to ensure that the participant could comfortably reach the stimulus. The head of the participant was tilted by ~20° to allow direct viewing of the stimuli. The height of the platform could also be adjusted to improve the view and the reachability of the object for each participant. The right upper arm of the participant was supported with foam.

The 3-D stimulus consisted of a white plastic cube (5 cm), which was affixed to the platform with Velcro. The surface of the platform where the object was attached was

covered with the complementary side of the Velcro. The platform was placed approximately 10 cm above the subject's pelvis at a comfortable and natural grasping distance. The stimulus was positioned in the same central location throughout the experiment, therefore the visual presentation of the object remained constant in all trials.

The starting position of the right hand was on a button box placed around the navel while the left hand rested beside the body.

The auditory cues were played through the software Presentation which was triggered by a computer that received a signal from the MRI scanner.

Localizer paradigms

We ran three sets of localizers to functionally identify ventral stream areas LO, LOtv, EBA and MT. The first two localizers were aimed to identify ventral visual stream areas LO, EBA and MT. Area LO is specialized in object recognition (Kourtzi et al. 2002), while areas EBA and MT are specialized in body-shape recognition and moving stimuli, respectively (Downing et al., 2001; Zeki et al., 1991). For this purpose, participants lay supine in the bed bore and viewed images displayed on a screen through a mirror affixed to the head coil. The third localizer was used to identify LOtv, an object-selective area with visual and tactile properties (Amedi et al., 2001). To this aim, participants tactilely explored objects or textures placed on an apparatus above their torso while fixating a cross viewed through the mirror. While all these areas are specialized in perception, they are also involved in action (Singhal et al., 2011; Monaco et al., 2017; Gallivan et al., 2013). In addition, while LO, EBA and MT are known as visual areas, area LOtv has

visual and tactile properties (Amedi et al., 2001). We examined whether the visual and somatosensory specialization of these areas is also present during action planning and execution. We ran *ad-hoc* contrasts to localize these areas based on their specialization (Figure 3A).

LO and EBA localizer

The BOT localizer included blocks of color photographs of headless Bodies, Objects and Tools (BOT), as well as scrambled versions of these stimuli (from Gallivant et al., 2013). Stimuli were presented into separate 16-s blocks, with 18 photographs per block, presented at a rate of 400 ms per photograph with a 490-ms inter-stimulus interval. Each run consisted of six stimulus blocks per condition, seven scrambled blocks, and two fixation/baseline blocks (20 s) at the beginning and end of each run. Stimulus blocks were organized into sets of three, separated by scrambled blocks, and balanced for prior-block history within a single run. All subjects participated in two of these localizer runs. Each stimulus block included either three or four repeated photographs, balanced across conditions. Participants were required to fixate a dot that was superimposed on the center of each image and performed an N-back task when the same stimulus was presented twice in a row. The duration of each BOT localizer was 7 min 30 s.

MT localizer

Stimuli were presented into 15-blocks of dots moving with center-out trajectories and static dots. Each run included four blocks per condition (Motion and Static) and each Static block was presented after a Motion block and was followed by a 15-s intertrial

interval (ITI). The Motion condition consisted of dots moving outwards from the center, while the Static condition consisted of fading non-moving dots. Participants participated in one of this localizer run and were required to fixate a dot placed in the center of the screen for the whole duration of the run. The duration of each MT localizer was 6 min 25 s.

LOtv localizer

Participants were required to tactilely explore objects or textures in separate blocks using their right dominant hand. The stimuli were attached on a custom-made wooden turntable placed above the torso of the participant. Two orthogonal separators were mounted on the turntable and divided it into four sectors (Figure 3B). Each sector contained three stimuli from one category (objects or textures). Participants rested the right hand on a flat surface located in middle of the chest and next to the turntable. In each block, participants were required to perform three sequential tactile explorations of the stimuli (objects or textures) in one sector of the turntable for 10.5 s. Blocks were spaced every 12.5 s during which participants rotated the turntable by 45° to bring the next set of stimuli next to the right hand for the subsequent exploration. Therefore, objects and textures were explored in alternating blocks with three items per block. In particular, at the beginning of each block a beep sound instructed participants to start to explore the first stimulus on the sector placed next to the right hand. After 4.5 s, two subsequent beep sounds separated by 4 s, cued participants to start to explore the second and third object. Following 4 s, another beep sound instructed the end of the exploration phase and participants were prompted to return the right hand to the home position and rotate the wheel with the left

hand. Stimuli were explored following the same order in all blocks: near-left, far-center and near right stimulus. Participants fixated a fixation cross projected on the screen and viewed through a mirror. Each run included 15 blocks of objects exploration and 15 blocks of texture exploration. Each participant completed three LOtv localizer runs for a total of 45 blocks per condition.

Imaging parameters

This study was done at the Center for Mind/Brain Sciences (Trento, Italy) using a 4-Tesla 4T Bruker MedSpec BiospinMRscanner and an 8 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°; 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 comprised 35 slices acquired in ascending interleaved order. During each experimental session, a T1-weighted anatomical reference volume was acquired using a MPRAGE sequence (TR = 2700 ms; inversion time TI = 1,020 ms; FA = 7°; FOV = 256 x 224, 176 slices, 1 mm isotropic resolution).

Preprocessing

Data were analyzed using the Brain Voyager QX software (Brain Innovation 2.8, Maastricht, The Netherlands). 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). The first four volumes 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 to ensure 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. Data from three participants, two of which also took part in the localizer study, showed abrupt head motion over 1 mm and were discarded from further analyses.

General Linear Model

In the experimental runs, the group random effects (RFX) GLM included twelve predictors for each participant. There was one predictor for each of the four conditions (Vision Grasp, Vision Open-hand, No Vision Grasp and No Vision Open-hand) by three Phases (Task Instruction, Delay and Action). Each predictor was derived from a rectangular wave function (1 volume or 2.5 s for the Task 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 predictors were: 1) Vision Grasp Instruction, 2) No Vision Grasp Instruction, 3) Vision Open-hand Instruction, 4) No Vision Open-hand Instruction, 5) Vision Grasp Delay, 6) No Vision Grasp Delay, 7) Vision Open-hand Delay, 8) No

Vision Open-hand Delay, 9) Vision Grasp Action, 10) No Vision Grasp Action, 11) Vision Open-hand Action, 12) No Vision Open-hand Action. In addition, we modelled movement parameters (3 rotations and 3 translations), and errors, if present, as predictors of no interest. Contrasts were performed on %-transformed beta weights (β).

Multivoxel Pattern Analysis

Linear Discriminant Analysis (LDA) single-trial classification

MVPA was performed with a combination of in-house software (using MATLAB) and the CoSMo MVPA Toolbox for MATLAB (http://cosmomvpa.org, Oosterhof et al. 2016), with an LDA classifier (http://cosmomvpa.org/matlab/cosmo_classify_lda.html#cosmo-classify-lda). For each participant, we estimated a GLM on non-smoothed data modelling every single trial for each experimental condition. A total of 420 regressors of interest were considered, originating from the four experimental conditions (Vision Grasp, Vision Open-hand, No Vision Grasp and No Vision Open-hand) x three time-phases (Task Instruction, Delay and Action) x 7 repetitions per run x 5 runs. In addition, we modelled movement parameters (3 rotations and 3 translations), and errors, if present, as predictors of no interest. We adopted a 'leave-one-run-out' cross-validation approach to estimate the accuracy of the LDA classifier. We used beta weights for classification and statistically assessed above chance decoding (50 %) significance across participants with a two-tailed one sample t-test.

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.

Cross-decoding

We tested whether an LDA classifier trained to discriminate between two conditions could then be used to accurately predict trial identity when tested on a different set of trials (i.e. cross-decode). The trials of the train and test runs were taken from different visual feedback conditions such that the training was performed considering the pairwise comparison between the two actions (Grasp vs. Open-hand) in the No Visual condition and tested in the Visual condition, and vice versa. The cross-decoding accuracies for each subject were computed by averaging together the results obtained in each cross-decoding (i.e., train on No Vision and test on Vision; train on Vision and test on No Vision).

ROI Analysis

Because we had *a priori* hypotheses about specific areas, we used independent localizer runs to identify regions of interest (ROIs) in the ventral visual stream (LO, LOtv, EBA and MT) and an independent contrast with the experimental runs to localize areas in the dorsal visual stream (SPOC, aIPS, M1/S1, vPM and dPM). The selection criteria based

on the localizer runs were independent from the key comparison and prevented any bias towards our predictions (Kriegeskorte et al. 2010; Vul et al. 2010).

We identified each ROI at the group level by using specific contrasts based on the known functional role of each area (see details below). Each ROI consisted of a sphere with radius = 9mm and volume = 3071mm^3 (or anatomical voxels). We centered the sphere on the voxel with peak activity for the contrast used to localize the area, and in the vicinity of the expected anatomical location of that area. This approach ensured that the same number of voxels was included in each ROI for adequate pattern classification, and that regions were selected objectively and independent of the planned comparisons for pattern classification in the experimental runs. As also shown in previous studies, we found some overlap between ventral stream areas. In particular, we found an overlap between area LO and EBA, MT and EBA (Downing et al. 2001), LO and MT (Kourtzi et al. 2002), LO and LOtv (Amedi et al. 2001) and MT and LOtv. The overlap between LO and EBA was 27% (840 voxels) in the left hemisphere and 6% (200 voxels) in the right hemisphere. Area MT and EBA overlapped by 60% (1832 voxels) in the left hemisphere and 26% (806 voxels) in the right hemisphere. Area LO and MT overlapped by 56% (1718 voxels) in the left hemisphere and 1% (20 voxels) in the right hemisphere. Area LO and LOtv overlapped by 7% (224 voxels) in the left hemisphere, and area MT and LOtv overlapped by 3% (80 voxels) in the left hemisphere.

Localization of ventral stream areas

The visual object-selective area LO was localized by using the contrast (Objects > Scrambled). LO was defined around the peak voxel of activity near the lateral occipital

sulcus (Malach et al., 1995; Grill-Spector et al., 1999, 2001). The body-selective area EBA was selected using the contrast (Bodies > Scrambled). The EBA was defined around the peak voxel of activity in the posterior inferior temporal sulcus/middle temporal gyrus (Downing et al., 2001; Peelen & Downing, 2005c), dorsal to LO. The motion-selective area MT was identified with the contrast (Motion > Static) with peak activity in the posterior middle temporal gyrus (Zeki et al. 1991). The tactile-visual object-selective area LOtv was identified with the contrast (Touch Object > Touch Textures) with peak activity located ventrally and anteriorly compared to LO.

Localization of dorsal stream areas

To localize areas involved in action execution (SPOC, aIPS, M1/S1, vPM and dPM) we use an RFX GLM of the experimental runs to generate an activation map computed by comparing the response during the execution of the two actions to baseline: [(Vision Grasp Action + No Vision Grasp Action + Vision Open-hand Action + No Vision Open-hand Action) > baseline). We selected the peak activation near the expected anatomical location of the ROI: superior end of the parietal occipital sulcus for SPOC (Gallivan et al. 2009; Cavina-Pratesi et al. 2010; Monaco et al. 2011), junction of the intraparietal sulcus and the inferior segment of the postcentral sulcus for aIPS (Binkofski et al. 1998; Culham et al. 2003; Frey et al. 2005; Begliomini, Caria, et al. 2007; Begliomini, Wall, et al. 2007), omega-shaped area of the central sulcus corresponding to the representation of the hand in M1/S1 (Hari et al. 1993; Yousry et al. 1997), T-junction of the superior precentral sulcus and the caudal end of the superior frontal sulcus for dPM (Cavina-

Pratesi et al. 2010; Monaco et al. 2011), inferior part of the junction between the inferior frontal sulcus (IFS) and precentral sulcus for vPM (Tomassini et al. 2007).

Information isolated for each condition and phase of the task

Cross decoding

The common aspect between Vision and No Vision conditions during the planning phase was the motor preparation for Grasp and Open hand movements. Since proprioceptive feedback is always available, even when we stay still and regardless of visual information, the motor preparation was likely based on the awareness of the current position of the hand relative to the target and the anticipation of somatosensory consequences of the upcoming action. During the execution of the movement, somatosensory feedback was available in addition to proprioceptive information regardless of the presence or absence of vision.

Vision

During the planning phase, vision of the target is available in addition to the proprioceptive information about the current state of our hand. During the execution phase, participants could rely on somatosensory and proprioceptive feedback as well as vision of the target and the hand approaching the target.

No Vision

During the planning phase, participants could rely on memory-information about the target and the proprioceptive information of the current position of the hand. During the

execution phase, somatosensory information was also available. Visual-memory processes might also take place to mentally update the estimated position of our hand relative to target, based on somatosensory and proprioceptive feedback.

Statistical analyses

Our initial approach was to use univariate analyses to test our hypotheses on the β weights extracted from each ROI using the group RFX GLM. First, we explored the extent to which the preparatory responses in ventral and dorsal stream areas are shaped by the upcoming action when the object is visible (in Vision condition) as well as when the object is not visible and has to be retrieved from memory (in No Vision conditions). To this aim, we performed our analysis on the planning phase preceding the movement. Second, we examined which brain areas are more strongly influenced by the view of the hand approaching the object (in Vision condition) as compared to performing actions in the dark (in No Vision conditions). To this goal, we performed the analysis in the execution phase. Notably, the involvement of brain areas in action planning and execution in Vision and No Vision conditions indicated by univariate analysis, include a somatosensory component elicited by predictive mechanisms, in the delay phase, and the movement itself, in the execution phase.

We then complemented these analyses using a multivariate classification method. The multivariate approach allowed us to isolate the somatosensory anticipation of the planned action as well as the somatosensory feedback during action execution by decoding action type (Grasp vs. Open hand) across visual conditions (train in Vision and test in No Vision condition, and vice versa). Indeed, the actions shared the same kinesthetic and

somatosensory aspects in Vision and No Vision conditions. In addition, MVPA enabled us to test our hypotheses when activation levels for key conditions did not differ from each other (i.e. Grasp Delay ~ Open-hand Delay). Indeed, MVPA has the advantage of revealing information carried by the activity pattern in a given area for two (or more) conditions with similar activation levels.

For the univariate analyses, for each ROI we used SPSS to perform one ANOVA for each phase of the task: Delay and Action. Each ANOVA had two levels for task (Grasp and Open-hand) and two levels for availability of vision (Vision and No Vision). When interactions reached significance, we further explored the nature of the interaction by performing post-hoc two-tailed t-tests for four comparisons: Grasp Vision vs. Open Hand Vision, Grasp No Vision vs. Open Hand No Vision, Grasp Vision vs. Grasp No Vision, Open Hand Vision vs. Open Hand No Vision.

For the multivariate analyses, for each ROI we performed two-tailed one sample t-tests on the decoding accuracy for the dissociation between Grasp and Open-hand in Vision, No Vision and across visual conditions against chance (50%) during the Plan and Execution phase. To further explore whether the decoding accuracy was higher in Visual conditions, we performed two tailed paired sample t-tests between the decoding accuracy in Vision vs. No Vision, Vison vs. across visual conditions and No Vision vs. across visual conditions.

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 number of t-tests performed within each time phase (Benjamini and Yekutieli 2001).

Results

Univariate analysis

The Talairach coordinates for each ROI are specified in Table 1. Statistical values of the main effects and post-hoc t-tests for each area are reported in Table 2.

Delay phase

As shown in figure 5, planning grasping movements elicited higher activation than planning open hand movements during the delay phase in left SPOC, right aIPS, vPM and LO. In addition, vision induced higher activation as compared to when no vision was available in bilateral SPOC. Conversely, bilateral EBA, left vPM and M1/S1 showed higher activation for No Vision than Vision conditions. Specifically, the ANOVA on the activation levels during the Delay phase showed a main effect of task in left SPOC, right aIPS, vPM and LO with higher activation for Grasp than Open hand movements. Further, there was a main effect of Vision in left SPOC, bilateral EBA and left M1/S1, with higher activation for Vision than No Vision in left SPOC and the opposite pattern in bilateral EBA, left vPM and M1/S1.

Action phase

As shown in figure 5, the execution of a grasping movement elicited higher activation than open hand movement in bilateral aIPS and dPM, left M1/S1, SPOC, EBA, LOtv, and MT. In addition, all areas, except left M1/S1 and bilateral vPM, showed higher activation in Vision than No Vision conditions. Specifically, we found a main effect of

action type in bilateral aIPS and dPM, left M1/S1, SPOC, EBA, LOtv, and MT, as well as a main effect of vision in bilateral aIPS, dPM, SPOC, EBA, LO, LOtv, and MT. In addition, there was a significant interaction in left aIPS, LO, MT, vPM and right dPM. However, post-hoc comparisons survived FDR correction ($p<0.011$) only for left aIPS, vPM and right dPM. In particular, the interaction in left aIPS was due to higher activation for Vision than No Vision conditions during the Open hand but not the Grasp movement. Given the well-known role of this area in grasping movements, it is likely that the execution of a grasp fully engaged area aIPS regardless of the presence of vision, while the activation for Open hand movements was enhanced when the hand was visible as compared to when it was not. In addition, the interaction in left vPM and right dPM was related to higher activation for Grasp than Open hand in No Vision but not in Vision conditions.

Multivoxel pattern analysis

Figure 6 shows the mean classification accuracy in each ROI for pairwise comparisons of movement type (Grasp vs. Open hand) in Vision and No Vision condition as well as across visual conditions. The Talairach coordinates and numbers of voxels of each ROI are specified in Table 1. Statistical values are reported in Table 4. We report only significant results that survived FDR correction for multiple comparisons.

Delay phase

We found significant decoding of movement type both within (yellow and red bars) and across (orange bars) visual conditions in LOtv, EBA, MT, SPOC, aIPS, dPM, and vPM

bilaterally, as well as in LO and M1/S1 in the left hemisphere. Area LO in the right hemisphere showed significant decoding accuracy in Vision and No Vision condition but not across visual conditions. In addition, there was higher decoding accuracy in Vision than No Vision conditions in left LO, higher decoding accuracy in Vision than cross-decoding in left LO, M1\S1 and bilateral SPOC, and higher decoding accuracy in No Vision than cross-decoding in right LO, dPM and vPM.

Action phase

We found significant decoding of movement type both within (blue and light green bars) and across (dark green bars) visual conditions in bilateral LOtv, MT, SPOC, aIPS, dPM, vPM and M1/S1, as well as in right LO and left EBA. Right LOtv showed above chance decoding accuracy for the dissociation between Grasp and Open hand movements in Vision and No Vision conditions but not across visual conditions. Right EBA showed above chance decoding accuracy in Vision and across visual conditions, but not in No Vision. In addition, LO in the left hemipshere showed higher decoding accuracy in Vision as compared to No Vision and across visual conditions, and LOtv and EBA in the left hemisphere showed higher decoding accuracy in Vision and No Vision conditions as compared to across visual conditions. Area MT in the left hemisphere showed higher decoding accuracy in Vision than across visual conditions. Area LOtv in the right hemisphere, as well as dPM and vPM in the left hemisphere showed higher decoding accuracy for No Vision than across visual conditions.

Discussion

Our results show two main findings. First, during the planning phase action intention can be reliably decoded in areas of dorsal and ventral visual stream regardless of the availability of visual information, as well as across visual feedback conditions. This suggests that in addition to vision, also proprioceptive, somatosensory, and memory-based information play a role in movement planning in dorsal as well as ventral stream areas. Second, during the execution phase we could decode actions in dorsal and ventral stream areas even when no vision was available. Importantly, we could also dissociate action types across visual conditions, suggesting that the activity pattern was modulated by the motor output and online somatosensory feedback.

Information driving preparatory signals in dorsal and ventral visual stream areas

In line with previous findings, our results show that the activity pattern in ventral stream areas during the planning phase preceding the action is modulated by the upcoming movement when visual feedback is available and the object is identical for both action types (Gallivan 2013, Freud 2108). This suggests that the critical factor that induces this effect is related to the visual anticipations of the upcoming action rather than the object itself. Indeed, the two movements elicit different hand configurations that lead to different perceptual expectations. An alternative and non-exclusive possibility is that the ventral stream contributes with dorsal stream areas to integrate of the visual goal into the action plan, and therefore the object is processed in an action-dependent manner. In fact,

grasping requires detailed information about object size and shape, while open hand movements do not.

Interestingly, we found that the activity pattern in ventral stream areas is also modulated by the upcoming action during the planning phase in No Vision conditions, and therefore driven by memory-based processes even in absence of any visual feedback. Ventral stream areas are known to have a crucial role in delayed actions that rely on memory-based information about the object, and consistently show reactivation during delayed actions performed in the dark (Fiehler et al. 2011; Singhal et al. 2013; Monaco et al. 2017). Further, patients with visual agnosia caused by lesions in the ventral stream show impairments in delayed grasping performed towards objects that are no longer visible (Milner and Goodale 1995), and transcranial magnetic stimulation in LOC impairs delayed but not immediate actions (Cohen et al. 2009). This evidence indicates a causal role of ventral stream areas in delayed actions, and our results extend previous findings by showing that the memory-based representation in ventral stream areas is not limited to the execution of the action, but encompasses also the planning phase that precedes the action. This memory-based information likely consists of the expected and well-known visual, somatosensory and motor responses generated by an action, as well as the proprioceptive inputs. Indeed, we are aware of this information even if we close our eyes.

Importantly, we could reliably decode action types in most ventral stream areas during the preparatory phase also across visual conditions. Crucially, the common aspect between the two visual conditions was action preparation. In fact, the same actions were being prepared during the delay regardless of the presence of visual guidance. One

possible explanation for these results is that cross-decoding reflects the integration of proprioceptive inputs about the current state of the hand into a forward model for the upcoming action towards the target. This seems plausible since proprioceptive inputs and final target locations remained unchanged in visual and no visual conditions. Although proprioceptive information per-se might not be processed in the ventral stream, it might contribute to building a perceptual and multisensory representation of limb position (Mercier et al. 2008). This explanation is supported by evidence showing that ventral stream area EBA has a causal role in combining perceptual information about body posture and desired action goal (Zimmermann et al. 2016) for the computation of forward models and state estimation that are part of action planning (Wolpert and Ghahramani 2000). Additional evidence showing functional connections between area LO and S1 during passive tactile stimulation of the hand in absence of any movement or motor task (Tal et al. 2016), might support an alternative explanation related to the anticipation of somatosensory consequences of the action via connections with dorsal stream areas. The second and non-exclusive possibility is that the cross-decoding reflects motor imagery related to the action, which might be present in vision and no vision conditions. Indeed, the neural processing of visual imagery is evident regardless of whether participants have their eyes open (Cichy et al. 2012) or closed (Kosslyn and Thompson 1995). Also, visual imagery can induce motion aftereffects regardless of whether participants have their eyes open or closed (Winawer et al. 2010). However, since our task involved the preparation of an action, the imagery component, if present, was likely more motor than visual. Visual and motor imagery might engage different neural mechanisms. Indeed, unlike visual imagery, the cortical representation of motor imagery, especially in the occipito-

temporal cortex, has given mixed results (Oosterhof et al. 2012). For instance, proprioceptive information plays an important role in motor imagery. In fact, it has been shown that peripheral proprioceptive information about hand posture induces stronger motor facilitations during motor imagery tasks when the hand posture is compatible with the imagined movement as opposed to when it is not (Vargas et al. 2004; Fourkas et al. 2006). Strong evidence comes from deafferented subjects who do not show any motor facilitation during motor imagery because of the lack of afferent feedback (Mercier et al. 2008). Despite the possibility that motor imagery might have driven our cross-decoding results, it is unlikely that participants were engaging in motor imagery for simple actions, such as grasping an object. Indeed, motor imagery requires a conscious effort, while planning a simple hand movement is a process that we perform effortlessly. In addition, planning a real movement and imagining one are processes that differ at several levels, as the former involves real consequences while the latter does not. Therefore, our cross-decoding possibly tackles information that is specific to anticipations of real movements in both visual conditions rather than motor imagery.

The decoding accuracy in Vision condition during the planning phase was higher than cross-decoding in LO, SPOC and interestingly in dPM and M1/S1. Additionally, LO showed higher decoding accuracy in Vision than No Vision condition. These results indicate a strong visual component in areas that are adjacent to the occipital lobe, such as LO and SPOC, that might be implicated in processing the visual anticipations of movements at the early stage of the planning phase. Subsequently, this information might be sent forward to premotor and motor areas for their integration in the motor plan at a later stage. The lack of a sensory specialization for the anticipation of actions in other

ventral and dorsal stream areas is likely due to the fact that anticipations of the consequences of an action are based on experience, and during the execution of actions in our everyday life, visual and somatosensory responses do not happen in isolation. In fact, they are naturally synchronized so that every visual frame of our hand movement corresponds to a specific somatosensory feedback. Thus, at the neural level, the strong experience-based association of visual and somatosensory feedback that we build throughout life might reinforce functional connections between ventral and dorsal stream areas. Indeed, evidence from neurophysiology and neuroimaging studies have shown anatomical and functional connections between dorsal and ventral stream areas (Borra et al. 2008; Verhagen et al. 2008; Bracci et al. 2012; Hutchison and Gallivan 2018), as well as between the primary somatosensory cortex and area LO in the ventral stream (Tal et al. 2016). These connections might allow cross-talks not only during movement execution, but also during the planning phase that precedes an action.

Feedback generated during action execution

Given the specialization of dorsal stream areas in processing visual and somatosensory information for action, as well as proprioceptive information about arm location (Sakata et al. 1973; Lacquaniti et al. 1995), it is not surprising that we can reliably use the activity pattern in areas of the dorsal stream to decode actions based on visual, somatosensory and proprioceptive feedback during action execution. Indeed, the known multisensory aspect of the parietal and frontal cortices makes of the dorsal stream a valuable site to integrate information coming from different senses (Buneo and Andersen 2006). Since experience allows for accurate anticipations, it follows that this information is also used

in these areas to anticipate the consequences of upcoming actions during the planning phase. The finding of a strong memory-based and somato-motor representation of actions performed with no visual guidance in ventral and dorsal premotor cortex is in line with neurophysiology studies showing that grasping actions elicit robust neuronal activity in macaque ventral and dorsal premotor cortex regardless of whether the action is performed with or without visual guidance (Raos et al. 2004, 2006).

Actions, and in particular grasping movements, also require a perceptual component in order to identify the target object that we intend to interact with as well as the hand approaching the object. Given the known role of ventral stream areas in perceptual identification of shapes (Kourtzi and Kanwisher 2000, 2001; James et al. 2003), body parts (Downing et al. 2001), and hands (Bracci et al. 2010), it is expected that visual information about any of these categories would modulate the activity pattern in ventral stream areas during the execution of the movement when vision is available. Therefore, the action-driven modulation of the activity pattern during action execution in ventral stream areas can easily be explained by the difference in visual feedback elicited by Grasp vs. Open hand movements.

Conclusions

Predictions are at the basis of skilled behaviors as well as simple hand actions. Although we perform grasping movements effortlessly, the motor plan is supported by a myriad of information that spans the visual, somatosensory, motor and cognitive systems. Therefore, the prediction of upcoming movements is based on several types of neural signals that we normally experience on a daily basis. Despite the specialization of ventral

stream areas in visual recognition of shapes and dorsal stream areas in somatosensory and motor processing, we used the activity pattern in both ventral and dorsal stream areas to reliably decode action preparation based on brain signals evoked by visual and non-visual (kinesthetic and motor) information. Our results show that visual, memory and somato-motor information similarly affect the pattern of activity in areas of dorsal and ventral visual streams for the representation of the motor plan, and allows predicting action intention across domains, regardless of the availability of visual information. In summary, the strong associations between visual and somato-motor information in our everyday life allows predicting action intention based on visual and non-visual inputs in dorsal and ventral visual streams.

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Tables

Table 1. Talairach coordinates for each ROI.

	Talairach coordinates		
	X	Y	Z
LH LO	-37	-82	-3
RH LO	46	-69	-7
LH LOtv	-43	-61	-11
RH LOtv	46	-49	-9
LH EBA	-48	-71	4
RH EBA	47	-70	7
LH MT	-44	-71	1
RH MT	51	-61	7
LH dPM	-30	-12	50
RH dPM	31	-12	49
LH vPM	-45	2	14
RH vPM	42	-2	12
LH M1/S1	-34	-32	48
LH aIPS	-37	-43	44
RH aIPS	38	-39	44
LH SPOC	-15	-73	32
RH SPOC	16	-73	36

Table 2. Statistical values for main effects and interactions in univariate results

	Delay phase				Action phase					
	ME task		ME vision		ME task		ME vision		Task by vision	
	$F_{(1, 15)}$	p	$F_{(1, 15)}$	p	$F_{(1, 15)}$	p	$F_{(1, 15)}$	p	$F_{(1, 15)}$	p
LHLO							65.4	0.001	19.6	0.001
RHLO	5.2	0.038					83.7	0.001		
LHLOtv					12.6	0.003	29.1	0.001		
RHLOtv							24.1	0.001		
LHEBA			7.2	0.017	4.9	0.04	42.2	0.001		
RHEBA			5.2	0.037			64.2	0.001		
LHMT					8.6	0.01	66.4	0.001	8.5	0.01
RHMT							28.7	0.001		
LHSPOC	4.7	0.046	11.4	0.004	7	0.018	29.3	0.001		
RHSPOC							52.9	0.001		
LH aIPS					33.4	0.001	9.5	0.008	11.6	0.004
RHaIPS	4.6	0.049			8.6	0.01	66.4	0.001		
LHdPM					18.7	0.001	2	0.172		
RHdPM					16.6	0.001	29.6	0.001	4.6	0.049
LHvPM			5.339	0.035					6.7	0.02
RHvPM	10.2	0.006							6.3	0.02
LHM1S1			8.8	0.01	83.5	0.001				

Note: Only significant results are shown

Table 3. Statistical paired-sample t-tests for univariate results

	Grasp > Open hand		Vision > No Vision	
	Vision	No Vision	Grasp	Open hand
LH aIPS				t=4.1 p<0.001
RHdPM		t=3.8 p<0.002		
LHvPM		t=2.9 p<0.011		

Note: Only significant results are shown

Table4. Statistical values for MVPA

	Delay phase: Grasp vs. Open-hand			Action phase: Grasp vs. Open-hand		
	Vision	No Vision	Across	Vision	No Vision	Across
LHLO	t=11.7 **p<0.001**	t=3.2 **p<0.007**	t=4.0 **p<0.001**	t=8.0 **p<0.001**	t=2.60 **p<0.022**	t=0.9 p<0.363
RHLO	t=3.3 **p<0.005**	t=5.0 **p<0.001**	t=2.0 p<0.061	t=4.6 **p<0.001**	t=4.5 **p<0.001**	t=2.4 **p<0.029**
LHLOtv	t=3.0 **p<0.009**	t=3.7 **p<0.002**	t=3.1 **p<0.007**	t=4.7p< **p<0.001**	t=5.9 **p<0.001**	t=3.5 **p<0.004**
RHLOtv	t=4.0 **p<0.001**	t=4.1 **p<0.001**	t=3.3 **p<0.005**	t=2.5 **p<0.024**	t=4.3 **p<0.001**	t=1.5 p<0.150
LHEBA	t=2.8 **p<0.014**	t=3.0 **p<0.008**	t=3.0 **p<0.009**	t=5.4 **p<0.001**	t=4.9 **p<0.001**	t=3.4 **p<0.004**
RHEBA	t=3.9 **p<0.001**	t=5.4 **p<0.001**	t=4.2 **p<0.001**	t=5.4 **p<0.001**	t=1.6 p<0.130	t=4.4 **p<0.001**
LHMT	t=3.4 **p<0.004**	t=3.1 **p<0.007**	t=3.9 **p<0.001**	t=5.5 **p<0.001**	t=4.4 **p<0.001**	t=2.9 **p<0.012**
RHMT	t=2.6 **p<0.019**	t=2.5 **p<0.025**	t=3.9 **p<0.002**	t=2.4 **p<0.031**	t=4.9 **p<0.001**	t=3.9 **p<0.001**
LHSPOC	t=7.0 **p<0.001**	t=3.3 **p<0.005**	t=4.4 **p<0.001**	t=4.6 **p<0.001**	t=4.8 **p<0.001**	t=3.6 **p<0.003**
RHSPOC	t=6.6 **p<0.001**	t=2.6 **p<0.020**	t=3.0 **p<0.008**	t=4.3 **p<0.001**	t=3.4 **p<0.004**	t=3.2 **p<0.006**
LH aIPS	t=5.0 **p<0.001**	t=10.2 **p<0.001**	t=7.4 **p<0.001**	t=5.6 **p<0.001**	t=7.1 **p<0.001**	t=6.5 **p<0.001**
RHaIPS	t=4.8 **p<0.001**	t=3.9 **p<0.002**	t=5.3 **p<0.001**	t=6.7 **p<0.001**	t=6.7 **p<0.001**	t=6.9 **p<0.001**
LHdPM	t=5.1 **p<0.001**	t=5.5 **p<0.001**	t=6.3 **p<0.001**	t=8.3 **p<0.001**	t=7.9 **p<0.001**	t=7.6 **p<0.001**
RHdPM	t=4.9 **p<0.001**	t=6.3 **p<0.001**	t=2.4 **p<0.03**	t=7.0 **p<0.001**	t=7.1 **p<0.001**	t=4.6 **p<0.001**
LHvPM	t=3.6 **p<0.003**	t=4.2 **p<0.001**	t=3.0 p<**0.008**	t=4.1 **p<0.001**	t=6.4 **p<0.001**	t=7.3 **p<0.001**
RHvPM	t=2.9 **p<0.012**	t=5.7 **p<0.001**	t=3.0 **p<0.008**	t=6.5 **p<0.001**	t=7.4 **p<0.001**	t=6.3 **p<0.001**
LHM1S1	t=7.1 **p<0.001**	t=5.7 **p<0.001**	t=5.4 **p<0.001**	t=7.7 **p<0.001**	t=8.7 **p<0.001**	t=8.4 **p<0.001**

Note: significant p values are indicated in bold

Figure legends

Figure 1

Set-up and experimental paradigm. A)The set-up required participants to maintain direct gaze at a fixation point on the object, when they had their eyes open. The object consisted of a cube and was placed on a platform placed above the participant's pelvis. After each movement, participants returned the hand on the button box above their abdomen. Participants wore headphone to hear auditory instructions about the task. B) Schematic timing of one trial. At the beginning of each trial, participants heard an auditory cue about the task. The cue was followed by a delay of 10 s, after which a Go cue prompted the participants to perform the action. The next trial started after 12.5 s of intertrial interval (ITI). In Vision trials, participants were instructed to open their eyes at the beginning of the trial until they heard "Eyes closed" at the end of the same trial. In No Vision conditions participants had their eyes closed for the whole duration of the trial.

Figure 2

Experimental design. We had a two by two factorial design with two Action types (Grasp and Open-hand) and two Vision conditions (Vision and No Vision), which gave rise to four conditions. We performed our analyses on the Plan (upper left panel) and Execution phase (upper right panel). During the planning phase (lower left panel), the classification between the two action types would allow isolating visual, memory-based predictions and motor preparation. During the execution phase (lower right panel), the classification

between the two action types would allow isolating visual and memory based information as well as sensory feedback originating from the execution of the movement.

Figure 3

Ventral stream localizers. A) The Talaraich coordinates of area MT, EBA, LO and LOtv are indicated with colored dots. Area LO was localized through a contrast of (Objects > Scrambled images), EBA was identified through a contrast of (Bodies > Scrambled images), MT was localized with the contrast (Motion > Static), and LOtv was identified with the contrast (Touch Object > Touch Textures). B) Apparatus used for the LOtv localizer. Objects and textures were attached on a custom-made wooden turntable and separated into four quadrants by two orthogonal separators. Each quadrant contained three stimuli from one category (objects or textures). In each block of the localizer, participants were required to perform three sequential tactile explorations of the stimuli (objects or textures) in one sector of the turntable. The first beep sound instructed the participant to start to explore the first stimulus on the sector placed next to the right hand (1). Two subsequent beeps separated by 4 s cued participants to start to explore the second and third object (2 and 3). Following 4 s, another beep sound instructed the end of the exploration phase and participants were prompted to return the right hand to the home position (HP) and rotate the wheel with the left hand.

Figure 4

Dorsal stream localizer. Dorsal stream areas were functionally localized by comparing the response during the execution of the two actions to baseline.

Figure 5

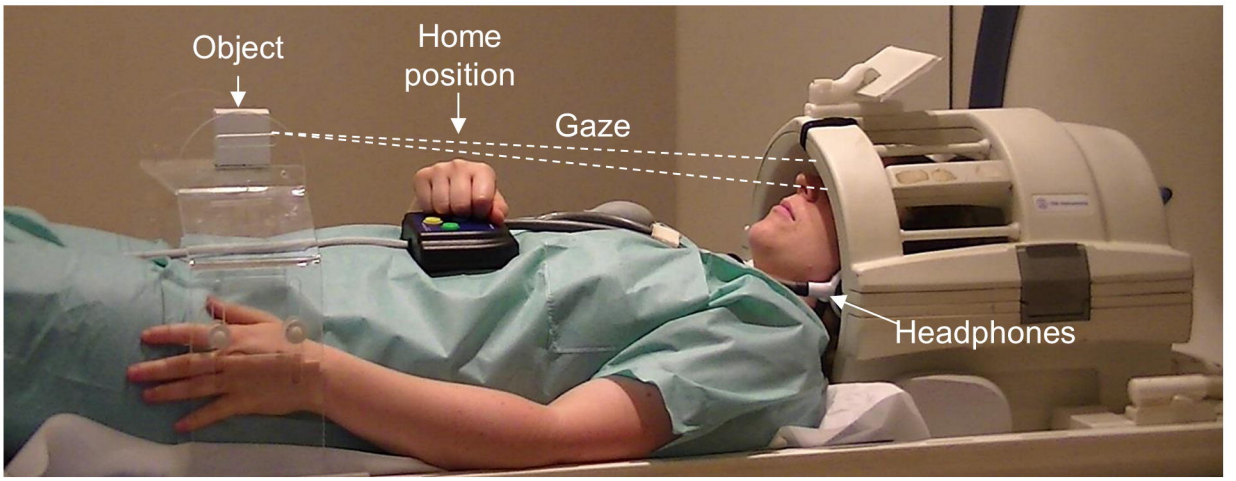
Activation levels in our ROIs. For each area, the bar graph indicate the β weights for the main effects of Task (Grasp and Open-hand) and the Vision (Vision and No Vision) in the planning phase (left) and execution phase (right). When interactions reached significance, post-hoc t-tests are shown between β weights of individual experimental conditions. Error bars show 95% confidence intervals.

Figure 6

Movement decoding from our ROIs. The plots show decoding accuracies for the dissociation between Grasp and Open-hand movements in Vision and No Vision condition as well as across Visual conditions during the planning phase (yellow, red and orange bars, respectively) and during the execution of the movement (blue, green and turquoise bars, respectively). Error bars show 95% confidence intervals.

Figure 1

A.


Object
Home position
Gaze
Headphones

B.

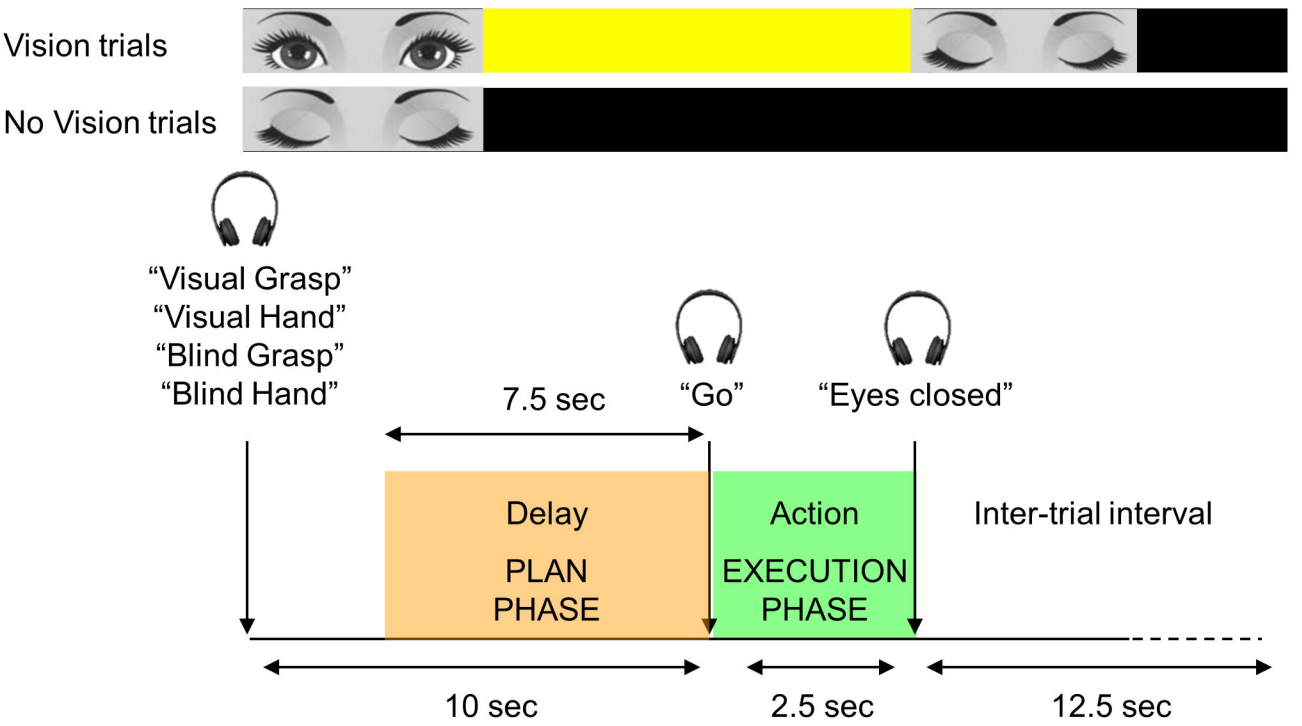
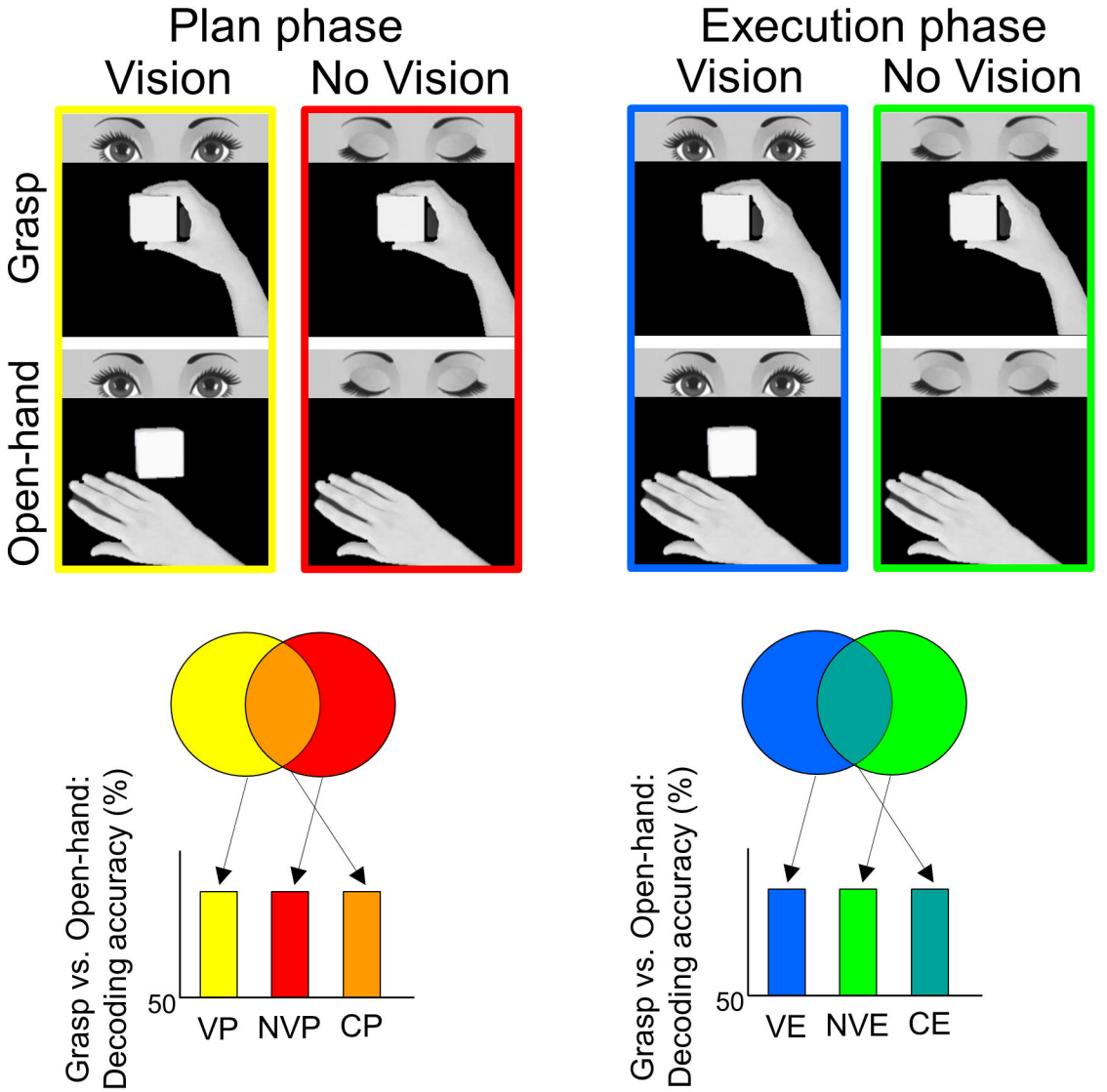

Vision trials
No Vision trials
"Visual Grasp"
"Visual Hand"
"Blind Grasp"
"Blind Hand"
7.5 sec
"Go"
"Eyes closed"
Delay
PLAN PHASE
Action
EXECUTION PHASE
Inter-trial interval
10 sec
2.5 sec
12.5 sec

Figure 2



Anticipations:

- Visual Plan (VP) = visual predictions + motor preparation
- No Vision Plan (NVP) = memory-based predictions + motor preparation
- Cross Plan (CP) = motor preparation

Feedback:

- Vision Execution (VE) = visual information + movement execution
- No Vision Execution (NVE) = memory-based information + movement execution
- Cross Execution (CE) = movement execution

Figure 3

Ventral Visual Stream areas

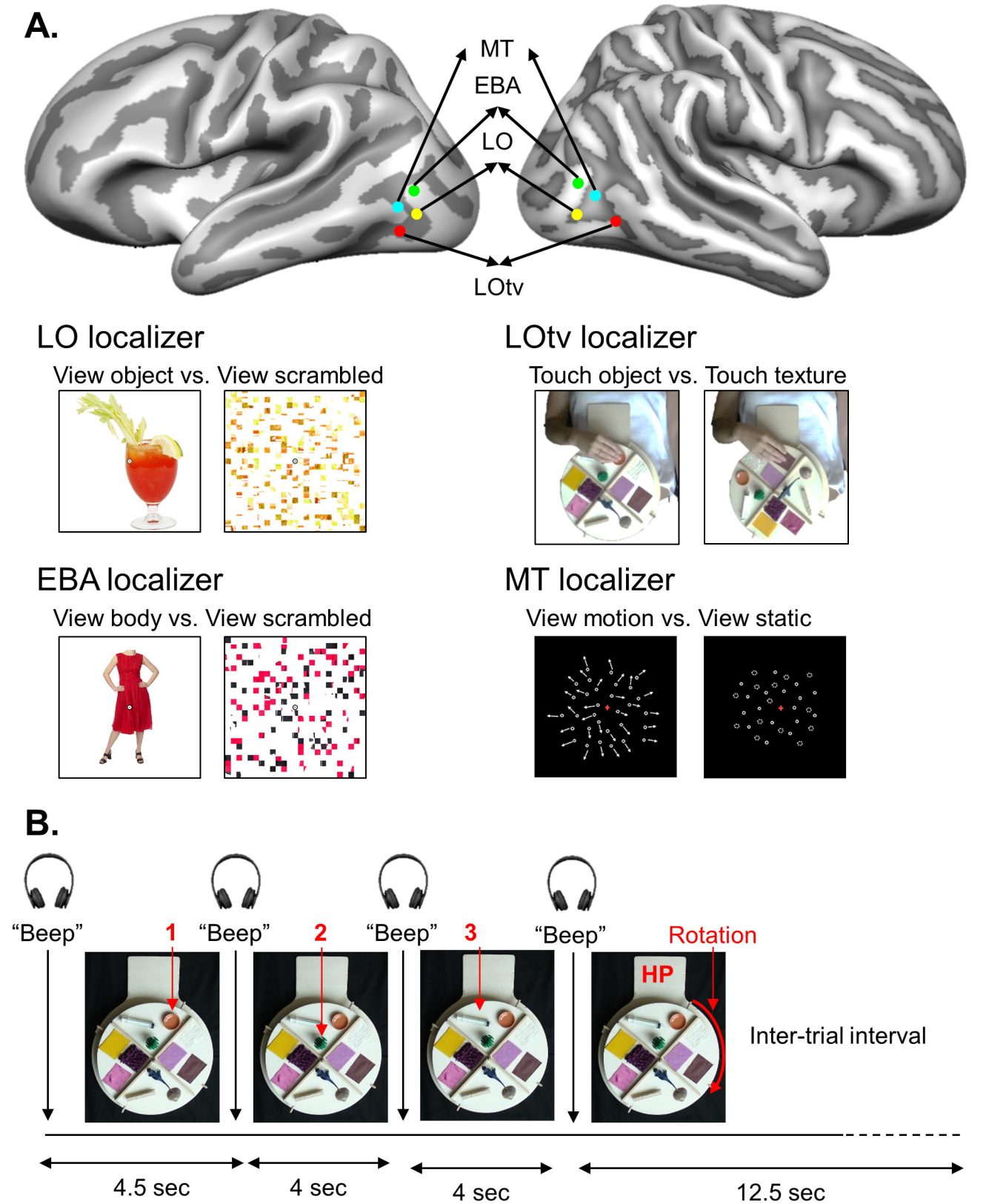


Figure 4

Dorsal Visual Stream areas

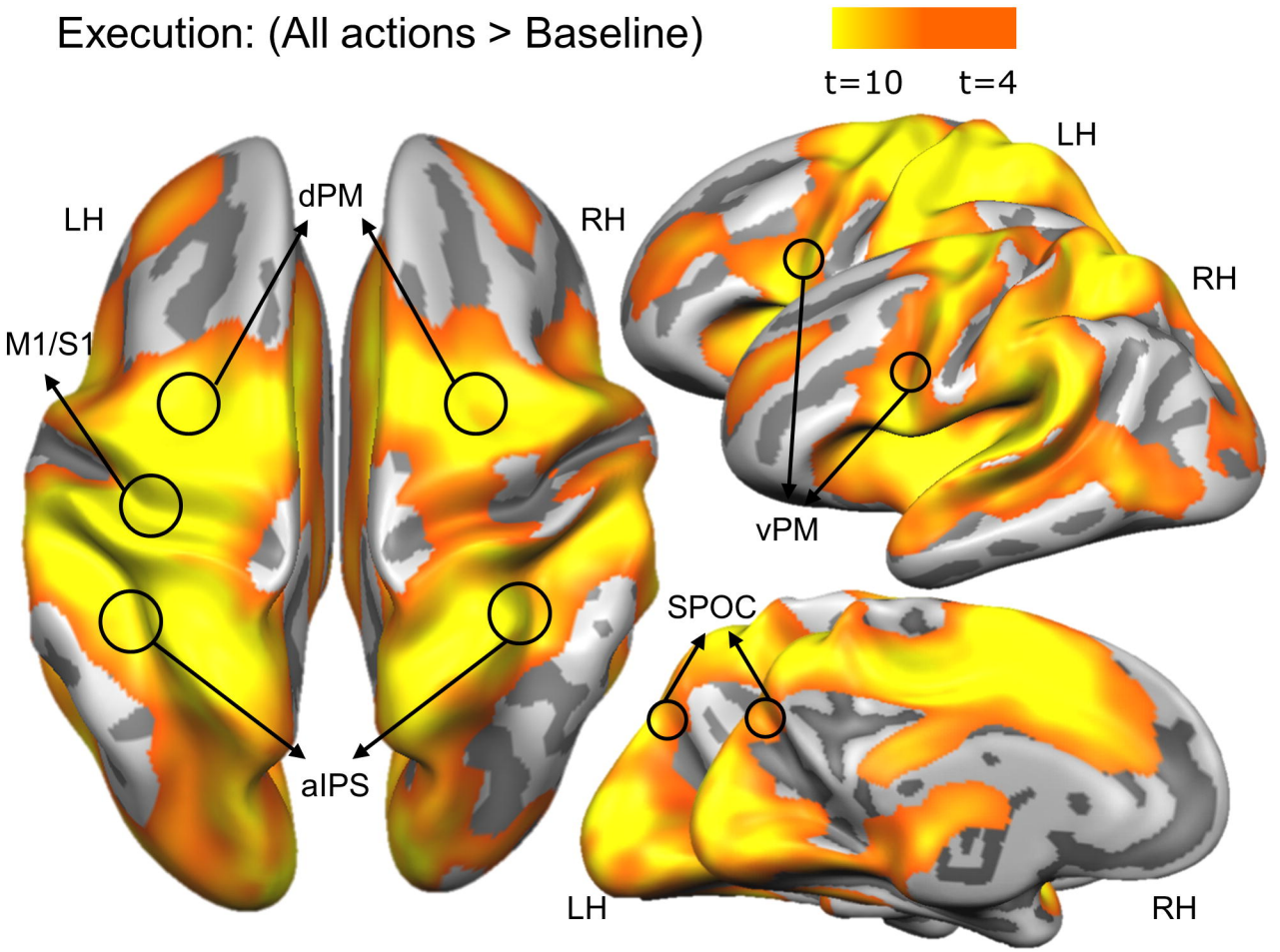


Figure 5

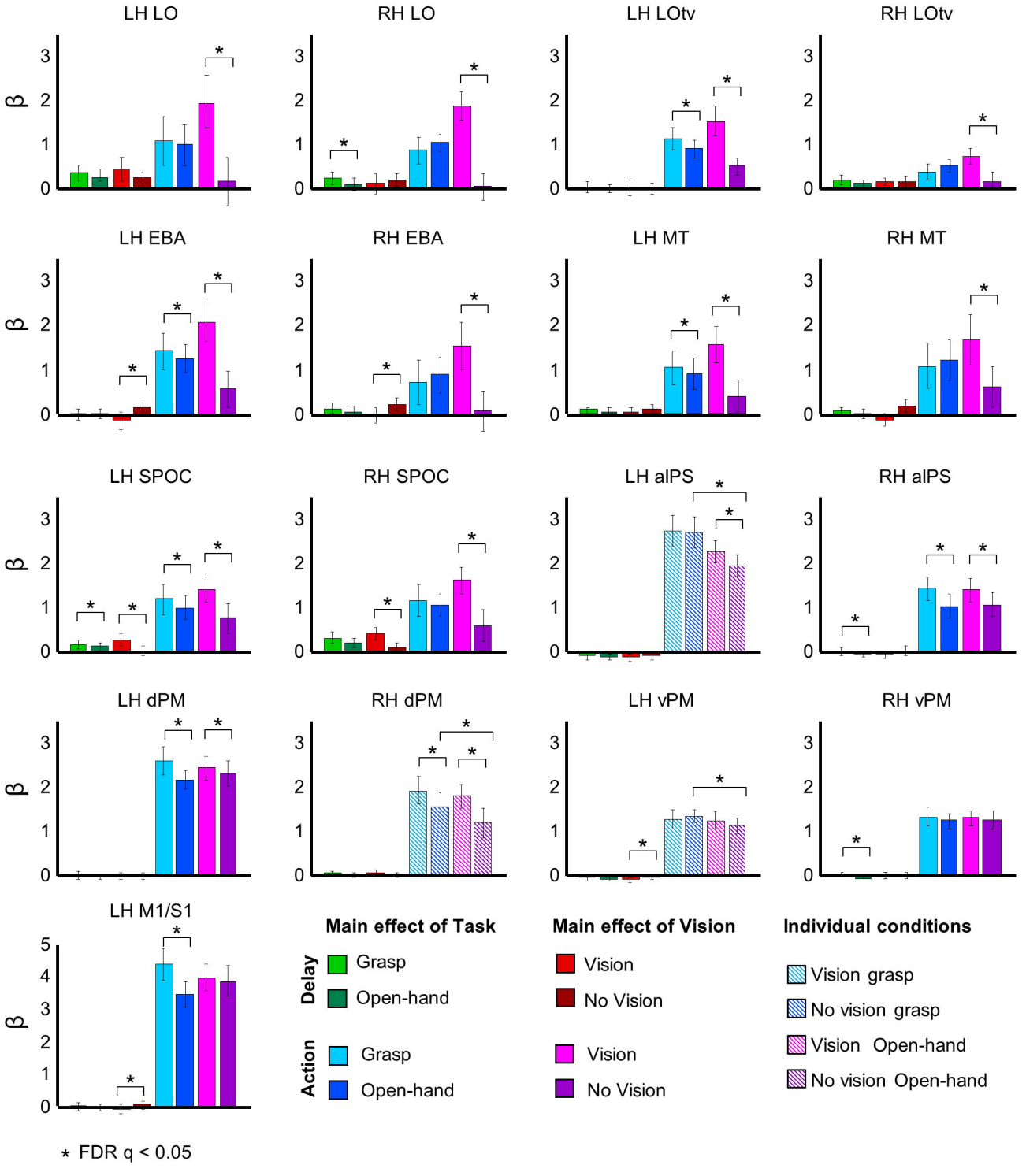
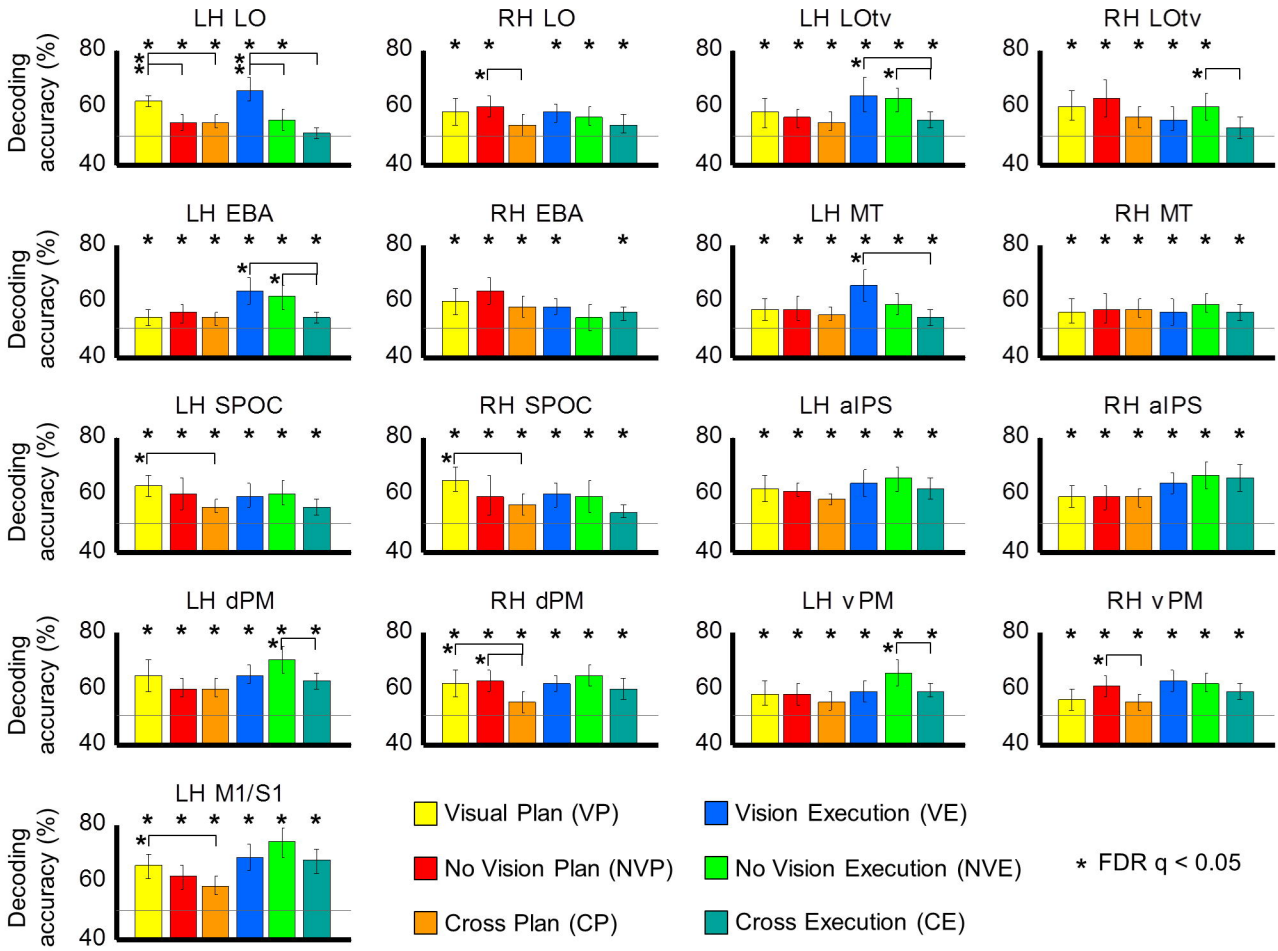

LH LO
RH LO
LH LOtv
RH LOtv
LH EBA
RH EBA
LH MT
RH MT
LH SPOC
RH SPOC
LH aIPS
RH aIPS
LH dPM
RH dPM
LH vPM
RH vPM
LH M1/S1
β
Main effect of Task
Delay
Grasp
Open-hand
Action
Grasp
Open-hand
Main effect of Vision
Vision
No Vision
Vision
No Vision
Individual conditions
Vision grasp
No vision grasp
Vision Open-hand
No vision Open-hand
* FDR q < 0.05

Figure 6


LH LO
RH LO
LH LOtv
RH LOtv
LH EBA
RH EBA
LH MT
RH MT
LH SPOC
RH SPOC
LH aIPS
RH aIPS
LH dPM
RH dPM
LH vPM
RH vPM
LH M1/S1
Decoding accuracy (%)
80
60
40
Visual Plan (VP)
No Vision Plan (NVP)
Cross Plan (CP)
Vision Execution (VE)
No Vision Execution (NVE)
Cross Execution (CE)
* FDR q < 0.05