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Getting a grip on reality: Grasping movements directed to real objects and images rely on dissociable neural representations



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ABSTRACT

In the current era of touchscreen technology, humans commonly execute visually guided actions directed to two-dimensional (2D) images of objects. Although real, three-dimensional (3D), objects and images of the same objects share high degree of visual similarity, they differ fundamentally in the actions that can be performed on them. Indeed, previous behavioral studies have suggested that simulated grasping of images relies on different representations than actual grasping of real 3D objects. Yet the neural underpinnings of this phenomena have not been investigated. Here we used functional magnetic resonance imaging (fMRI) to investigate how brain activation patterns differed for grasping and reaching actions directed toward real 3D objects compared to images. Multivoxel Pattern Analysis (MVPA) revealed that the left anterior intraparietal sulcus (aIPS), a key region for visually guided grasping, discriminates between both the format in which objects were presented (real/image) and the motor task performed on them (grasping/reaching). Interestingly, during action planning, the representations of real 3D objects versus images differed more for grasping movements than reaching movements, likely because grasping real 3D objects involves fine-grained planning and anticipation of the consequences of a real interaction. Importantly, this dissociation was evident in the planning phase, before movement initiation, and was not found in any other regions, including motor and somatosensory cortices. This suggests that the dissociable representations in the left aIPS were not based on haptic, motor or proprioceptive feedback. Together, these findings provide novel evidence that actions, particularly grasping, are affected by the realness of the target objects during planning, perhaps because real targets require a more elaborate forward model based on visual cues to predict the consequences of real manipulation.

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1. Introduction

One of the most influential conceptualizations of the visual system suggests that the visual system is segregated, anatomically and functionally, into two visual pathways (Goodale & Milner, 1992). In this view, the ventral pathway supports visual perception, while the dorsal pathway subserves goal-directed actions. Most of the research on the cognitive and neural mechanisms underlying goal-directed actions utilized real 3D objects. Importantly however, with the proliferation of touchscreens in the last decade, humans now commonly perform visually guided actions upon two-dimensional images of objects. Although such interactions share some features with visuomotor control of real 3D objects, they provide a limited range of actions and have limited consequences. For example, using a hammer to pound a nail will have real consequences (which may contribute to achieving goals, such as successfully hanging a portrait, or failure, such as a bruised thumbnail). In stark contrast, even though a picture of a hammer may invoke the *concept* of hammering, one would certainly never try to pound a nail with a picture of a hammer. Thus, despite the similarity between actions directed to real 3D objects and images, given the differential effects, the underlying neural representations may be expected to differ.

Consistent with this conjecture, recent behavioral evidence shows that while visually guided grasping of real 3D objects can be performed using only visuomotor processing (within the dorsal visual stream, Goodale & Milner, 1992), grasps performed upon images show properties consistent with greater reliance on perceptual representations. First, the simulated grasping of object images, like purely visual perceptual tasks, follows a fundamental psychophysical principle (Weber's Law); whereas, grasping of real 3D objects does not (Ganel, Chajut, & Algom, 2008; Holmes & Heath, 2013). Second, grasping of images relies on holistic representation of shape (Freud & Ganel, 2015) while grasping of real 3D objects relies on analytic representation of object features (Ganel & Goodale, 2003). Third, crowding (i.e., the presence of flanking objects in a scene) impairs size perception but not grip scaling of 3D objects; whereas for 2D objects, the effect of crowding is similar for perception and action (Chen, Sperandio, & Goodale, 2015).

Given this psychophysical evidence that grasping is affected by stimulus realness, we expected differences in the neural processing of actions upon real and simulated objects. Recent human neuroimaging evidence has shown that even during passive viewing, the neural processing of real objects and images may differ (Snow et al., 2011). Thus, during manipulative actions it is likely that object realness may be expected to modulate the neural representations. Alternatively, there may be reasons to expect no such differences. For example, if precision grasping is akin to reaching to two locations with the index finger and thumb (Smeets & Brenner, 1999), one may expect similar neural representations for the grasping of real objects and images because the digit positions are similar.

Here we tested whether regions within the visual pathways generate distinct visuomotor representations that carry information regarding object realness in addition to the expected movement. We might expect differences between real objects and images in the ventral visual stream, where we

have previously found such differences during passive viewing (Snow et al., 2011) and where we have found that realism of an action task affects activation (Kroliczak, Cavina-Pratesi, Goodman, & Culham, 2007). However, we might expect clearer differences, and differences that are specific to grasping, in the dorsal visual stream, specifically the anterior intraparietal sulcus (aIPS), which combines visual and motor cues to plan and execute visually guided actions (Culham et al., 2003; Gallivan & Culham, 2015; Singhal, Monaco, Kaufman, & Culham, 2013).

Grasping of a real 3D object evokes real consequences that must be anticipated even during action planning; whereas, action consequences are fairly minimal for simulated objects. Hence we predict that the distinction between object format would be evident in aIPS. Since such regions rely on visual information available before movement execution, this hypothesis predicts that the differences between object formats would be manifested in the planning phase and not just during execution. Finally, this hypothesis predicts that object realness will matter more for grasping of a real 3D object, which requires greater planning accuracy and anticipation of action consequences than reaching to touch the object. That is, errors in grasping real 3D objects will lead to consequences, corrections and recalibrations that are not necessary when grasping images; whereas, errors in reaching towards real 3D objects and images will lead to similar mislocalizations.

One important consequence of actions upon real 3D objects is tactile feedback that can be used to optimize manipulation (such as adjusting digit positions or grip force) and to “calibrate” forward models for better performance on subsequent trials (Säfstrom & Edin, 2008). However, this haptic feedback is absent for actions upon images (though visual feedback may still be available) and may be a critical factor in observed behavioral differences. Despite the fact that even simple terminal feedback can still engage the dorsal visual pathway (Whitwell, Ganel, Byrne, & Goodale, 2015), differential haptic feedback is thought to mediate the differences between actions directed to real 3D objects and images of the same objects (Hosang, Chan, Jazi, & Heath, 2015). Hence, to examine the sensitivity to object realness beyond the differences induced by the haptic feedback, we employed an experimental design that minimized the differences between the haptic feedback provided for real objects and images (see method for details).

We used functional magnetic resonance imaging (fMRI) to investigate the human neural representations of real objects versus images during two action types, grasping (for which object attributes like size and shape are highly relevant) and reaching to touch (which relies predominantly on object location) (Fig. 1). Because of the obvious differences in haptic feedback during execution of a grasp towards real objects versus images, we focussed our analyses on the planning period when stimuli were in view but before the action was initiated. We expected that the neural representations across sensory and sensorimotor brain regions, as inferred from MultiVoxel Pattern Analysis (MVPA), would differ during the planning of actions towards real objects versus images. Moreover, we predicted that the difference may be particularly marked during grasping movements, where object

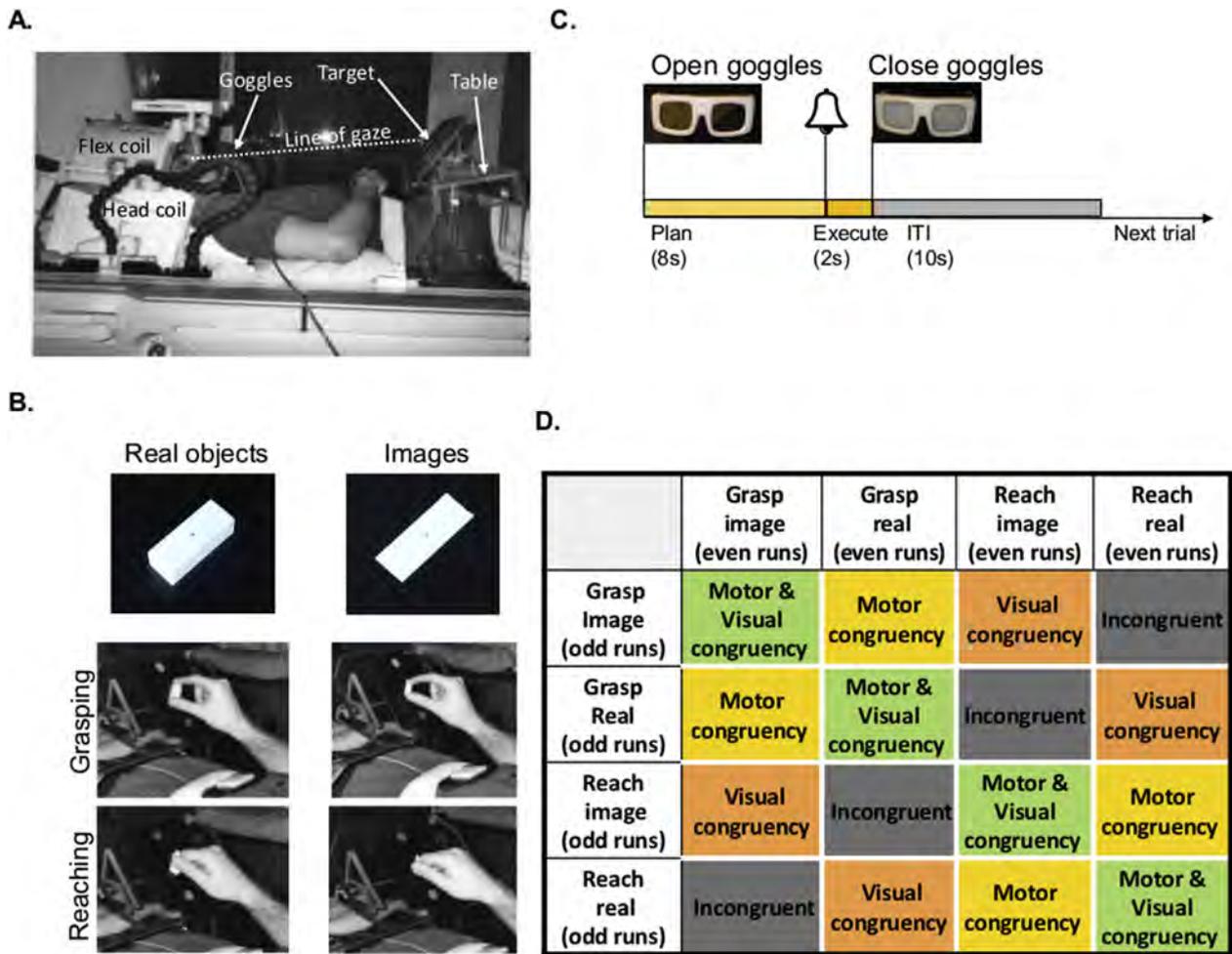


Fig. 1 – Experimental methods. (A) Participant setup shown from a side view. (B) Experimental apparatus and target objects shown from the participant's point of view. Participants performed grasping movements (upper row) and reaching-to-touch movements (lower row) to real objects (left column) and to similar images (right column). (C) Timing of each trial. Trials began with the opening of the goggles such that participants could see the object and which movement they should perform based on the sticker attached above the object. After 8 sec an auditory cue was given and participants executed the appropriate movement (grasp/reach). After an additional 2 sec, the goggles were closed and participants returned their hand to its starting location. (D) Analysis approach. Spatial activation patterns within a region were correlated across odd and even runs for each combination of 4 conditions in the 2×2 factorial experimental design, yielding 16 pairwise correlation coefficients. Correlations were grouped into four categories as a function of the congruency between any two conditions: motor & visual congruency, motor congruency (grasp/reach), visual congruency (real/image) and incongruency.

properties such as shape and size are relevant for grasp planning and are coded by areas like aIPS, compared to reaching, where only information about location is essential.

2. Experimental procedure

2.1. Participants

Data was analyzed from 13 right-handed volunteers who participated in the experiment (eleven females; mean age: 24.5 range: 22–29 years) and were recruited from the University of Western Ontario (London, Ontario, Canada). The data obtained from two additional participants were excluded. One of the subjects has excessive head and body movements

during the scan and the other subject had only six runs available, which is not sufficient for the main analysis in which the data was divided for odd and even runs. All participants had a normal or corrected-to-normal vision and were financially compensated for their participation. Informed consent was obtained prior to the study. All experimental procedures were approved by the University of Western Ontario's Health Sciences Research Ethics Board using principles consistent with the Declaration of Helsinki.

2.2. Setup and apparatus

Participants planned and performed reach-to-touch and reach-to-grasp movements towards a centrally located object. Each participant's workspace consisted of a turntable with

four compartments placed over the waist (Fig. 1A). Objects were three real, 3D, white-plastic blocks that varied in height (20, 30 or, 40 mm; with a constant width of 15 mm and a constant depth of 10 mm) mounted on a black background and three printed 2D images simply depicting flat white rectangles with the same facing dimensions as the real objects (but no depth or simulated depth) upon a black background (Fig. 1B). All objects were located at the center of a black square plate (13.7 cm × 13.7 cm) tilted toward the participant (Fig. 1B). Note that the different object sizes were mainly used to reduce predictability and were not analyzed separately. Green and red stickers were placed at the two ends of the plate to cue the type of action (grasping/reaching) participants were instructed to complete.

To facilitate direct viewing of the workspace, we tilted the head coil (~20°) and used foam cushions to give an approximate overall head tilt of 30° (Fig. 1A). To minimize limb-related artifacts, participants had the right upper arm braced, limiting movement to the elbow, enabling reaching movements along an arc. Computer controlled PLATO goggles (Translucent Technologies, Toronto, ON) with liquid-crystal shutter lenses were used to control stimulus exposure time.

2.3. Experimental design and timing

The design was a 2 × 2 factorial design, with movement type (grasping/reaching) and object type (real/image) as within-subject variables (Fig. 1B). We used slow-event related paradigm with 20-sec trials each consisting three phases. Each trial began with the planning phase (8 sec) that was followed by the execution phase (2 sec) and then an inter-trial interval (ITI) (10 sec) (Fig. 1C). The goggles were open from the beginning of the planning phase until the end of the execution phase such that actions were performed with visual feedback (in closed loop). Participants were cued about the required movement by the color of the sticker located above the object (red-reach, green-grasp) and execute the movement after they heard an auditory cue. In the grasping movements, participants grasped the long axis of the object using a precision grip with their index finger and thumb. Given the tilt of the plate upon which stimuli were displayed, this grasp meant the index finger landed above and behind the thumb (Fig. 1B). To minimize motor and haptic differences between real object and images, participants were asked not to lift the object from the black plate. In the reaching movements, participants transported their arm to the target location, but rather than forming a grip, they touched the object with the knuckles. Following each of the two movement types, participants were asked to return their hand to its central starting position when goggles were closed.

A total of 192 trials (48 trials per condition) were conducted. These trials were randomized and balanced across eight runs. The fMRI testing session for each participant included set-up time, eight functional runs (although two participants completed only seven runs) and one anatomical scan, for a total duration of approximately 2 h.

2.4. MRI acquisition

Participants were scanned in a 3-T Siemens Prisma MRI scanner at the Robarts Research Institute. To enable direct

viewing without occlusion while providing whole-brain coverage, the bottom 20 channels of a 32-channel head coil were positioned below the head (occiput) while a 4-channel flex coil was suspended over the forehead. Measures of the blood-oxygenation-level-dependent (BOLD) signal were acquired using a T2*-weighted, single-shot, gradient-echo echo-planar imaging acquisition sequence. Specific scanning parameters were as follows: whole brain coverage, 36 slices, transverse orientation, voxel resolution (3 mm)³, no gap, TR = 2000 ms, TE = 30 ms, flip angle = 70°, 259 volumes. High-resolution anatomical volumes were acquired with a T1-weighted 3D MPRAGE sequence (TR = 2300 ms, field of view 256 × 256, flip angle = 9°, (1 mm)³, 176 slices).

2.5. Data analysis

fMRI data was processed using BrainVoyager 2.8QX software (Brain Innovation, Maastricht, Netherlands.), Neuroelf package (<http://neuroelf.net/>), and in-house software written in Matlab (The MathWorks, Inc, Natick, MA, USA.). Preprocessing included 3D motion correction, slice-time correction, filtering of low temporal frequencies (slow drifts below 3 cycles/run). Given the application of MVPA, no spatial smoothing was applied.

2.5.1. Regions of interest (ROI) selection

We examined six regions of interest (ROIs) based on our theoretical expectations. The aIPS (bilaterally) was chosen as a key region of interest in the dorsal visual stream because it has reliably been shown to be a key region in visually guided grasping by neuroimaging studies (for review see Gallivan & Culham, 2015), a neuropsychology study (Binkofski et al., 1998), and neurostimulation studies (reviewed in Tunik, Rice, Hamilton, & Grafton, 2007). Moreover, aIPS has previously been shown to be sensitive to the realness of the action (Kroliczak, McAdam, Quinlan, & Culham, 2008). The lateral occipital cortex (LOC) (bilaterally) was chosen as a key region of interest in the ventral visual stream because it has reliably been shown to be a key region in visual object recognition by neuroimaging studies of control participants (reviewed in Grill-Spector, Kourtzi, & Kanwisher, 2001) and patients with object recognition disorders (Bridge et al., 2013; Freud, Ganel, Sheleff, et al., 2015; James, Culham, Humphrey, Milner, & Goodale, 2003; Ptak, Lazeyras, Di Pietro, Schneider, & Simon, 2014). Moreover, LOC activation (specifically fMRI adaptation) has been shown to be affected by the realness of objects (Snow et al., 2011). In addition, we examined two unilateral control regions. We identified M1/S1, in the hand area of the central sulcus, which due to their proximity in volumetric space likely includes both primary motor cortex area M1 (on the precentral bank of the central sulcus) and part of primary somatosensory cortex (Brodmann area 3 on the postcentral bank of the central sulcus). We also identified another somatosensory area (SS) in the postcentral sulcus that likely includes parts of somatosensory cortex (Brodmann area 2 on the anterior bank of the postcentral sulcus) and Brodmann area 5 (on the posterior bank of the postcentral sulcus).

Each ROI was defined as a sphere (radius 5 mm for a total volume of 515 mm³). All ROIs were defined for each individual participant based on statistical map that was acquired from the contrast of all conditions > baseline ($p < .05$, false discovery rate

(FDR corrected) and anatomical landmarks. The motor cortex was defined by selecting voxels around the left ‘hand knob’ landmark in the Central Sulcus (CS). The somatosensory cortex was defined by selecting voxels encompassing the post-central gyrus and postcentral sulcus (PCS) anterior to the aIPS (Gallivan, McLean, Valyear, & Culham, 2013; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011). The aIPS was bilaterally defined by selecting voxels located in the vicinity of the junction of the intraparietal sulcus and the post-central sulcus. The LOC was bilaterally defined by selecting voxels located at the posterior portion of the inferior temporal gyrus/sulcus. Average ROIs (across participants) are projected on the average cortical surface derived from cortex-based alignment of the anatomical scans of all the participants (Fig. 2).

2.5.2. Multivoxel pattern analysis (MVPA)

MVPA was conducted separately for each ROI using the following steps: First, the beta weights for each condition (grasp real, grasp image, reach real, reach image) in each phase (planning, execution) were calculated separately for each voxel, using a General Linear Model (GLM). Next, the data was separated for odd and even runs and all pairwise correlations between the response patterns across combinations of the four conditions (separately for each participant) were calculated and Fisher transformation was applied on the correlation values to ensure normal distribution and to enable further parametric statistical analysis (As was done in previous fMRI studies-e.g., Freud, Rosenthal, Ganel, & Avidan, 2015; Jeong & Xu, 2016). Finally, since the correlation of a condition with itself (e.g., grasp image-grasp image), happens only between runs (while other types of correlation occur also within run), and temporal proximity is known to inflate correlations, further analysis were focused only on the correlations between the odd and even runs.

This approach yields a four by four asymmetrical correlation matrix between different conditions (Fig. 1D). We classed each of these correlation coefficients based on whether they involved motor congruency and/or visual congruency. Four correlations reflect trials that were fully congruent (motor & visual congruency, green cells, Fig. 1D). Four correlations reflect trials that share congruent movement types (yellow cells, Fig. 1D). Four correlations values reflect trials that share congruent object formats (orange cells, Fig. 1D). Finally, four correlations reflect incongruency of both movement type and

object format (gray cells, Fig. 1D). The logic of this analysis is that if a given region processes both visual and motor information, greater correlations are expected for the full congruency trials compared with the motor congruency/visual congruency trials. Further evidence could come from the comparison between motor/visual congruency with the incongruent trials. If a region is sensitive to a particular type of information (motor or visual), the correlations between congruent types, which share this information, should be higher than the correlations between incongruent types.

Finally, to examine whether the sensitivity to object realness differently modulates the representations during grasping versus reaching movements, the correlations between the grasping movements ($r_{\text{grasp real: grasp image}}$) and the correlation between the reaching movements ($r_{\text{reach real: reach image}}$) were compared. Higher correlations reflect more similar representations while lower correlation between two conditions, reflect more dissociable representations. To visualize the multidimensional results of the MVPA we generated hierarchical clusters plot using the average distance between all pairs of objects in any two clusters (Matlab functions “linkage” and “dendrogram”).

2.5.3. Searchlight analysis

To test whether different other regions along the ventral and dorsal pathways were sensitive to motor and visual information, an exploratory whole-brain searchlight analysis using a 5 mm diameter sphere, was employed. Three models were generated (a motor model, a vision model, and a visuomotor model, see Fig. 5) and a second-level analysis was employed to generate t maps ($t > 3.5$; $p < .005$) with a cluster correction using a Monte Carlo simulation method (Forman et al., 1995) performed with the function AlphaSim in NeuroElf (<http://neuroelf.net/>). We note that this threshold might yield a higher-than-expected false positive rate due to violated statistical assumptions (Eklund, Nichols, & Knutsson, 2016), and therefore a careful interpretation of the searchlight results is required; however the main goal of this exploratory analysis was to detect whether other regions, outside the predefined ROIs were also sensitive to the different conditions.

The first two models were defined based on sensitivity to one modality (vision or motor), and insensitivity to the other modality. Hence, each of these models predicts greater correlation

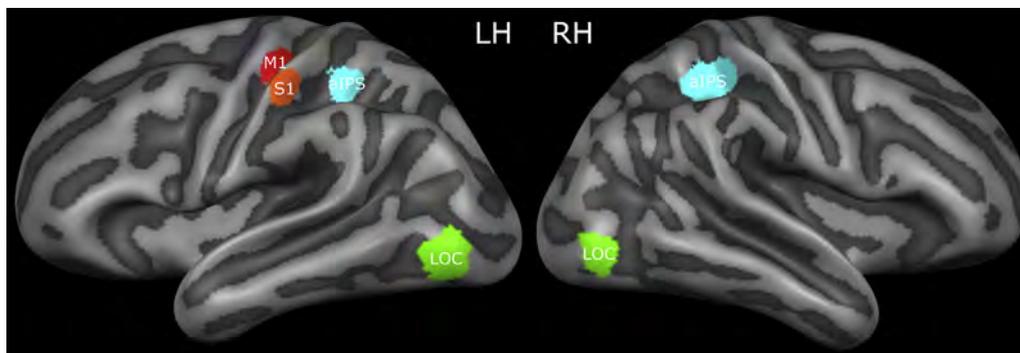


Fig. 2 – Regions of interest (ROIs). ROIs and anatomical landmarks are overlaid on a group-averaged folded cortical mesh. ROIs: M1-Motor cortex (Talairach coordinates $x = -33$ (left), $y = -25$, $z = 50$). SS- Somatosensory cortex ($x = -48$ (left), $y = -25$, $z = 46$). aIPS- Anterior Intraparietal Sulcus ($x = -36$ (left)/31(right) $y = -44/-40$ $z = 44/46$). LOC- Lateral Occipital Cortex ($x = -44$ (left)/42(right) $y = -71/-70$ $z = -3/-4$).

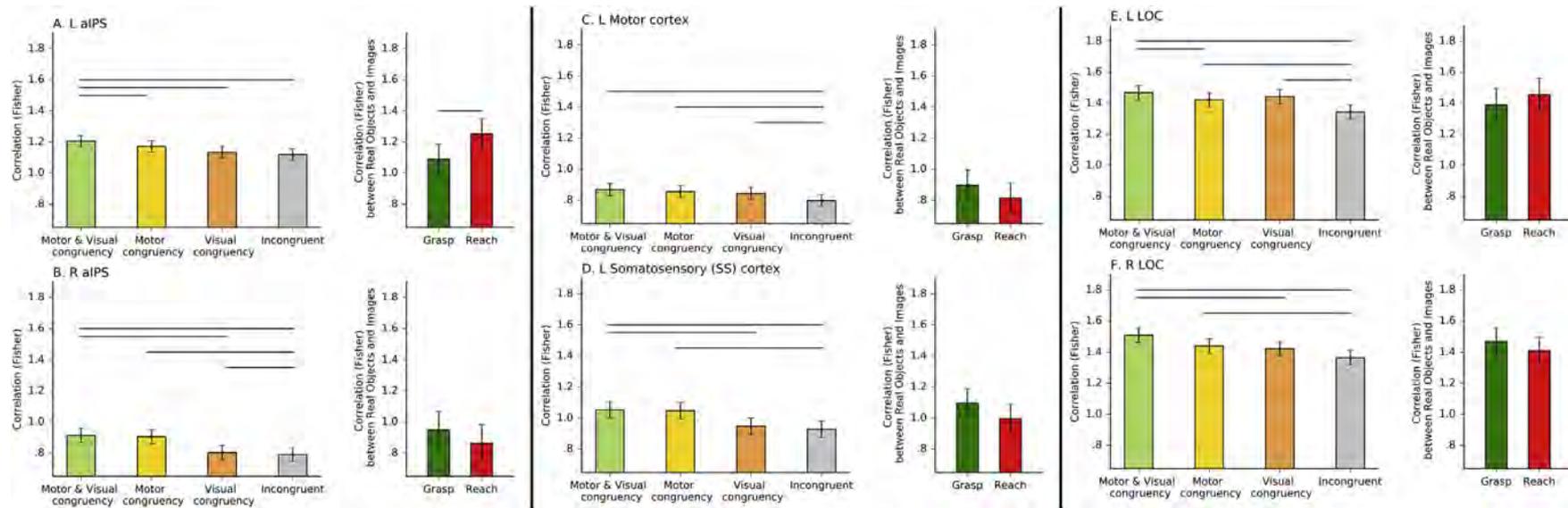


Fig. 3 – Results, planning phase. (A) Left aIPS showed sensitivity to motor information and to visual information, as evident from the greater correlation induced by the full congruency trials (left panel). Grasping movements were found to be more segregated by object-reality compared to reaching movements (right panel). (B) Right aIPS was mainly sensitive to motor congruency, but did show higher correlation for visual congruency compared with incongruent trials. No modulation of object reality on movement type was found. (C) Motor cortex did not exhibit a main effect of congruency, and sensitivity to the movement congruency, was not modulated by object reality. (D) Somatosensory cortex exhibited sensitivity to movement congruency but not to format congruency. No modulation of object reality on movement type was found. (E) left LOC showed sensitivity to visual congruency and to movement congruency. In contrast to left aIPS, sensitivity to the movement congruency was not modulated by object reality, suggesting the LOC is sensitive to the visual differences between real object and images and does not combine visual and motor information. (F) Right LOC was sensitive to motor information, while no sensitivity observed for visual information. Horizontal lines mark significant simple effects ($p < .05$). Error bars in all figures represent 95% confidence intervals for the main effect as calculated from repeated measure ANOVAs (Jarmasz & Hollands, 2009).

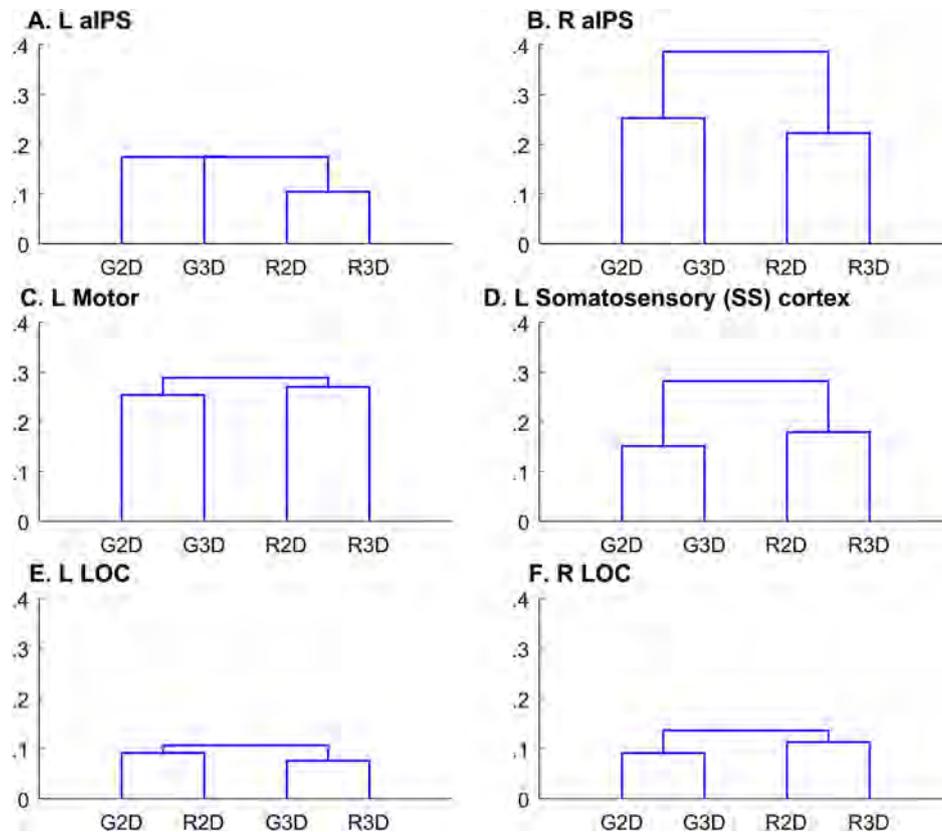


Fig. 4 – Hierarchical clustering of conditions within ROIs. Each clustering tree shows the conditions grouped by the similarity of their representations. Note that most ROIs were clustered predominantly based on the motor information (movement type). However, the left aIPS representations (A) were found to be different, showing three clusters (see text for details). In addition, left LOC (E) was clustered predominantly based on visual information (object type).

values between to any two conditions that share the relevant information (i.e., movement type for the motor model, object type to the vision model) and lower correlation values for all other cells. The third model predicts equal sensitivity to both visual and motor information. Thus, for this model the highest sensitivity is predicted only along the diagonal, while cells that correspond along one dimension are correlated, but not as trials that correspond across the two dimensions (i.e., the diagonal).

2.5.4. Univariate analysis

In addition to the main MVPA, a whole brain, univariate analysis was conducted. GLM analysis was used to calculate the beta values for each condition and a Random effect (RFX) analysis with a cluster correction using a Monte Carlo simulation method was applied ($p < .005$). We tested whether main effects of object type or movement type or interaction between these variables were evident.

3. Results

3.1. Planning phase

3.1.1. MVPA

First, we analyzed the neural representations of the left aIPS, a key region for the computation of visually guided hand

actions. As presented in Fig. 3A, full congruency (i.e., motor and visual congruency) induced greater correlation (i.e., more similar representations) than motor congruency, visual congruency and incongruent trials, suggesting that the left aIPS represents both motor (reach/grasp) and visual information regarding object realness during action planning. To statistically estimate this effect, a repeated-measures analysis of variance (ANOVA) was employed and revealed a main effect of condition [$F_{(3,36)} = 4.58, p < .01, \eta_p^2 = .27$, Fig. 3A left panel]. Planned comparisons ensured that full congruency induced greater correlations relative to motor congruency [$F_{(1,12)} = 6.64, p < .05$], visual congruency [$F_{(1,12)} = 7.02, p < .05$] and incongruent trials [$F_{(1,12)} = 8.18, p < .01$]. No differences between the visual congruency and motor congruency were found, suggesting that these two cues were equally effective [$F_{(1,12)} = 2.8, p > .1$].

Yet, if the aIPS truly processes object realness to generate a forward model of the action to be performed, a critical prediction is that the representations of real objects and images would be more similar during the planning of reaching movements than grasping movements. Accordingly, the correlation between reaching to real objects and reaching to images was greater (i.e., less dissociable) than the correlation between grasping real objects and grasping images [$F_{(1,12)} = 6.65, p < .05, \eta_p^2 = .35$] (Fig. 3A, right panel).

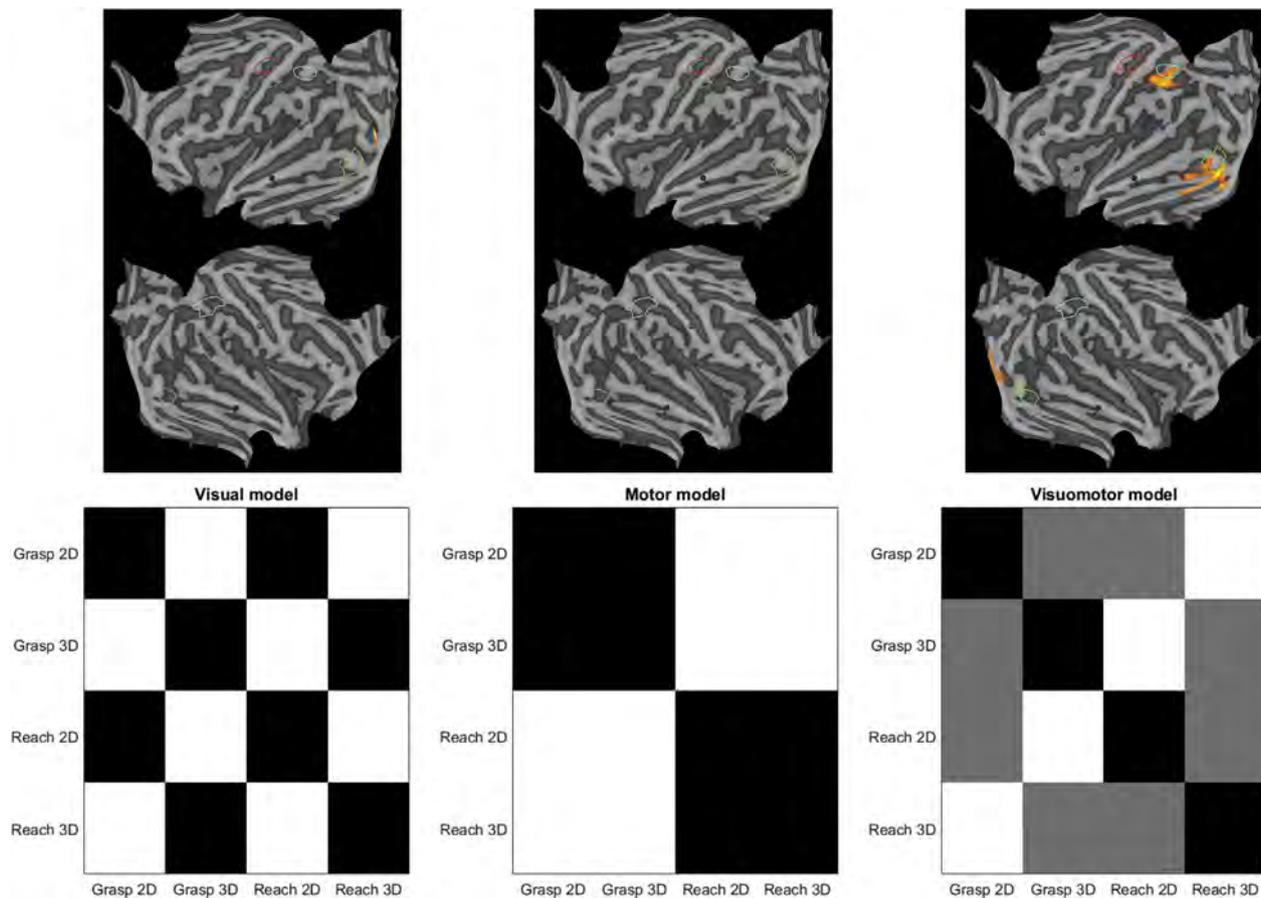


Fig. 5 – Group *t* maps for the searchlight whole-brain analysis of the planning phase, presented on flattened hemispheres of a group-averaged cortical mesh. ROIs were overlaid as indicated by colored outlines corresponding to the respective colors in Fig. 2. Patterns of activation were correlated with three models (bottom panels). The visual model (left panel), the motor model (middle panel) and visuomotor model (right panel). Black cells reflect perfect similarity, white cells reflect complete dissimilarity, and gray cells reflect an intermediate level of similarity.

To further visualize the representational space of the left aIPS we generated a hierarchical clustering plot in which the degree of similarity between two conditions is reflected by the height of the inverted U shape that connects them. Interestingly, for the left aIPS (and only for this ROI), three clusters were found. Reaching movements were clustered together (i.e., similarly represented) while grasping movements, directed to pictures and pictures, were separated from the reaching movements but also from each other (Fig. 4A).

To demonstrate the specificity of the neural representations in the left aIPS, the response pattern in the right aIPS was also analyzed. Since participants always completed the action with their right hand and aIPS activation (Culham, Cavina-Pratesi, & Singhal, 2006) and coding (Gallivan et al., 2013) is strongest for actions with the contralateral hand, the homotopic right aIPS would not be expected to differentially represent grasping and reaching movements based on the realness of the object. Nevertheless, some motor and visual aspects might still be coded even in the right aIPS (Gallivan et al., 2011), possibly as a product of functional coupling between homotopic cortical regions (Konen, Behrmann, Nishimura, & Kastner, 2011). Accordingly, full congruency induced greater correlations than visual congruency

[$F_{(1,12)} = 7.07, p < .05$] and incongruent trials [$F_{(1,12)} = 18.79, p < .01$], while no difference was found between full congruency and motor congruency [$F_{(1,12)} < 1$] (Fig. 3B, left panel). In addition, both motor congruency and visual congruency induced greater correlation than incongruent trials [$F_{(1,12)} > 5.75, p < .05$], suggesting that motor and visual cues were represented, at least partially, in the right aIPS. Importantly, the critical comparison between grasping movements and reaching movements did not reveal any differences [$F_{(1,12)} < 1$], suggesting that the right aIPS does not differentially represent grasping movements directed to real objects and images (for further visualization see Fig. 4B).

Although the present experimental design tried to minimize the differences between the movements directed to real objects and images, movement and haptic expectations could still convey information about object realness, which is not related to movement planning *per se*. To examine this issue, we also analyzed the response patterns in the motor and somatosensory cortices during the action planning phase. As presented in Fig. 3C and D, in the motor cortex, despite a trend, no main effect of object congruency was found [$F_{(3,36)} = 2.47, p = .07$], while the somatosensory cortex was robustly sensitive to the upcoming movement to be

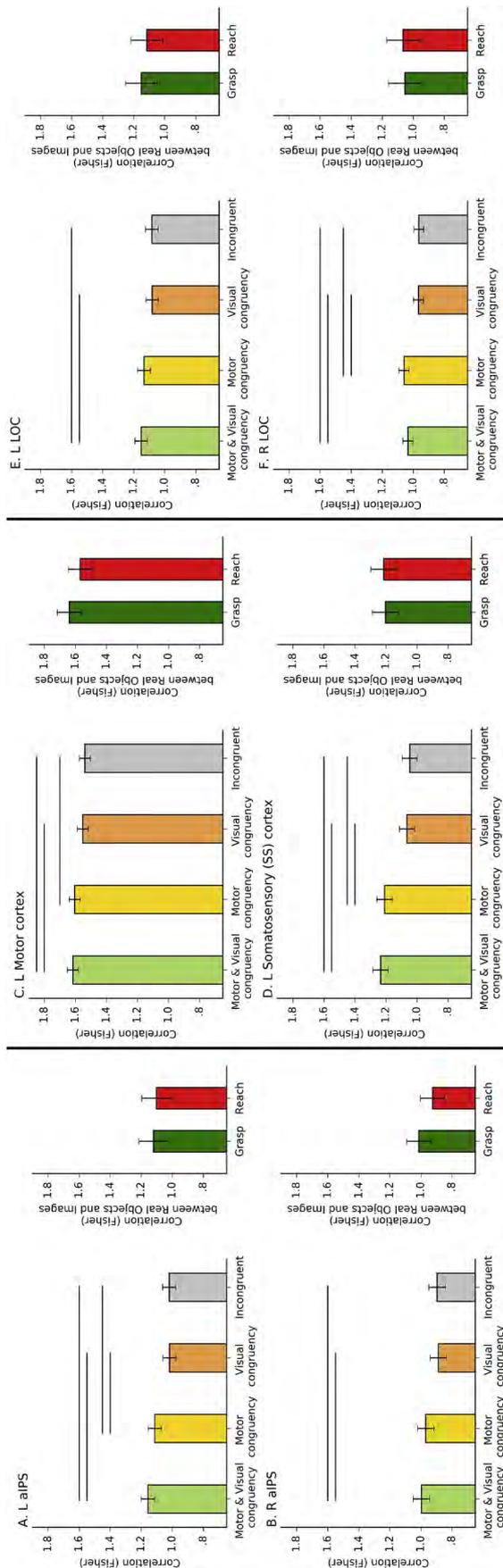


Fig. 6 – Results, execution phase. (A–F) All ROIs were sensitive to motor information, and none of the ROIs were sensitive to visual information (left panel). In contrast to the planning phase, movement congruency was not modulated by object realness in all ROIs (right panel).

performed, but not to object type. Together, these findings suggest that object realness was not encoded in these regions. In the somatosensory cortex the ANOVAs revealed a reliable main effect of congruency [$F_{(3,36)} = 6.19, p < .01, \eta_p^2 = .34$] and simple comparisons demonstrated that full congruency induced greater correlations than visual congruency [$F_{(1,12)} = 7.21, p < .05$] and incongruent trials [$F_{(1,12)} = 16.77, p < .01$] while motor congruency induced greater correlation than incongruent trials [$F_{(1,12)} = 8.36, p < .05$]. Interestingly, motor congruency and full congruency induced a similar level of correlations [$F_{(1,12)} < 1$], further suggesting that motor, but not visual information related to object realness was encoded in somatosensory cortex. The cluster plot (Fig. 4D) further demonstrates this point.

Critically, for both somatosensory and motor cortices the comparisons between reaching movements versus grasping movements showed that object realness did not interactively modulate one type of a movement [Motor $F_{(1,12)} = 1.65, p > .2$; Somatosensory: $F_{(1,12)} = 2.95, p > .1$]. Together, the results obtained from the motor and somatosensory cortices suggest that motor information is strongly encoded prior to movement initiation, while object realness is not.

Finally, we also analyzed the representational content in the right and left ventral-pathway region LOC. Consistent with the well-documented sensitivity of LOC to object shape in general (Malach et al., 1995), to 3D object structure in particular (Freud, Ganel, & Avidan, 2015; Moore & Engel, 2001), and to object realness (Snow et al., 2011), we found a robust sensitivity to object type in the left hemisphere. That is, although both the real objects and the images conveyed rectangular objects of the same dimensions, their neural representations during object planning differed. In addition, LOC in both hemispheres showed sensitivity to the type of movement that was planned, with representational differences between upcoming grasping versus reaching movements. This finding is consistent with past results showing that areas of the ventral visual stream are activated during and causally involved in hand actions (as in the extrastriate body area Astafiev, Stanley, Shulman, & Corbetta, 2004; Zimmermann, Verhagen, Lange, & Toni, 2016) and may code upcoming actions (including LOC, Gallivan, Chapman, McLean, Flanagan, & Culham, 2013), perhaps because they share connections with dorsal stream areas such as aIPS (Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012; Hutchison, Culham, Everling, Flanagan, & Gallivan, 2014) and have been proposed to anticipate the visual consequences of actions (Gallivan, Chapman, et al., 2013; Zimmermann et al., 2016).

In the left LOC, the ANOVA revealed a main effect for conditions [$F_{(3,36)} = 5.56, p < .01, \eta_p^2 = .31$] which stemmed from a higher correlation for visual congruency [$F_{(1,12)} = 13.52, p < .01$], full congruency [$F_{(1,12)} = 18.79, p < .01$] and motor congruency [$F_{(1,12)} = 5.74, p < .05$] compared with incongruent trials (Fig. 3E). Notably, no difference was found between full congruency and visual congruency [$F_{(1,12)} < 1$] further demonstrating the importance of visual information in this region (see Fig. 4E for cluster plot). Importantly, and in contrast to the left aIPS, similar correlations were found for grasping and reaching movements [$F_{(1,12)} < 1$], suggesting that LOC sensitivity to object realness reflects the representation of object

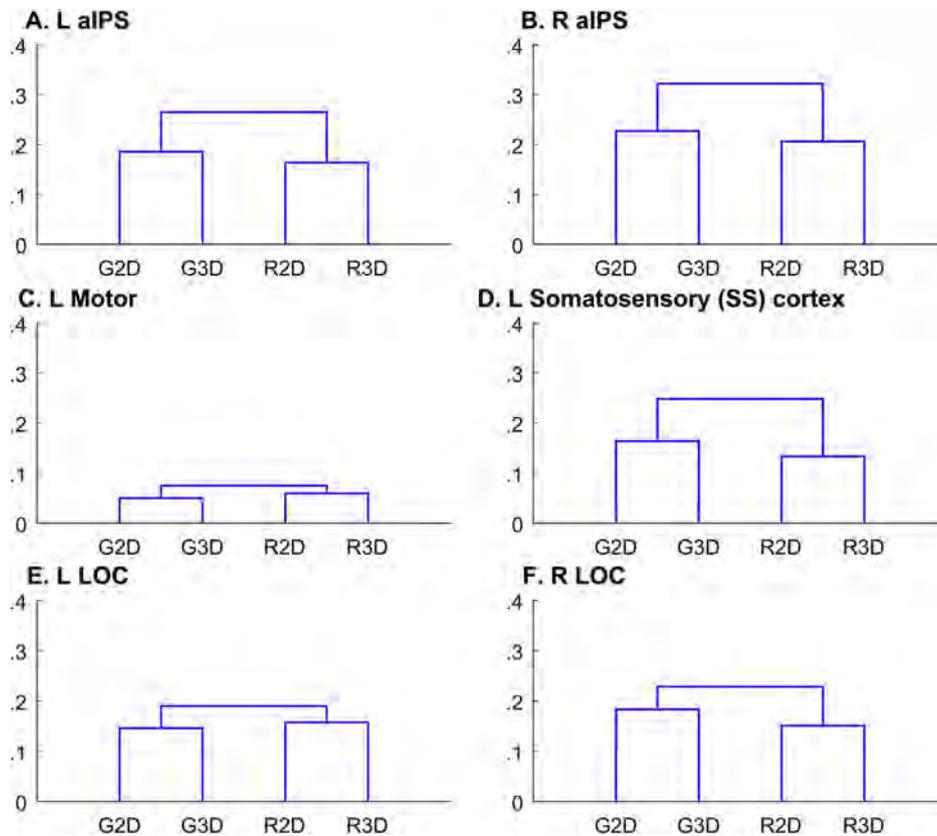


Fig. 7 – Hierarchical clustering reveals that in the execution phase all regions were clustered based on motor congruency.

shape or object 3D status and not a combination of visual and motor information.

The right LOC exhibited somewhat differential representational pattern than the left LOC. A main effect for condition [$F_{(3,36)} = 6.71, p < .01, \eta_p^2 = .35$], but it was derived from higher correlation for motor congruency [$F_{(1,12)} = 10.58, p < .01$] and full congruency [$F_{(1,12)} = 16.08, p < .01$] versus incongruent trials, while only a trend was found for visual congruency [$F_{(1,12)} = 3.17, p = .1$]. Finally, similar correlations were found for grasping and reaching movements [$t_{(14)} = 1.24, p > .2$] (Fig. 3F).

3.1.2. Searchlight analysis

To test whether additional regions were involved in the coding in visuomotor control of real 3D objects and images we applied a searchlight analysis. Three models were tested, a motor model (i.e., sensitivity to movement type, insensitivity to visual information), a visual model (i.e., sensitivity to visual information, insensitivity to motor information) and a visuomotor model (an average of the two models described above) (Fig. 5, bottom panel).

The searchlight analysis mainly confirmed the findings of the ROI analysis. Specifically, the visuomotor model was found to be correlated with voxels in the proximity of the left aIPS and left LOC, further reflecting the coding of both motor and visual information by these regions. Note that the searchlight analysis was not aimed to detect the differential representation of grasping movements and reaching movements directed to images and real 3D objects.

The motor model was not correlated with the representational content obtained in the planning phase, while a small cluster, in the posterior part of the right parietal cortex was found to be correlated with the visual model. This cluster might be related to the coding of disparity information that differentiate between real 3D objects and 2D images (Freud, Plaut, & Behrmann, 2016; Orban, 2011).

3.1.3. Univariate analysis

The univariate analysis did not reveal an interaction between object type and movement type, and further suggests that MVPA offers greater sensitivity than the univariate analysis in the investigation of the neural mechanisms of visuomotor control (e.g., Gallivan et al., 2011,2013). An unexpected main effect of movement type, with greater activation for reaching movements was found. However, in contrast to the findings from the MVPA, this effect was evident in all ROIs of the dorsal pathway, and was not specific to the aIPS. In addition, a main effect for object type was found in early visual cortex, with greater activation for 2D objects compared with real 3D objects.

3.2. Execution phase

3.2.1. MVPA

Similar analysis was applied on the responses obtained from the execution phase. This analysis revealed a main effect for full congruency in all ROIs, with no differences between the motor congruency and the full congruency. In contrast to the planning phase, no evidence was found for effects of format

congruency, nor for a modulation of movement congruency by object type (Figs. 6A–F and 7A–F). The detailed statistics of this analysis can be found in Table 1.

These results suggest that during movement execution the neural representations of real objects and images are similar and indistinguishable (for further visualization see Fig. 7), and therefore further reinforce the notion that the differential representations observed in the planning phase are independent from potential kinematic and haptic differences.

3.2.2. Searchlight analysis

In agreement with the ROI analysis, the motor model was found to be correlated with regions in the proximity of the aIPS, somatosensory cortex and motor cortex in both right and left hemisphere. Moreover, some early visual regions, in the left hemisphere were found to be correlated with the motor model, and this might be attributed to feedback connections (Fig. 8, middle panel). Note that the visuomotor model was also found to be correlated with the data in the execution phase (Fig. 8, right panel), but this might be related to the internal correlation between the visuomotor model and the motor model.

3.2.3. Univariate analysis

The univariate analysis did not reveal an interaction between object type and movement type nor an effect of object type. As found in previous studies (Culham et al., 2003), a bilateral main effect of movement type, with greater activation for grasping movements was found in the motor cortex, somatosensory cortex and in the aIPS.

4. Discussion

The present study investigated the neural representations that dissociate visually guided actions directed to images from those directed to real objects. Although previous behavioral studies suggested that actions directed to real objects rely on differential representations than actions directed toward images (Freud & Ganel, 2015; Holmes & Heath, 2013; Hosang et al., 2015), the neural underpinnings of this dissociation have not been investigated before. Our findings add to the understanding of the two visual streams (Goodale & Milner, 1992) by showing that the dorsal pathway is sensitive to object realness, specifically in the context of a visuomotor task. Along with earlier work suggesting that the distinction between action and perception does not generalize to artificial actions such as pantomimed grasping (Goodale, Jakobson, & Keillor, 1994; Kroliczak et al., 2007), the emerging view is that the dorsal stream processes vision for real actions upon real objects.

Specifically, we found that the left aIPS, a key region for the computation of visually guided grasping actions (Culham et al., 2003; Gallivan & Culham, 2015), is sensitive to object realness before movement initiation, especially for grasping actions. These differences support the established notion that the visuomotor system generates a forward model of the planned actions that takes into account the constraints and outcomes associated with real objects, which are different from those associated with images.

The lower correlation values between grasping movements directed to real object and images relative to reaching

Table 1 – Repeated measures ANOVAs results of the execution stage.

| ROI | Congruency (Main effect) | Motor & visual congruency > incongruent (Simple effect) | Motor congruency > incongruent (Simple effect) | Motor & Visual congruency > Motor congruency (Simple effect) | Motor & Visual congruency > Vision congruency (Simple effect) | $I(\text{reaching real-reaching image}) > I(\text{grasping real-grasping image})$ |
|------------------------|--------------------------------------|---|--|--|---|---|
| L aIPS | $F_{(3,26)} = 11.02, \eta_p^2 = .47$ | $F_{(1,12)} = 24.06, p < .01$ | $F_{(1,12)} = 6.75, p < .05$ | $F_{(1,12)} = 2.81, p > .1$ | $F_{(1,12)} = 26.2, p < .01$ | $F_{(1,12)} < 1$ |
| R aIPS | $F_{(3,26)} = 4.31, \eta_p^2 = .2$ | $F_{(1,12)} = 6.26, p < .05$ | $F_{(1,12)} = 3.5, p = .08$ | $F_{(1,12)} = 1.94, p > .15$ | $F_{(1,12)} = 5.87, p < .05$ | $F_{(1,12)} < 2.9, p > .1$ |
| L motor Cortex (M1/S1) | $F_{(3,26)} = 4.53, \eta_p^2 = .27$ | $F_{(1,12)} = 10.34, p < .01$ | $F_{(1,12)} = 7.14, p < .05$ | $F_{(1,12)} < 1$ | $F_{(1,12)} = 4.93, p < .05$ | $F_{(1,12)} = 1.9, p > .15$ |
| L somatosensory cortex | $F_{(3,26)} = 16.04, \eta_p^2 = .57$ | $F_{(1,12)} = 21.8, p < .01$ | $F_{(1,12)} = 17.5, p < .01$ | $F_{(1,12)} = 17.5, p < .01$ | $F_{(1,12)} = 17.35, p < .01$ | $F_{(1,12)} < 1$ |
| L LOC | $F_{(2,26)} = 9.17, \eta_p^2 = .43$ | $F_{(1,12)} = 9.73, p < .01$ | $F_{(1,12)} = 2.66, p = .12$ | $F_{(1,12)} < 1$ | $F_{(1,12)} = 5.75, p < .05$ | $F_{(1,12)} < 1$ |
| R LOC | $F_{(2,26)} = 3.15, \eta_p^2 = .26$ | $F_{(1,12)} = 7.36, p < .05$ | $F_{(1,12)} = 16.79, p < .01$ | $F_{(1,12)} = 1.87, p > .15$ | $F_{(1,12)} = 11.06, p < .01$ | $F_{(1,12)} < 1$ |

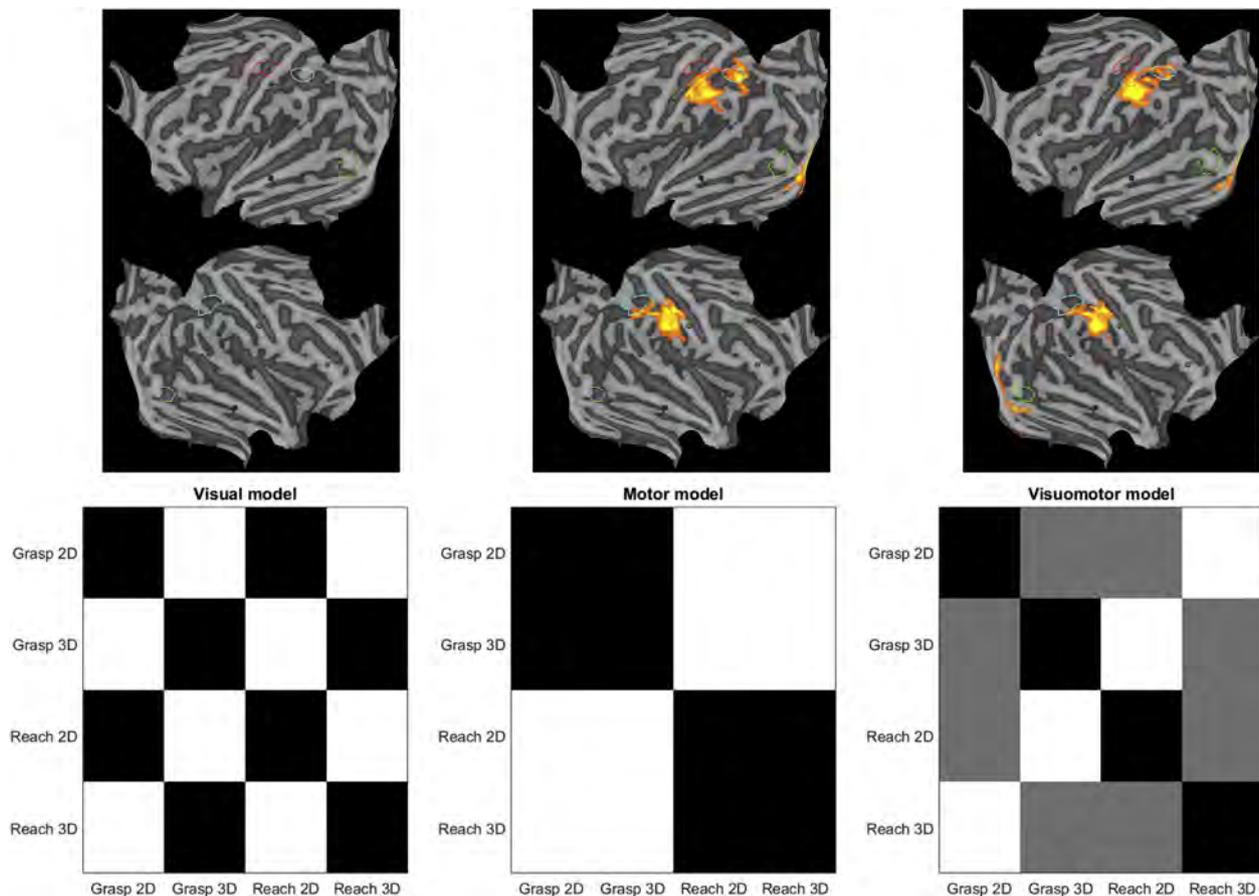


Fig. 8 – Group t maps for the searchlight whole brain analysis of the execution phase, presented on flattened hemispheres. ROIs were overlaid as indicted by colored outlines corresponding to the respective colors in Fig. 2. Patterns of activation were correlated with three models (bottom panel).

movements might be interpreted as reflecting greater noise rather than distinctive representations. Yet several lines of evidence suggest that this is not the case in the present investigation. First, the overall level of correlations was high ($r > .7$), pointing to a reliable measurement. Moreover, the comparison between the fully congruent trials and the partially congruent trials, revealed sensitivity to both visual and motor information in the left aIPS, suggesting that the signal is reliable enough to reveal subtle differences between the experimental conditions. Most importantly, the differentiation between grasping and reaching based on the object realness was unique to the left aIPS, and was not found in other predefined ROIs (including the homotopic right aIPS). If a particular condition (e.g., grasping 2D) had induced more noise, then lower correlations would be expected to be manifested not only in a particular region, but rather in a more distributed fashion. Thus, the uniqueness of the effect in aIPS suggests that the lower correlations between grasping 3D and grasping 2D, could not be attributed to noise, but rather reflect distinctive representations of grasping movements in the left aIPS.

Notably, the unique representations in aIPS also stand in contrast to the representations in the motor and somatosensory cortices which demonstrated no sensitivity to object realness during planning and execution, although, like aIPS,

they had strong sensitivity to the movement type (grasping versus reaching). This finding suggests that the sensitivity observed in the left aIPS could not be attributed to different kinematics or haptic feedback associated with the two object categories.

Finally, left LOC, located in the ventral pathway, was also sensitive to object format. Importantly, and in contrast to the left aIPS, the sensitivity to the visual information in the ventral pathway did not interact with movement type (that is, it was equally evident for grasping and reaching movements). Thus, the representations in LOC appear to reflect sensitivity to the visual differences between the two object categories (Snow et al., 2011), rather than the integration of visual and motor information that supports movement planning. Nevertheless, these results indicate that LOC does not code the real (3D) and pictorial (2D) versions of a shape as equivalent. This conclusion is also in accordance with previous studies that demonstrate the role of LOC in 3D object representation (Freud, Ganel, & Avidan, 2013, 2015; Moore & Engel, 2001).

4.1. Does the potential for action affect object representations in the dorsal pathway?

The dorsal pathway is known to be crucial for the computations that support visuomotor control (Goodale & Milner, 1992;

Goodale, 2014). However, object representations have also been reported in the dorsal pathway for perceptual tasks, in the absence of actions (Freud, Ganel, Shelef, et al., 2015; Konen & Kastner, 2008; for a recent review see; Freud et al., 2016). One possibility is that these dorsal-stream object representations are the product of computations related to the potential actions associated with specific objects, which are evoked even for passive viewing of images. This notion is in line with the well-documented sensitivity of the left IPS to real tools (Macdonald & Culham, 2015), pictures of tools (Chao & Martin, 2000; Macdonald & Culham, 2015) and graspable objects in general (Creem-Regehr & Lee, 2005).

Importantly, if action-related cues truly play a role in the process of object representations in the dorsal pathway, a plausible prediction is that real objects would elicit different activation effects than images in the dorsal pathway, even in the absence of a visuomotor task. In accordance with this hypothesis, Snow and colleagues have shown that real objects and images of the same objects elicit differential degrees of fMRI adaptation in the ventral and dorsal pathway (Snow et al., 2011). Such differential adaptation could reflect either differences between real objects and images in the potential actions they enable and/or to the availability of binocular depth cues for real objects but not images. Differences in stereoscopic vision may be highly relevant for the dorsal pathway, which processes 3D information from disparity (Georgieva, Peeters, Kolster, Todd, & Orban, 2009, 2011; Sakata, Taira, Kusunoki, Murata, & Tanaka, 1997; Theys, Romero, van Loon, & Janssen, 2015). Nevertheless, binocular differences alone cannot account for the results of the present experiment because object realness modulated the pattern of responses, in the left aIPS, differentially for grasping and reaching movements even though the visual information during planning was identical.

4.2. Movement type is encoded in the dorsal and ventral pathways

In addition to the sensitivity to object realness, all ROIs exhibited robust sensitivity to motor congruency (grasping/reaching). While this finding is not surprising for the ROIs of the visuomotor system (namely, aIPS, somatosensory cortex and motor cortex), it is more unexpected to find sensitivity to this information in the ventral LOC, which is known to be sensitive to object shape (Kourtzi & Kanwisher, 2000; Malach et al., 1995) and correlated with perceptual performance (Grill-Spector, Kushnir, Hendler, & Malach, 2000).

The sensitivity of LOC to motor congruency, particularly during the execution phase could be attributed to the differential visual feedback obtained from grasping and reaching movements. Yet, such sensitivity was also observed in the planning phase, in which the visual information is identical. One possibility is that the LOC activation pattern was modulated by the differential perceptual expectations generated for the two movement types (Gallivan, Chapman, et al., 2013; Summerfield & de Lange, 2014; Summerfield, Trittschuh, Monti, Mesulam, & Egner, 2008). Another possibility, which is nonexclusive to the first one, is that the LOC activation pattern was modulated by dorsal pathway inputs. For example, in a recent study it was found that during action

observation, visuomotor regions contribute to object recognition by influencing the activation in the ventral pathway (Sim, Helbig, Graf, & Kiefer, 2015).

4.3. What constitutes “real” objects?

Our results here showed distinct representations for actions upon real objects compared to images; however, there is a continuum of object representations between these two extremes. With the proliferation of virtual reality in our daily lives, it remains to be determined which aspects of realness are essential for full recruitment of the dorsal stream. Our results suggest that while the availability of 3D depth cues (such as stereo vision) may affect processing in many regions, they cannot fully account for dorsal-stream activation, in which the representations were affected by the combination of these cues with the task at hand. As such, we expect that virtual reality systems that add realness of depth cues may not suffice to evoke the full perception-action dissociation. However, some virtual reality systems also provide sensory consequences of actions such as haptic feedback through technology like cyber gloves and visual feedback of action consequences (such as virtual objects that respond to actions on touchscreens). One open question is whether these simulations are sufficient for perception-action dissociations or whether some higher-level sense of realness or “presence” is required (e.g., Lok, Naik, Whitton, & Brooks, 2003).

Note that in the present study we have used simplified 2D versions of the real objects. The choice of stimuli was done in accordance with the current behavioral literature in which grasping movements directed to real 3D objects were found to be dissociated from grasping movements directed to simplified 2D images (Freud & Ganel, 2015; Holmes & Heath, 2013; Hosang et al., 2015) while basic kinematic properties, such as movement times and reaction times, were similar. Importantly, since behavioral measurements of movement kinematic were not available in the MRI scanner, we chose to utilize simplified 2D images for which behavioral performance were already characterized. Nevertheless, future studies should investigate whether more realistic images differentially modulate object and movement representations.

5. Conclusion

The present study examined the neural mechanisms that dissociate visuomotor control of actions directed to real 3D objects versus images. In line with previous behavioral investigations (Freud & Ganel, 2015; Holmes & Heath, 2013), we found that actions directed to images rely on distinct neural representations than those directed to real 3D objects. These dissociable representations may reflect the operation of a forward model generated by the visuomotor system, which integrates visual information about object realness with motor information about the expected movement. Based on these results, we propose that the two-streams model (Goodale & Milner, 1992) could benefit from increased emphasis on the role of the dorsal visual stream not just in “vision for action” but “vision for real actions”.

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