

Disentangling Visual from Motor Information in Reaching Movements: A New Paradigm for

Solving an Old Problem

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Abstract

When making a reach movement, sensory information about the object and the motor plan associated to the upcoming reach coincide in space. In order to study how both these types of representations are represented across the brain, we implemented a paradigm that differentiates visual and motor information of an action by comparing reach movements with swipe movements. Differently from reach movements, during swipe movements, participants do not physically start the movement on the object location. Hence, the visual and motor information about a future action are separated. We found that, during the planning period, the primary visual cortex represents both visual and motor information associated with a motor movement. The parietal reach region, involved in the planning and control of reach movements, represents the motor goal of a movement. The primary motor cortex represents both visual and motor components of an upcoming motor movement.

Keywords: fMRI, reach, swipe, motor, MVPA, representational similarity analysis, posterior parietal cortex

Disentangling Visual from Motor Information in Reaching Movements: A New Paradigm for Solving an Old Problem

Moving is an essential part of life most species undertake in order to interact with the world around them. Even the simplest of movements one can imagine, reaching for your headphones, poses an intricate problem to the brain as a computational system: what type of mechanism is used to translate the sensory information we perceive into a motor intention we later execute? Answering this question requires uncovering the neural underpinnings of motor movements and their corresponding intentions, an exciting and challenging task that was taken on in this paper. Adding insight into the topic allows researchers to convert theory into practice, devising technologically innovative solutions for patients who lost the ability to move some or all parts of their bodies (for a short review see Courtine, Micera, DiGiovanna, Del R, & Millan, 2013).

One pillar region in the brain that is involved in action-related cognitive functions is the posterior parietal cortex (PPC) (Andersen & Buneo, 2002), initiating the planning and control of motor movements, either of the eyes or the limbs (Mountcastle, Lynch, Georgopoulos, Sakata, & Acuna, 1975). Its anatomical segregation contains the inferior parietal lobule (IPL), comprised of area 7a and lateral intraparietal area (LIP) which shows strong activation from the earliest stages of eye-movement planning (Corbetta et al., 1998; Kustov & Robinson, 1996). Conversely, movements of the arm (Galati et al., 2011) as well other limbs (Heed et al., 2011) are mostly encoded in the superior parietal lobule (SPL) (Marconi et al., 2001) comprising of posterior reach region (PRR) and the dorsal area 5 (PE), PEc and PEa (see Figure 1). The higher activation of PRR during movement planning in comparison to saccade planning has been shown both in

monkeys (e.g., Snyder, Batista, & Andersen, 1997) as well as in humans (Connolly, Andersen, & Goodale, 2003).

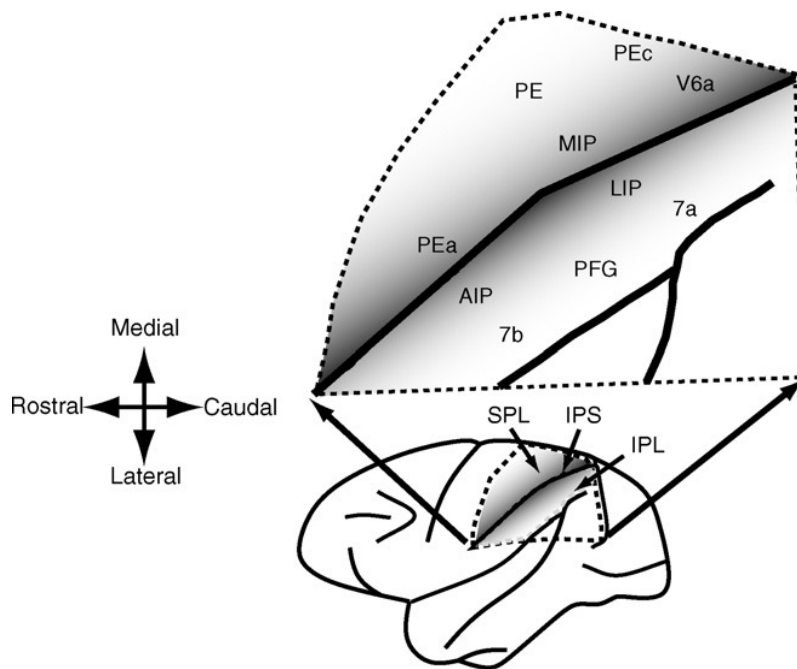


Figure 1. Lateral view of the macaque brain depicting the expanded view of several PPC regions. From “The posterior parietal cortex: sensorimotor interface for the planning and control of visually guided movements” by Buneo & Andersen, 2006.

Literature disagrees on whether activation in PPC regions such as the PRR represents a future motor goal (Zhang & Barash, 2000) or a memory of the visual target (Gottlieb & Goldberg, 1999). This question has been difficult to address because normally both targets coincide in space: the headphones you reach for provide visual input regarding the object’s location (i.e., visual target), but they are also the target of your reach movement (i.e. motor target). Fernandez-Ruiz and colleagues used an optical reversing prism paradigm to dissociate the visually perceived pointing movement direction from the physical pointing direction (Fernandez-Ruiz, Goltz, DeSouza, Vilis, & Crawford, 2017). In this case, a leftward pointing movement towards a visual cue on the left was perceived as a rightward movement towards a visual cue on the right. During the planning period, the authors found higher activation in the

PRR contralateral to the perceived visual cue and movement location (i.e., ipsilateral to the actual location) for conditions with the prism and higher activation contralateral to the visual cue and actual movement in conditions without the prism (Fernandez-Ruiz et al., 2007). Put differently, the PRR showed higher activation contralateral to the visual cue (whether actual or perceived) and not the actual movement direction (in conditions with the prism), which the authors as evidence towards the encoding of the visual information and not the intention of the physical movement (Fernandez-Ruiz et al., 2007).

A different line of research used a context-rule task during which participants were instructed to reach either toward (pro rule) or in the opposite direction (anti rule) of the visual cue (Gertz, Lingnau, & Fiehler, 2017). The authors used MVPA, a powerful statistical tool that allowed them to train and test a classifier on trials that decoded either the visual cue or the motor goal. This task, however, did not allow the classifier to decode better than chance neither the visual cue nor the movement goal from the anterior and posterior superior parietal lobule (SPL) that we refer here as the PRR (Gertz et al., 2017). This result is puzzling, since a good deal of research (e.g., Gail. & Andersen, 2006; Gail, Klaes, & Westendorff, 2009; Westendorff, Klaes, & Gail, 2010; Klaes, Westendorff, Chakrabarti, & Gail, 2011) has adopted context-rule tasks to address whether, during the planning period, the PPC maintains information regarding the memory of a visual cue or a motor goal.

A recent paradigm implemented by Fabbri and colleagues has behaviorally dissociated the motor and visual targets by comparing reaching and swiping movements (Fabbri, Selen, van Beers, & Medendorp, 2017). During the reaching task the position of the visual cue coincided with the location participants had to touch on the screen in order to drag the target. Put differently, there was a spatial match between the visual and the motor target (Fabbri et al.,

2017). During the swiping task, however, participants could touch anywhere on the screen in order to move the target. In this case, the authors observed a spatial mismatch between the visual and motor target (Fabbri et al., 2017). This mismatch during swiping is associated with the way people interact with objects on touchscreens. For instance, when trying to locate a city on a map, swiping left anywhere on the screen would lead to bringing an unseen point from the right of the map into view. The authors reported that such a flexible way of interacting with ‘virtual’ objects can be explained by a desire to start the movement near the visual target, while at the same time not obscuring it and minimizing the total predicted distance from the target to its final destination (Fabbri et al., 2017).

The swiping task during which the motor and visual target are separated offers a unique opportunity to study motor intentions and the transformations associated to them in the brain. The current study adopted the paradigm from Fabbri et al., (2017) in a fMRI setting. Participants were first presented with an instruction screen which indicated the type of task for that run (i.e., reach or swipe). After a delay during which the movement was planned, participants could bring the object from the side of the screen to the center. We compared the two different tasks and their respective activation patterns during the planning (i.e., delay) period, with the rationale that they would differ in their motor targets but not in their visual targets. We used Representational Similarity Analysis (RSA), a derivative of MVPA that has previously been used to describe processes associated with spatial encoding (Gertz et al., 2017; Fabbri, Stubbs, Cusack, & Culham, 2016). RSA is considered a more sensitive and powerful tool than univariate analyses being able to detect subtle differentiations within patterns in data (Haxby, 2012).

We assessed the representation of the visual and motor targets in 3 regions of interest (ROIs) in the brain. First, we expected to find the representation of the visual target in early

visual area V1. This prediction is in line with most current literature that posits the primary visual cortex (V1) as a low-level visual area, which responds to basic features (Hubel & Wiesel, 1959). One of the most distinct patterns found in the visual system relates to the lateralization of stimulus presentation. Visual areas in the occipital cortex respond to stimuli presented on the contralateral side of the visual hemifield (Tootell, Dale, Sereno, & Malach, 1996; Wandell, Dumoulin, & Brewer, 2007). Thus, in this ROI we expected to decode the visual target that was kept identical during the reach and the swipe task. Our next region of interest is the parietal reach region (PRR) that literature describes as being involved in the planning of reach movements (Mountcastle et al., 1975; Snyder et al., 1997; Marconi et al., 2001; Battaglia-Mayer, Caminiti, Lacquaniti, & Zago, 2003). The PRR has also been described as an interface between the visual and motor cortices (Mountcastle et al., 1975), hence we expected to find representation of both the visual and motor targets. Finally, we will assess representations in the primary motor cortex (M1). Literature describes this ROI as encoding various intrinsic parameters related to muscle movements (Evarts, 1968; Sergio & Kalaska, 2003). Due to this muscular specificity exhibited in M1, we expected to find representation of the motor target specific to each motor action.

Methods

Participants

16 neurologically healthy participants (3 women, mean age = 27.2) took part in the experiment. All participants were right-handed and reported normal or corrected-to-normal vision. Due to the technical setup of the study, only participants with a height of at least 1.80m were selected. Four participants were excluded from the analyses; two were excluded because of not completing the experiment due to technical issues and another two due to reported difficulties with seeing the screen. Another 6 participants were excluded after the pre-processing

due to abrupt head movements. Informed consent was obtained from all participants prior to the study, in accordance with the Donders Institute Ethics Board (Nijmegen, The Netherlands) and the Declaration of Helsinki.

Procedure

The experiment contained two different kinds of tasks. In the Instructed Reach task, participants were instructed to start the movement on the target location and drag the target into the goal area. As such, the visual target in the Reach task coincided with the motor target. In the Swipe task, participants could move the target by freely choosing where to position their index finger (on the visual target or near it), since both actions would allow to move the target into the goal area. Hence, during the swipe task, the visual target differed from the motor target in terms of spatial location (i.e., spatial mismatch). The spatial mismatch between the visual and motor targets would allow for differentiating visual and motor information in the brain during the planning period of a movement. Participants first performed a practice session to make sure they understood the task. Each experimental trial started with the instruction for the specific task, as is shown in the far-left panel in Figure 2. Next, a planning phase consisting of 2, 4 or 6 seconds followed indicated by a red fixation dot during which participants kept their index finger in the goal area (i.e., center of the screen). When the fixation turned green, participants were instructed to bring the visual target into the goal area as fast and as accurately as possible. When participants touched the start, the visual target and the goal appeared on the screen, while the start disappeared. A time limit was imposed, so that two seconds after the presentation of the visual target and goal, both items disappeared from the screen. We jittered the ITI (i.e., 2s, 4s, 6s) in order to decorrelate the hemodynamic responses of successive trials. The experiment

presented participants with the 2 tasks blocked within runs; each run occurred (in alternating orders) four times for each participant.

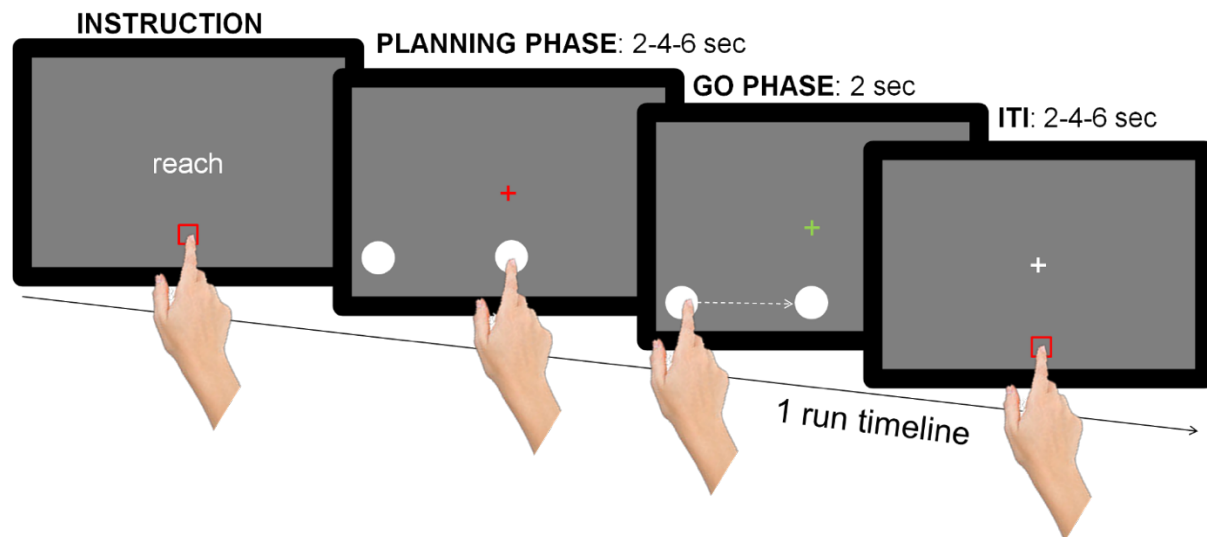


Figure 2. A schematic trial example of the reach task. To move the visual target into the goal, participants had to lift their index finger from the start, position it on the visual target (or anywhere else on the screen if the instruction was “free swipe”) and drag the target into the goal area.

Stimuli and Task Design

The experiment was programmed in PsychoPy (Pierce, 2009). All stimuli in the study appeared 3cm below the center of the screen, allowing participants to execute the task using their right lower arm. The stimuli were presented horizontally on a grey background. The stimuli consisted in: a 1x1cm red square indicating the start location of the hand on the screen (i.e., the “start”), a 1cm-radius white dot (i.e., the “visual target”) and a 1 or 2cm radius white dot representing the end location of the hand (i.e., “the goal”). The size of the goal area was varied in order to manipulate task difficulty: a smaller goal area would require a more accurate movement to fit the goal inside it than a larger goal area. The visual target could appear 6 or 9cm to the left

or the right side of the center of the screen, while the start and the goal were always presented at the center of the screen.

Apparatus

Participants lay supine in the scanner with their head tilted 20° to allow for direct viewing and hand contact with the MR-compatible 10.4inch LCD touch screen with Texim Europe monitor. The touch screen was positioned just outside the bore of the scanner so that participants could execute swiping movements on its surface with their right index fingers (see Figure 3). In order to limit hand/body movements, we fixated participants' arms with upper arm cushions as well as forearm straps.



Figure 3. Image of the setup used in the fMRI scanner.

Data acquisition

Data was acquired at the Donders Institute (Nijmegen, The Netherlands) on a 3T Siemens Magnetom Skyra scanner using a 32-channel head coil. A multiecho sequence (TE 1 = 9.0 ms, TE 2 = 19.30 ms, TE 3 = 30 ms, TE 4 = 40 ms) was used to improve signal strength. Each functional volume comprised 34 slices acquired at at ~30° caudal tilt with respect to the plane of

the anterior and posterior commissure (ACPC), covering the whole brain (TR: 2070, voxel size: 3.5 x 3.5 x 3.0 mm, FOV: 224 mm, flip angle = 90°). The T1-weighted anatomical image was collected using an MPRAGE sequence (TR = 2300ms; TE = 3.03ms; flip angle = 8°; in-plane FOV = 256 x 256mm; GRAPPA acceleration factor PE = 2; voxel resolution = 1mm³; duration = 5:21min).

Preprocessing and Data Analysis

Imaging data were preprocessed using the following steps: slice timing correction (using sinc interpolation), 3D motion correction (sinc interpolation), high-pass temporal filtering (default cutoff frequency of 3 cycles/run), Functional images were aligned to the run closest to the anatomy that was used for functional-anatomical coregistration. Both functional and anatomical runs were aligned to the ACPC plane and Spatial normalized to a Talairach template. Given that data were analyzed using Representational Similarity Analysis, no spatial smoothing was applied. 15 functional runs were excluded after the pre-processing due to abrupt movements. Data analysis was performed using Brain Voyager QX 2.8 (Goebel, Esposito, & Formisano, 2006). All statistical tests were conducted in JASP 0.8 (JASP Team, 2018).

Definition of regions of interest

All ROIs were based on a contrast between all conditions versus the baseline, which included activation related to the visual and motor features of the current task. Only regions that were active in all participants were included as ROIs. All ROIs were determined based on activation-related and structural information from previous studies (Fabbri et al., 2016). Still, to allow for comparison with other studies, Talairach coordinates were computed for each individual ROI and can be seen in Table 1. More so, given that activation of the ipsilateral hemisphere might not reliably indicate activity related to motor movements performed with the

right hand, we limited our analysis of ROIs to the left hemisphere, as done in previous studies on motor control (Gertz et al., 2017; Fabbri et al., 2016). For each individual participant, each ROI was centered on the hotspot of activation.

We investigated 3 regions of interest (ROIs) from the visual, posterior parietal and motor cortices in which we expected to find representation of the visual, visuomotor and motor targets, respectively. The putative V1 was selected based on active voxels in or near the calcarine sulcus (Snow, Strother, & Humphreys, 2014). The parietal reach region (PRR) was located along the medial surface of the superior aspect of the PPC (Connolly et al., 2003). Lastly, the primary motor cortex (M1) was localized at the “hand knob” in the central sulcus (Yousry et al., 1997).

Table 1. ROI Talairach coordinates (Mean \pm SD x, y, z center of mass)

ROIs	X	Y	Z
V1	-6 ± 3.25	-88 ± 1.8	-5 ± 3.9
PRR	-19 ± 3.18	-60 ± 2.76	51 ± 2.87
M1	-33 ± 1.59	-26 ± 2.8	49 ± 3.99

Representational Similarity Analysis (RSA)

Analyses for the current study were conducted following the principles of Multivariate Pattern Analysis, a set of methods that assesses patterns of activity within a neural system rather than the extent to which a system is globally engaged, as done with univariate analyses (Haxby et al., 2001). MVPA is based on the idea that encoding perceived stimuli in finite categories is rather unlikely given the amount of neural circuitry needed each time a new category arises. More so, such an absolute categorization based on peak responses within a region would ignore similarities or differences between stimuli on the basis of which these categories are formed (Haxby, 2012). Hence, multivariate methods such as Representational Similarity Analysis (RSA)

compare the similarity between experimental conditions in terms of their BOLD-related activity patterns in order to uncover the neural mechanisms that instantiate them (Kriegeskorte, Mur, & Bandettini, 2008b). RSA has proved to be an advantageous method that allows for condition-rich designs. It also allows researchers to integrate computational modelling into analyses of data obtained from different modalities, whether that be fMRI, behavioral measures or single-cell recordings (Kriegeskorte et al., 2008b). In the current study, RSA allowed us to compare how similar the models generated by brain-activity data are to our theoretical models that distinguish between the visual and motor target.

We extracted parameter estimates (B weights) for all conditions for each voxel in each ROI, repeating this procedure for all runs. Next, Pearson correlations were calculated between each pair of conditions for all runs per ROI and for each individual participant (i.e., 1-level RSA). The resulting representational similarity matrices (RSMs) allowed us to estimate how similar the activity pattern of each condition is to every other condition within each task as well as across tasks. In the following steps we assessed how well our models that captured the visual and motor target could explain brain data in each ROI. To do so, Pearson correlations were computed between each model and the RSMs (2-level RSA). To assess the strength of models within each ROI, we computed pairwise t-tests for all examined models within a region. Lastly, we used MDS transformation to visualize, in 2D space, the neural similarity resulting from the 2-level RSA.

Theoretical Models

We used three models that represent the encoding of the visual and motor targets in each ROI. Each model included predictions for all the conditions within each task modality as well as across task modalities. Behavioral results of the paradigm implemented in the current study

indicate that the size goal area (meant to manipulate task difficulty) had no effect on the spatial mismatch employed by participants during the swiping task (Fabbri et al., 2017). Hence, our predictions for the current models group conditions with small and large goal areas. Figure 4 depicts the models used to represent the visual and motor targets; strong similarity between conditions of interest is shown in light colors, while no similarity is shown in black. In the Visual Target Model, we assumed that irrespective of goal size, proximity of the target from the center of the screen and task modality, conditions where the visual target is presented in the same hemifield (left-left, right-right) are very similar to each other. Conversely, when comparing conditions where the visual target was presented in different hemifields (left-right), these would be less similar to each other. This is in accordance with literature on the visual system, where activation in V1 follows patterns of lateralization and responds to stimuli presented in the contralateral visual hemifield (Wolynski, Schott, Kanowski, & Hoffmann, 2009). For the Motor Target Model, we assumed no similarity when comparing conditions belonging to different tasks. This representation of the motor target is based on literature that finds the primary motor cortex as an area encoding specific action-related movement parameters (Eisenberg, Schmuelof, Vaadia, & Zohary, 2011). The comparison of conditions between tasks (reach versus swipe) is the key difference between our Visual Target Model and Motor Target Model: while the visual target is assumed to be identical during both reach and swipe, the motor target would differ for these two tasks, akin to differing motor actions and parameters associated with each condition in each of the two tasks. Lastly, we tested a Task Separation Model that assumes high similarity between conditions that belong to the same task modality and no similarity between conditions if they belong to different task modalities.

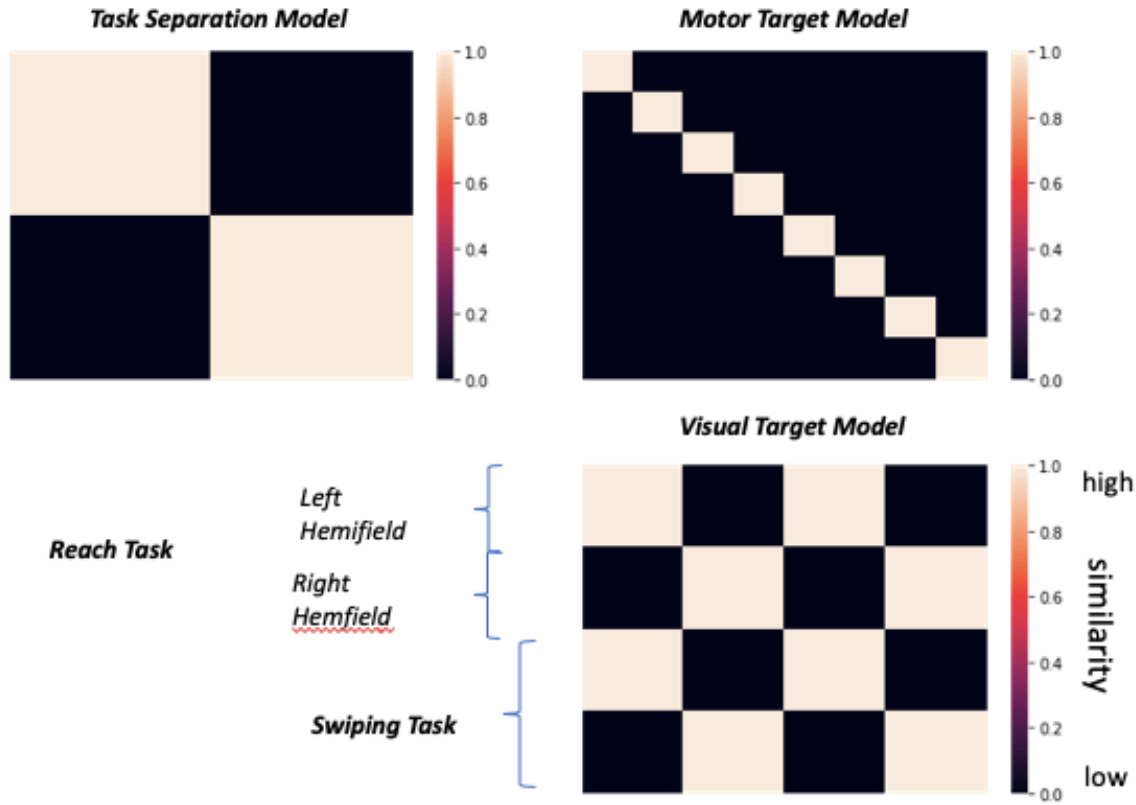


Figure 3. Models tested in each ROI.

Results

Representational similarity between all conditions in each ROI

The current study aimed to distinguish between the visual and motor target during the planning stage of reach and swipe movements. As such, we expected to find representation of the visual target (i.e., Visual Target Model) in early visual ROIs, namely the putative V1. Conversely, we expected to find representation of the motor target in the primary motor area M1, as assessed by our Motor Target Model. Lastly, we expected to find representations of both the visual and motor targets in PRR, an area that has previously been found to encode reaching movement goals (Gertz et al., 2017; Mountcastle et al., 1975).

The RSMs depicted in Figure 5 represent the neural similarity between all 16 conditions (8 conditions in each of the 2 tasks) averaged across 6 participants for each of the ROIs. It is

important to note that visual inspection of the following RSMs is part of an exploratory approach, given that the swipe task is a new paradigm that has not been previously studied. As such, no statistical tests were conducted on these RSMs. Each cell in the matrices expresses the similarity between the neural pattern elicited by each condition when compared to another condition. Light colors in the matrices indicate stronger neural similarity between conditions during the two tasks, with a maximum of 1 on the diagonal of the matrix, in which identical conditions are compared. In contrast, darker colors indicate low neural similarity between conditions, with a minimum of 0 for conditions that are uncorrelated to each other. For example, as can be seen in the RSM for V1, the squared checkboard-like pattern in the upper left corner indicates higher similarity between conditions where the target was presented in the left visual field during the reach task. For the visual area V1 (Figure 5) this pattern reflects the lateralization of the visual target: in V1, there is strong similarity between conditions where the target was presented in the same hemifield (either left or right), both in the reach task as well as in the swipe task. Still, in the swipe task this pattern reflecting the lateralization of the visual target is more pronounced i.e., there is less similarity when comparing conditions where the visual target was presented in different hemifields. The RSM for the PRR shows that the distinction between the left and the right visual field is no longer as clearly visible as in V1. Instead, conditions are more similar when they belong to the same task modality, and less so when the two different tasks are compared. Lastly, the RSM for M1 indicates that conditions from the swipe task where the visual target was presented in the left hemifield are less similar to all the conditions in the reach task, no matter if the target was presented to the left or to the right during the reach task.

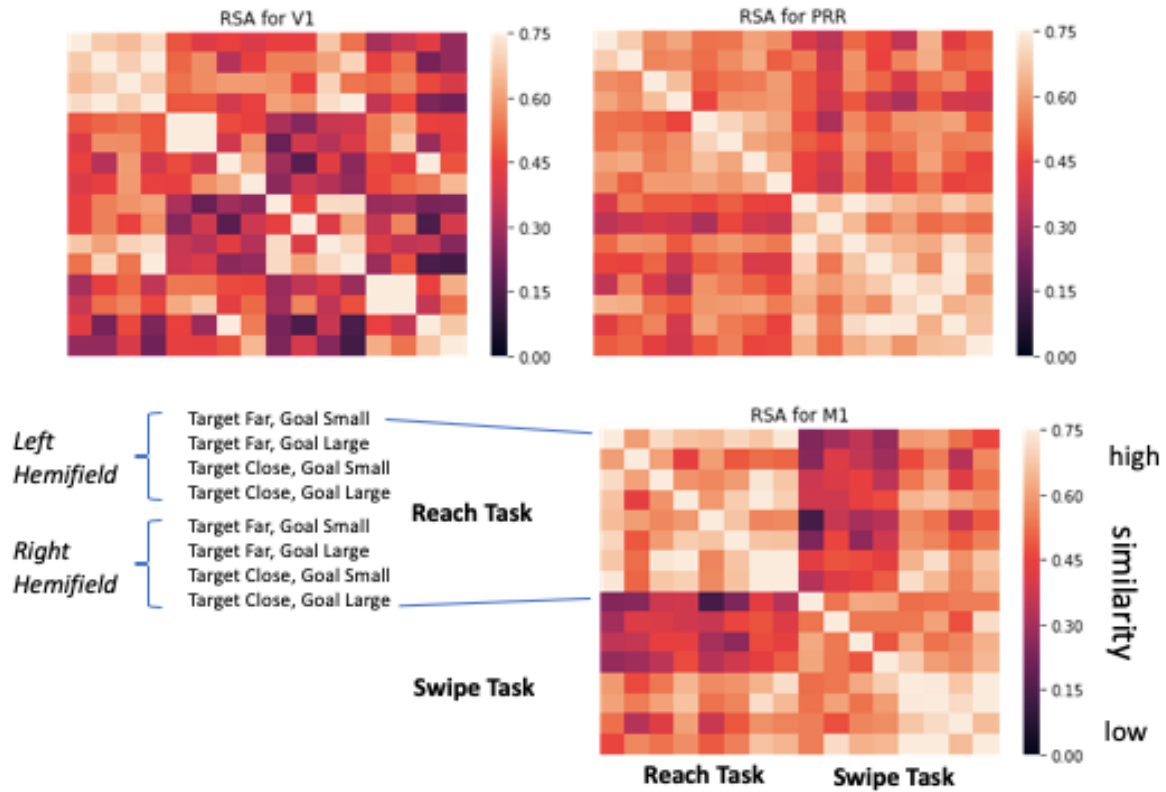


Figure 5. Representational Similarity Matrices in V1, PRR and M1, respectively. The scale used in the current figure runs to the maximum level of similarity in the data (0.75).

The neural similarity between the models of interest and the average RSMs computed in each ROI are depicted through a 2D MDS plot in Figure 6. MDS plots allow for a bottom-up visualization of data for easier and more intuitive interpretation of the results, since the grouping of the points in the plot is uninfluenced by any categorical assumptions about the data (Fabbri et al., 2016). The proximity of the points is indicative of neural similarity between data in the 3 ROIs and the theoretical models assessed in the current study. Visual inspection of the plots indicates that data in V1 is most similar to the model representing the visual target, as predicted by our hypotheses. Next, the close proximity between the points depicting the RSM in PRR and the Task Separation Model indicates that conditions in the posterior parietal cortex are

distinguished based on task modality or types of motor behavior (reach or swipe). Lastly, the third grouping of points depicts the neural proximity between the data in the primary motor cortex (M1) and the model representing the motor behavior, where differently from the visual target, the motor actions associated with each visual target would be different for each task.

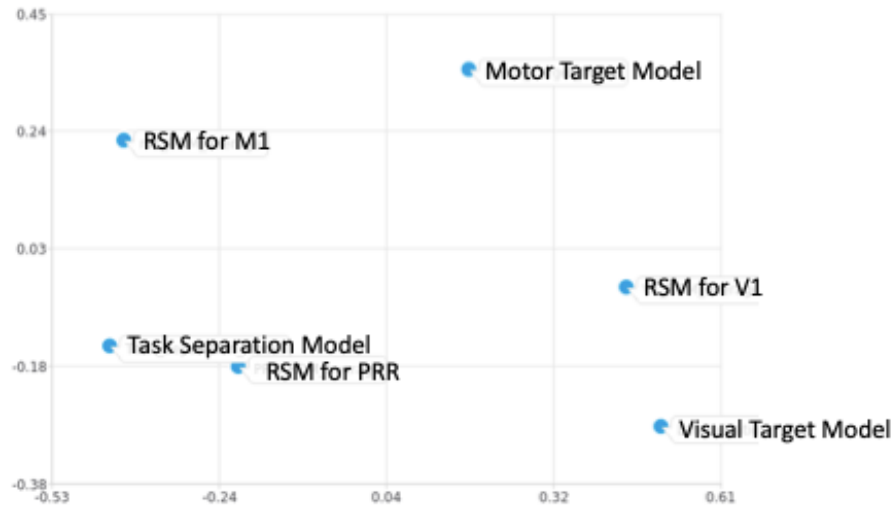


Figure 6. MDS plot indicating the neural similarity between the data in each ROI and the theoretical models.

Correlations between the Neural Data and the Theoretical Models

We assessed the degree to which different ROIs – from the visual, motor and posterior parietal cortex – represent information regarding the visual and motor targets within and between tasks. This was done by computing correlations between the RSMs of each participant and theoretical models of interest. Each model was tested in each ROI in order to obtain a measure of the extent to which visual and motor information are represented in the three ROIs. A summary of how each model performed in each ROI can be seen in figure 7.

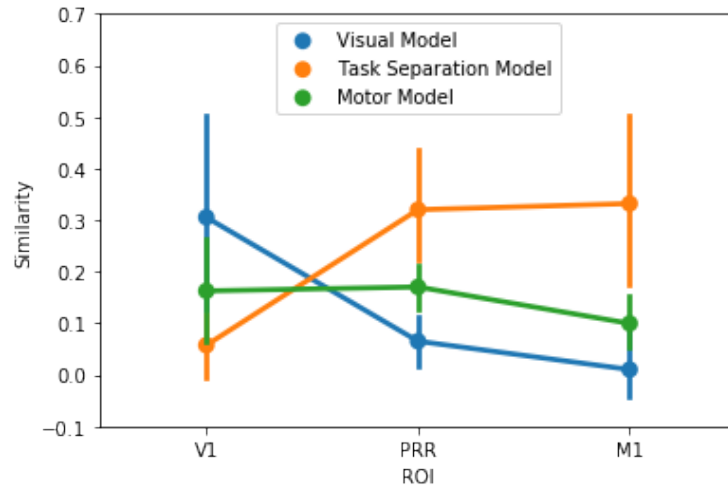


Figure 7. Similarity values among theoretical models and RSMs for each region of interest. Error bars represent Confidence Intervals of 95%.

In order to establish which models performed better than chance, we conducted one sample t-tests for each model in every ROI, correcting for the number of t-tests performed using the Bonferroni correction ($p < 0.004$). All models performed significantly better than chance in all ROIs. Next, to compare how well the models performed in each ROI, we conducted pairwise t-tests for all pairs of models in that ROI.

As can be seen in Table 2, there was no significant difference between the 3 models in early visual area V1. This could suggest that all models assessed here were descriptive of the neural data in the visual system. In contrast to V1, in the posterior parietal region PRR, both the Motor Model as well as the Task Separation Model performed significantly better than the Visual Model ($p = 0.004$, $p = 0.003$, respectively). This could suggest that as we move up the cortical stream, visual information plays a lesser role in explaining data in PRR and is likely replaced by motor sensitivity related to the motor intentions associated to each particular task. There was no significant difference between the Motor Model and the Task Separation Model in PRR, which could suggest that both these models explained the neural data in this ROI to the same extent.

Lastly, there was no significant difference between the 3 models in the primary motor cortex (M1), suggesting that all 3 models might be representative of the data in M1.

Table 2. *p* values resulting from Pairwise t-tests of all models in each ROI.

			V1	PRR	M1
Visual M.	-	Motor Model	0.080	0.004*	0.192
Motor M.	-	Task Separation M.	0.177	0.018	0.022
Visual M.	-	Task Separation M.	0.109	0.003*	0.050

Note. * Significant p-values (p corrected for the number of tests performed; $p < .0055$)

Discussion

Studying motor intentions in the brain has posed researchers with the challenge of untangling the sensory information about the objects we interact from the motor plan of each future movement. So far, this problem has been solved through experimental means, with paradigms asking participants to make a movement in the opposite direction from the visual stimulus they are presented with (i.e., anti-reach tasks). However, just how often would such a behavior be implemented in real-life situations? The swipe task implemented in this study bridges the gap between laboratory and natural settings by allowing participants to perform a motor movement they would usually perform when using touchscreens. As such, our goal was to assess the extent to which differing regions in the brain represent visual and motor information as distinguished by reaching and swiping movements.

Representation of visual and motor targets in PRR

Current literature assessing the role of regions within the PPC places the parietal reach region at the boundary of sensory-motor integration, involved in the planning of an upcoming reach movement (Mountcastle et al., 1975; Johnson et al., 1996; Snyder et al., 1997; Marconi et al., 2001; Battaglia-Mayer et al., 2003). As such, we expected to find representation of both the

visual and motor targets in PRR. Our results suggest that the Motor Target Model and the Task Separation Model performed significantly better in this ROI than the Visual Target Model. This is in line with previous studies that decoded motor goals from the PRR (Gail & Andersen, 2006; Gertz & Fiehler, 2017). Thus, the current study meaningfully contributes to the debate about whether PRR maintains the location of the visual target (Bisley & Goldberg, 2003) or the prospective motor movement associated with it (Andersen & Cui, 2009; Filimon, 2010), in favor of the latter. Previously, target-selection tasks as well as rule-selection tasks have been used to answer this question (Gail et al., 2009; Westendorff et al., 2010). The Swiping task is a novel way of testing these hypotheses, under conditions that are similar to real-life, non-laboratory settings (Fabbri et al., 2017).

More so, as indicated by the significant performance of the Task Model (in comparison to the Visual Target Model) in this ROI, the PRR seems to be modulated by information given prior to the planning phase (i.e., whether the movement is a reach or a swipe) and thus might be involved in grouping the tasks according to this modality. As such, this higher-level cortical area seems to encode the category (reach vs swipe) associated to each type of motor movement. The results of this study provide additional proof to a functional segregation within the PPC next to an anatomical one (Heed et al., 2011; Andersen & Cui, 2009). In this case, different motor intentions associated to different motor behaviors are differentiated at the level of category they are grouped by. It is this level of abstractness in which PRR codes motor goals that makes the region a suitable candidate for neural prosthetics (Buneo & Andersen, 2006).

Representation of visual and motor targets in Early Visual Area V1

We expected to find representation of the visual target, as assessed by the Visual Target Model, in the visual system (i.e., V1). This hypothesis was based on current literature that posits

visually-driven areas in the occipital cortex to respond to stimuli presented on the contralateral visual hemifield (Engel, Glover, & Wandell, 1997). However, the results of the current study indicate that none of the models in V1 were significantly different from each other, suggesting that more than one model is representative of the information decoded in V1 during the planning stage of a motor movement. This finding is insightful because it counters the view that V1 is just a passive transmitter of sensory information (Gullivan et al., 2019) and is sensitive only to basic visual features such as line orientations (Hubel & Wiesel, 1959). Indeed, some studies suggest that the PPC participates in sensory information processing in V1 through feedback modulations (Borra and Rockland, 2011; Hishida et al., 2018). As such, recent fMRI studies have decoded motor-specific parameters of a task from V1 during the planning period, among which the effector used to perform a movement (Gallivan et al., 2019) as well as the type of movement performed (i.e., reach or grasp; Chapman, Gallivan, Culham, & Goodale, 2011; Gutteling et al., 2015). Our study provides additional support for this line of argument: in addition to processing visual information related to the task, early visual areas also encode motor parameters relevant for an upcoming motor action.

As argued by Gallivan and colleagues (2019), one possible reason for transmitting this type of information to V1 could be to amplify the processing of target dimensions most relevant to upcoming motor movements. Our exploratory analyses of the averaged RSMs in V1, though not subjected to statistical testing, point towards a stronger lateralization in the swipe task compared to the reach task. This could indicate that the dimension most relevant to future motor behavior in the swipe task is target direction (i.e., left/right). This preliminary conclusion is supported by Fabbri and colleagues', (2017) behavioral results of the same paradigm: participants employ a spatial mismatch (i.e., start the movement next to the visual target rather

than on the target) when swiping, irrespective of whether the visual target is far or close from the center. The reliance on target direction when swiping in favor of the specific spatial location of the visual target (i.e., central versus periphery) could make target direction a likely candidate for encoding as early as in V1. Future studies could assess the extent to which specific target dimensions relevant to different types of motor movements can be decoded from the visual system.

Representation of visual and motor targets in M1

The primary motor cortex (M1) has mostly been described in the literature as a lower-level motor output structure, due to its direct connections with the corticospinal cord (Choinard & Paus, 2006). Due to this low level of abstractness, M1 has been thought to encode motor information at the level of joint angles and muscle movements (Todorov, 2000). Consequently, we expected to find representation of the motor target in this area, as assessed by our Motor Target Model. However, akin to the results in V1, we found no significant difference between the models in the primary motor cortex. Finding visual as well as motor representations in M1 could speak of a more prominent role this region has in planning motor movements (Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011). Indeed, some studies have found neuronal populations in M1 sensitive to target position (Eisenberg et al., 2011; Shen & Alexander, 1997b) as well as target color (Zach, Inbar, Grinvald, Bergman, & Vaadia, 2008) when these aspects were relevant for an upcoming movement. Lurito, Georgakopoulos, & Georgopoulos (1991) found that neuronal populations in M1 contribute to both visual and motor representations at different timepoints during a trial, initially being sensitive to target location, and later becoming sensitive to movement direction. Thus, it might be more feasible to think of a time-dependent aspect

underlying sensory-motor dynamics in regions involved in movement planning such as the primary motor cortex (Gail & Andersen, 2006).

Conclusion

Studying the neural underpinnings of motor intentions requires experimentally disentangling the sensory information from the motor information. We did so by introducing an ecologically plausible task (i.e., swiping) that formerly proved to differ from reaching in its motor behavior, while relying on the same visual input (Fabbri et al., 2017). Using a statistically powerful procedure, namely Representational Similarity Analysis (Kriegeskorte et al., 2008), we investigated how similar the two tasks are in terms of representing visual and motor targets in visual, posterior parietal and motor areas in the brain. Our findings suggest a gradient of visual to visuomotor to motor representations in the brain during the planning phase of both types of movements. Importantly, our study points to the fact that during the planning phase of a movement, PRR mainly represents motor goals of an upcoming movement. More so, both visual as well as motor information regarding a future movement are represented in primary visual and motor cortices.

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