Overlapping representations for grip type and reach direction

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To grasp an object, we need to move the arm toward it and assume the appropriate hand configuration. While previous studies suggested dorsomedial and dorsolateral pathways in the brain specialized respectively for the transport and grip components, more recent studies cast doubt on such a clear-cut distinction. It is unclear, however, to which degree neuronal populations selective for the two components overlap, and if so, to which degree they interact. Here, we used multivoxel pattern analysis (MVPA) of functional magnetic resonance imaging (fMRI) data to investigate the representation of three center-out movements (touch, pincer grip, whole-hand grip) performed in five reach directions. We found selectivity exclusively for reach direction in posterior and rostral superior parietal lobes (SPLp, SPLr), supplementary motor area (SMA), and the superior portion of dorsal premotor cortex (PMd). Instead, we found selectivity for both grip type and reach direction in the inferior portion of dorsal premotor cortex (PMd), ventral premotor cortex (PMv), anterior intraparietal sulcus (aIPS), primary motor (M1), somatosensory (S1) cortices and the anterior superior parietal lobe (SPLa). Within these regions, PMv, M1, aIPS and SPLa showed weak interactions between the transport and grip components. Our results suggest that human PMd and S1 contain both grasp- and reach-direction selective neuronal populations that retain their functional independence, whereas this information might be combined at the level of PMv, M1, aIPS, and SPLa.

Introduction

The ability to reach for and grasp objects is fundamental for our interaction with the environment. Reaching refers to the transport phase of the hand toward the object, while grasping includes the preshaping of the hand in relation to the shape and size of the object. It has been suggested that the transport component relies on a dorsomedial pathway consisting of superior parieto-occipital cortex (SPOC) in the medial wall of the parietal cortex, medial intraparietal area (MIP) and the dorsal premotor cortex (PMd); the grip component is thought to rely on a dorsolateral pathway consisting of the anterior intraparietal sulcus (aIPS) and the ventral premotor cortex (PMv) (Culham et al., 2006; Jeannerod et al., 1995; Tanné-Gariépy et al., 2002; Vesia and Crawford, 2012).

One of the best studied parameters of the transport component is directional tuning, identified as maximal activity during reaching in the preferred direction and a gradual decrease of activity with increasing angular difference from the preferred direction. In line with the view of separate streams for transport and grip, directionally tuned neurons have been found in monkey PMd (Caminiti et al., 1991) and parietal area V6A (Fattori et al., 2001, 2005). Likewise, the human SPOC and the rostral superior parietal lobe have been reported to show stronger activation during reaching to far locations in comparison to near locations, indicating a general preference for the transport in comparison to the grip component (Cavina-Pratesi et al., 2010). However, directionally tuned neurons have also been reported outside dorsomedial areas, like monkey PMv (Kakei et al., 2001; Stark et al., 2007), primary motor cortex (M1) (Georgopoulos et al., 1982), and the cerebellum (Fortier et al., 1989). Using fMRI adaptation, directional selectivity has been demonstrated both in regions of the human dorsomedial and the dorsolateral pathway (Fabbri et al., 2010, 2012; Lingnau et al., 2014). Taken together, these studies indicate that the representation of the transport component is not restricted to the dorsomedial pathway.

A number of studies support the view of a specialized role of the dorsolateral stream for the representation of the grip component. Macaque area AIP contains neurons selective for the grip used to grasp a specific object (Murata et al., 2000; Taira et al., 1990). This area projects to area F5, which also shows grip selectivity (Fluet et al., 2010; Rizzolatti et al., 1988; Umiltà et al., 2007). Inactivation of both areas causes impairment in appropriately grabbing an object (Fogassi et al., 2001; Gallese et al., 1994). Human fMRI studies demonstrated that both aIPS and PMv...
respond more strongly during grasping in comparison to reaching movements (Binkofski et al., 1999; Cavina-Pratesi et al., 2010; Culham et al., 2003; Frey et al., 2005). Moreover, permanent as well as temporary lesions to both human aIPS and PMv lead to an impairment in shaping the hand in relation to the shape and size of the object (Binkofski et al., 1998, 1999; Dafotakis et al., 2008; Davare et al., 2006, 2007; Rice et al., 2006).

Whereas the studies reported above support the view of a relative specialization of the dorsolateral pathway for the grip component, it has been shown that monkey PMd (Stark et al., 2007) and parietal area V6A (Fattori et al., 2010) in the dorsomedial pathway also contain grip selective neurons. Furthermore, it has been found, using multivoxel pattern analysis (MVPA) to decode brain activity, that precision grasps of different object sizes can be distinguished both in regions of the dorsolateral and the dorsomedial pathway (Gallivan et al., 2011b).

The fact that both the dorsomedial and the dorsolateral pathway seem to be sensitive to certain aspects of the transport and grasp components suggests that the functional distinction between these two components is not as clear-cut as originally thought. Little is known, however, about the combined representation of transport and grip. Stark et al. (2007) recorded from neurons in monkey PMd and PMv. For each recording site, the authors determined whether intracortical microstimulation (ICMS) evoked movements of proximal (shoulder, elbow) or distal (finger) joints. In line with previous studies, ICMS in PMd and PMv led to activation of muscles involved in the transport and in the grip component, respectively. Surprisingly, the authors observed that roughly the same proportion of neurons modulated by either reach direction or grip type were observed both within PMd and PMv. Moreover, in about 1/4 of all recorded neurons, the effect of reach direction and grip type interacted. They proposed that directionally tuned neurons in PMv and grip selective neurons in PMd might serve the purpose of relaying directional information through horizontal connections from proximal to distal sites, and information about grip type from distal to proximal sites.

Previous studies aiming to distinguish between the reach and grasp components compared brain activity during reach-to-grasp movements versus point-to-touch movements (Cavina-Pratesi et al., 2010; Desmurget et al., 2001; Faillenot et al., 1997; Konen et al., 2013). Such paradigms, however, are limited by the fact that the spatial accuracy demands of these two movements are clearly different. Here we used an innovative approach that does not rely on this assumption, varying both reach direction and grip type and measuring their selectivity across the entire brain. This allowed us to ask the question whether selectivity for reach direction and grip type are present within the same region, and if so, whether these two components interact. In addition to areas that are either grip selective but not directionally tuned (Fig. 1a) or vice versa (Fig. 1b), we aimed to identify areas that contain both grip-type and reach-direction selective neuronal populations. Such areas might contain neuronal populations that are directionally tuned irrespective of the type of grip (Fig. 1c). Alternatively, they might consist of neuronal populations that are both grip-type and reach-direction selective, as it was reported in monkey PMd and PMv by Stark et al. (2007); such areas should show an interaction between the two parameters (see Fig. 1d).

To test these predictions, we instructed participants to perform simple non-visually guided center-out reach-to-grasp movements (touch, pincer grip, whole-hand grip) in five different reach directions (0, 45, 90, 135, 180°, where 90° is straight ahead; see Figs. 2a–c). To measure selectivity for grip type, reach direction and their interaction, we performed multivoxel pattern searchlight analysis.

Materials and methods

Participants

Sixteen volunteers (9 males) took part in the experiment (age range: 21–52 years). All but one were right handed. Participants had normal or corrected-to-normal vision using MR-compatible glasses. Two of the authors (L.S., A.L.) took part in the experiment, while the other participants were naïve to the purpose of the study; all gave written informed consent for their participation. The experimental procedures were approved by the ethics committee for research involving human subjects at the University of Trento. Data recorded from one participant were excluded from the analysis because it became clear throughout the experiment that she did not properly understand the task.

Procedure and visual stimulation

During each trial, participants were presented with an arrow at the center of the screen for 2 seconds (s), followed by an inter-trial-interval (ITI) of 1 s (see Fig. 2a). Using their right hand, participants had to execute a center-out reach-to-grasp task on a device attached to their chest. Visual feedback was not provided so as to exclude confounds such as systematic eye movements toward the target object and uncontrolled visual stimulation by the sight of the participant’s own hands (see also Fabbri et al., 2010, 2012; Lingnau et al., 2014). The device consisted of 5 half-spheres of polystyrene (3 cm diameter) glued on a black plastic surface. They were placed at five equidistant positions on a virtual circle (8 cm radius) as well as at the center of that circle.

Fig. 1. Hypothetical Fisher-transformed correlations between odd and even runs as a function of angular difference in reach direction (x-axis) and combination of grip types (black circles: same grip type, white circles: different grip type). a–d: Hypothetical data from a ROI that contains neuronal populations that are grip-type selective, but not directionally tuned (a), directionally tuned, but not grip-type selective (b) selective for grip-type and reach-direction, but not for their interaction (c), selective for grip-type and reach-direction, as well as to their interaction (d). Note that the interaction depicted in (d) is only one out of several possible examples.
At the beginning of each trial, participants positioned their index finger on the central half-sphere (Fig. 2b). They were instructed to execute center-out movements in one of the five possible directions using one of the three different movement types as soon as the arrow appeared on the screen, and to then move back to the start position. Reach direction was indicated by the orientation of the arrow presented on the screen, while the type of movement was specified by its color (see Fig. 2c). Note that both whole-hand and pincer grip differ from touching in that they require grasping a target. The two grasps differ in the configuration of the hand: whole-hand grasp requires the use of all fingers while pincer grip uses only thumb and index fingers (see Fig. 2c).

Altogether there were 3 (movement type) × 5 (reach direction) conditions (Fig. 2c). In addition, 12% of the trials were null trials in which participants had to maintain fixation while keeping the hand at the center position for 3 s (2 s trial duration + 1 s ITI).

Instructions were counterbalanced between participants: for 8 out of 16 participants, a green arrow instructed them to reach the target using a whole-hand grip, a yellow arrow instructed to touch the target, and a red arrow instructed to reach the target using a pincer grip. For the other half of the participants, the green arrow instructed to touch the target, the yellow arrow instructed to use a pincer grip, and the red arrow instructed to use a whole-hand grip.

To reduce visual similarity between trials, we varied the visual appearance of the arrow that indicated the reach direction and type of grasp on each trial (see Materials and methods for details). Hand movements differed in the way the hand made contact with the target object (touch: using the index finger; pincer grip: index finger and thumb; whole-hand grip: all fingers).

At the beginning of each trial, participants positioned their index finger on the central half-sphere (Fig. 2b). They were instructed to execute center-out movements in one of the five possible directions using one of the three different movement types as soon as the arrow appeared on the screen, and to then move back to the start position. Reach direction was indicated by the orientation of the arrow presented on the screen, while the type of movement was specified by its color (see Fig. 2c). Note that both whole-hand and pincer grip differ from touching in that they require grasping a target. The two grasps differ in the configuration of the hand: whole-hand grasp requires the use of all fingers while pincer grip uses only thumb and index fingers (see Fig. 2c).

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To reduce visual similarity between trials, we varied the visual appearance of the arrow that indicated the reach direction and type of grasp on each trial (see Fabbri et al., 2010 for a similar approach). Arrow width and length were varied randomly from 0.41° to 1.22° in steps of 0.405°. The x- and y-center coordinates of the arrow were jittered in a range of ±0.07° in steps of 0.035°. Stimuli were back-projected onto a screen by a liquid-crystal projector at a frame rate of 60 Hz and a screen resolution of 1280 × 1024 pixels. Participants viewed the stimuli binocularly through a mirror above the head coil. The screen was visible as a rectangular aperture of 17.5 × 14.3°. Visual stimulation was controlled by ASF (Schwarzbach, 2011) based on the MATLAB Psychtoolbox-3 for Windows (Brainard, 1997; Pelli, 1997).

Instructions and training

Before entering the scanner, participants learned to execute center-out movements corresponding to the visual instructions, and they familiarized themselves with the location of the half-spheres on the device such that they were able to perform the movements accurately in the absence of visual feedback (see also Fabbri et al., 2010, 2012; Lingnau et al., 2014). The experimenter instructed participants to execute each movement within a constant time window of 2 s corresponding to the
presentation time of the arrow, rather than trying to move as fast as possible and thus risking head movements. Participants were asked to move their hand back to the center position before the arrow disappeared, and to start each trial from the center position.

fMRI design

The entire experiment consisted of 12 event-related runs. Each run consisted of 75 experimental trials and 10 null trials for a total of 85 trials, and lasted 4.2 min. For each participant, each of the 15 conditions (5 reach directions × 3 types of movement) was repeated 5 times in a run for a total of 60 repetitions per condition.

Data acquisition

We acquired fMRI data using a 4T Bruker MedSpec MRI scanner and an 8-channel birdcage head coil. Functional images were acquired with a T2*-weighted gradient-recalled echo-planar imaging (EPI) sequence. Before each functional scan, we performed an additional scan to measure the point-spread function (PSF) of the acquired sequence, which serves for correcting of the distortion expected with high-field imaging (Zaitsev et al., 2004). We used 34 slices, acquired in ascending interleaved order, slightly tilted to run parallel to the calcarine sulcus (TR (time to repeat): 2000 ms; voxel resolution: 3 × 3 × 3 mm; TE (echo time): 33 ms; flip angle (FA): 73°; field of view (FOV): 192 × 192 mm; gap size: 0.45 mm). Each participant completed 12 scans of 126 volumes each.

To be able to co-register the low-resolution functional images to a high-resolution anatomical scan, we acquired a T1 weighted anatomical scan (MP-RAGE; voxel resolution: 1 × 1 × 1 mm; FOV: 256 × 224 mm; GRAPPA acquisition with an acceleration factor of 2; TR: 2700 ms, inversion time (TI): 1020 ms; FA: 7°).

Data analysis

Data analysis was performed using BrainVoyager QX 4.1 (Brain Innovation), the BVQX Toolbox (http://support.brainvoyager.com/available-tools/52-matlab-tools-bvqtools.html) and custom software written in MATLAB (MathWorks).

Preprocessing, segmentation, and cortex-based alignment

To correct for distortions in geometry and intensity in the EPI images, we applied distortion correction on the basis of the PSF data acquired before each EPI scan (Zeng and Constable, 2002). Before further analysis, we removed the first 4 volumes to avoid T1-saturation. Next, we performed 3D motion correction with trilinear interpolation for estimation and sinc interpolation for resampling using the first volume as reference followed by slice timing correction with ascending interleaved order. Functional data were temporally high-pass filtered using a cut-off frequency of 3 cycles per run. The time course of each voxel was normalized to reflect percent signal change. We aligned the first volume of each run to the high resolution anatomy of the respective participant. Both functional and anatomical data were transformed into Talairach space using trilinear interpolation.

To obtain a better spatial correspondence across participants, we segmented and inflated both hemispheres of each participant, and morphed them into a spherical representation for cortex-based alignment (Fischl et al., 1999). Using the curvature information of each individual hemisphere, we performed cortex-based alignment (BrainVoyager 4.1) in an iterative procedure, starting with a strongly smoothed curvature map and progressing towards less smoothed curvature maps. Cortex-based alignment resulted in a correspondence mapping relating each vertex in the individual sphere to the group-aligned sphere. These correspondence mappings were used to transform the statistical map, computed in 3D and projected to each individual surface, to a group-aligned map. For better orientation of functional data with respect to anatomical landmarks, we reconstructed the inflated left and right hemisphere that represents the average curvature maps of all 15 participants who took part in the study. Since we used right-hand movements that are known to preferentially recruit the left hemisphere, only data from the left hemisphere are presented.

Univariate analysis

At the first level, we estimated beta weights for each combination of type of movement (touch, pincer grip, whole-hand grip) and reach direction (0°, 45°, 90°, 135°, and 180°), time-locked to the onset of the arrow, separately for each participant. Altogether, we included 3 × 5 = 15 predictors. Moreover, we added six parameters (x, y, z translation and rotation) resulting from 3D motion correction as predictors of no interest. The time course of each predictor of interest was convolved with a dual-gamma hemodynamic impulse response function (Friston et al., 1998), and the resulting reference time courses were used to fit the signal time course of each voxel. Beta estimates derived from the first-level analysis were projected on the surface and aligned to the group average inflated hemisphere of all participants using the correspondence mapping obtained during cortex-based alignment. The cortex-based aligned individual maps were entered into a second level random effects (RFX) general linear model (GLM) analysis carried out on the surface. To identify areas recruited during movement execution, we computed the RFX GLM contrast “all conditions versus baseline”, where baseline refers to all periods not explicitly modeled in the GLM. Statistical maps were corrected for multiple comparisons using a False Discovery Rate (FDR) < .01.

Searchlight-based multivoxel pattern analysis

We performed correlation-based multivoxel pattern analysis (MVPA, Haxby et al., 2001) using a searchlight approach (Kriegeskorte et al., 2006). First of all, we created beta maps using a cortex mask that restricts the analysis to voxels falling within −3 to +1 mm of the gray–white matter boundary determined during segmentation. To do so, we extracted the time course for each combination of movement type (touch, pincer grip, whole hand grip) and reach direction (0°, 45°, 90°, 135°, 180°), separately for each participant for each voxel in the cortex mask. Next, we calculated z-transformed β-estimates of the BOLD response separately for each participant, condition and run. Then, we averaged β-estimates across odd and even runs, resulting in a 15 × N voxels correlation matrix for each of the odd and even runs, separately for each participant. Data were normalized by subtracting the grand mean response across conditions from each voxel, separately for odd and even runs (Haxby et al., 2001).

Second, in each participant, for each voxel in the cortex mask, we determined a small region (the searchlight) containing all voxels falling within a radius of 5 mm of the central voxel. Since the analysis was restricted to voxels along the gray–white matter boundary, the number of voxels falling within each single searchlight varied between 5 and 19 (mean: 16; std: 3). Within each searchlight, we computed the correlations between odd and even runs for all combinations of movement types and angular differences between odd and even runs using the values stored in the beta maps. Next, we collapsed correlations across same grip types (pincer/pincer; whole-hand/whole-hand), different grip types (pincer/whole-hand; whole-hand/pincer), all combinations of same reach directions (e.g. 0°/0°, 45°/45°) and different reach directions (e.g. 0°/45°, 0°/90°). We assigned these four correlation values to the center of each searchlight, and stored them in a volumetric map, separately for each participant. Next, we generated surface maps from these volumetric maps and aligned them to the group average inflated hemisphere using the correspondence mapping derived during cortex-based alignment.

Third, for each vertex in the group average inflated hemisphere, we read the four correlation values (grip type × reach direction) for each participant, resulting in a 15 (participants) × 4 (conditions) matrix for...
each vertex. For each of these matrices, we computed a repeated-measures ANOVA with the factors grip type (same, different) and reach direction (same, different), separately for each vertex. The resulting F-values for the two main effects and the interaction were saved into a new surface map.

We used two different approaches to threshold the three maps containing the F-values of the two main effects and their interaction resulting from the repeated-measures ANOVAs as described above. First, we applied family-wise error correction using a false-discovery rate (FDR) <.05 (Genovese et al., 2002). Second, we thresholded the three maps retaining only those vertices with the top 1, 5 and 10% of the highest F-values.

Results

Univariate analysis

As a first step, we identified areas involved in the execution of center-out reach-to-grasp movements by running a RFX GLM contrast between all movement types versus baseline, collapsed across reach direction. At a threshold of FDR <.01, this contrast revealed a recruitment of primary motor cortex (M1), the dorsal premotor cortex (PMd), ventral premotor cortex (PMv), primary somatosensory cortex (S1), the rostral part of the superior parietal lobe (SPLr), anterior SPL (SPLa) and posterior SPL (SPLp/anterior precuneus), anterior intraparietal sulcus (aIPS), and the supplementary motor area (SMA) in the left hemisphere known to be part of the prehension network (Fig. 3; see Table 1 for Talairach coordinates).

Rostral SPL most likely corresponds to area IPS4 (Mars et al., 2011) or area 5L (Schepersjans et al., 2008), whereas SPLa most likely resembles area VIP (Mars et al., 2011) or area 7PC (Schepersjans et al., 2008).

Searchlight-based multivoxel pattern analysis

Fig. 4 shows the results of the searchlight analysis, thresholded with an FDR <.05. This analysis revealed a widespread network of areas within and beyond the dorsomedial pathway, in particular, SPLp, SPLr, SMA, and the superior portion of the PMd (PMDs) that were sensitive to reach direction (blue). By contrast, the inferior portion of PMd (PMDi), PMv, M1, S1, SPLa and aIPS showed selectivity for both reach direction and grip type. At this statistical threshold, none of the areas showed an interaction between reach direction and grip type. Next, instead of FDR correction, we thresholded all three maps, retaining only those vertices containing the top 5% F values, corresponding to uncorrected min. p-values of .0012, .000023 and .041 for the main effect of reach direction, grip type and their interaction, respectively. The results are shown in Fig. 5. As can be seen, areas showing the strongest effect of reach direction are located along the dorsomedial pathway (blue) and consist of PMDi, PMv, aIPS, and M1 also showed a weak interaction between reach direction and grip type (yellow).

To examine whether the results of the searchlight analysis change qualitatively depending on the threshold applied to each map, we repeated the analysis described above, showing the top 1, 5 or 10% of all vertices for each of the three maps. The corresponding maps can be seen in Supplementary Fig. 1. As it becomes clear, the qualitative pattern is invariant across the three different thresholds, with dorsomedial areas showing the strongest effect of reach direction and dorsolateral areas showing the strongest effect of grip type.

Directional tuning and grip selectivity across regions

Fig. 6 shows correlations for same (black circles) and different (white circles) grip types as a function of the angular difference between odd and even runs (0°, ±45°, ±90°, ±135°), separately for each region revealed by the searchlight analysis. The boundaries of the regions used for this analysis are shown in Supplementary Fig. 2. Supplementary Fig. 3 shows the same as Fig. 6, but distinguishes between the two grip types instead of collapsing across them. Note that the results shown in Fig. 6 and Supplementary Fig. 3 are biased by the searchlight analysis and thus just serve as an additional visualization of the results of the searchlight analysis shown in Figs. 4 and 5.

Table 1

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Table 1

Talairach coordinates of regions of interests. PMv, ventral premotor cortex; SMA, supplementary motor area; PMDi, dorsal premotor cortex, inferior portion; PMDs, dorsal premotor cortex, superior portion; M1, primary motor cortex; S1, somatosensory cortex; SPLr, superior parietal lobe, rostral portion; aIPS, anterior intraparietal sulcus; SPLa, superior parietal lobe, anterior portion; SPLp, posterior parietal lobe, posterior portion.

Fig. 3. Statistical map resulting from the contrast “all conditions > baseline”, superimposed on the averaged folded inflated brain of all N = 15 participants (FDR < .01). Major sulci and gyri are denoted by white lines. SMA, supplementary motor area; PMd, dorsal premotor cortex; M1, primary motor cortex; SPLr, superior parietal lobe, rostral portion; S1, somatosensory cortex; SPLp, posterior parietal lobe, posterior portion; SPLa, superior parietal lobe, anterior portion; aIPS, anterior intraparietal sulcus.
Compatible with the results obtained in Figs. 4 and 5, tuning curves for same grip type (black circles) and different grip type (white circles) were very similar in SMA, PMDs, SPLr and SPLp/aPCu, suggesting that neuronal populations in these regions are mainly selective for reach direction, irrespective of grip type, similar to the predictions illustrated in Fig. 1b. By contrast, PMDi, M1, and S1 showed strong effects of grip type, as evidenced by the differences between the curves for same and different grip types. The effect of reach direction in these regions was weaker in comparison to those obtained along the dorsomedial stream, as evidenced by broader tuning curves, in line with the results of the searchlight analysis (Figs. 4 and 5), similar to the predictions illustrated in Fig. 1c. Finally, the effect of grip type and reach direction tended to interact in SPLa, PMv, and aIPS, with the strongest effect in SPLa, similar to the predictions shown in Fig. 1d.

Discussion

The hypothesized distinction between independent transport and grip components of the prehensile action has been challenged by growing evidence that areas in both streams are involved in processing both components (Cavina-Pratesi et al., 2010; Fattori et al., 2010; Kakei et al., 2001). However, studies that examined both reach and grip type selectivity within the same experimental paradigm are scarce (Stark et al., 2007). Consequently, it is unclear to which degree neuronal populations sensitive to grip type are sensitive also to the transport component and vice versa. Here, we used multivoxel pattern searchlight analysis of fMRI data in a paradigm that required participants to perform three different types of movements (touch, pincer grip, whole-hand grip) in five different reach directions. We found that regions of the dorsomedial pathway are selective for reach direction, while areas of the dorsolateral pathway were selective for both grip type and reach direction. Whereas using a family-wise error correction of FDR < .05 did not reveal any interaction, a more liberal selection of the top 1%, 5%, and 10% of all vertices suggested a weak interaction between the reach and grasp component in SPLa, aIPS, PMv and M1, with the strongest effect in SPLa.

Areas specialized for reach direction

Figs. 4, 5, and 6 show a main effect of reach direction, and no sensitivity for grip type, in SMA, PMDs, SPLr and SPLp/aPCu, suggesting that these areas preferentially code the transport component of the action. Results in PMd and SMA are consistent with previous findings reporting selectivity for reach direction in various regions of the monkey (Mahan...
and Georgopoulos, 2013) and human fronto-parietal network including PMd and SMA (Fabbri et al., 2010, 2012; Lingnau et al., 2014). Likewise, the results in SPLr and SPLp/aPCu are consistent with the preference for the reaching component previously reported in these areas (Cavina-Pratesi et al., 2010; Filimon et al., 2009; Konen et al., 2013).

Visually vs non-visually-guided reaching

As one moves along the posterior–anterior axis of the posterior parietal cortex, the proportion of visually responsive neurons decreases whereas the proportion of movement-related neurons increases (Battaglia-Mayer, 2001; Battaglia-Mayer et al., 2000; Burnod et al., 1999; Galletti et al., 1996, 1997; Johnson et al., 1996; Marconi et al., 2001). A similar visuo-motor gradient is present in frontal areas from dorso-rostral premotor cortex (F7) to dorso-caudal premotor cortex (F2) and M1 (Battaglia-Mayer, 2001; Marconi et al., 2001). Neuroimaging studies have suggested a similar functional organization in the human brain, where the superior parieto-occipital sulcus is more active during visually than non-visually guided actions and anterior precuneus is equally active in both conditions (Filimon et al., 2009).

Here we focused on the neuronal basis of proprioceptively-guided actions, excluding visual information from the hand and the target. As one would expect on the basis of the literature reported above, we did not obtain any involvement of the superior parieto-occipital cortex that is known to show a preference for visually compared to non-visually guided actions (Filimon et al., 2009). Other than that, we found the same set of parietal and frontal areas that are typically reported to be involved during visually-guided actions (e.g. Cavina-Pratesi et al., 2010; Filimon et al., 2009; Gallivan et al., 2011a,b). It should be noted, however, that the rather weak grip selectivity we observed in areas aIPS and PMv that are known to contain visually responsive neurons (Murata et al., 2000; Raos et al., 2006) is likely to be due to the fact that we used non-visually guided movements in the current study.

In contrast to visually-guided actions where the required reach direction is typically given by a spatial cue indicating the target location (see for example Filimon et al., 2009), here we used a centrally presented arrow to instruct reach direction. In comparison to spatially guided actions, movements instructed by arbitrary stimulus–response associations have been shown to lead to a stronger recruitment of ventral prefrontal cortex, the putamen/globus pallidus and dorsal premotor cortex/BA6 (Toni et al., 2001). Whereas we obtained no recruitment of ventral prefrontal cortex, one might argue that the results we obtained in dorsal premotor cortex to some degree reflect the association between the orientation of the arrow and the required reach direction. Whereas we cannot fully exclude this possibility, it is important to point out that PMd has been consistently shown to be recruited in previous studies using visually-guided reaching using spatially congruent cues (Cavina-Pratesi et al., 2010; Filimon et al., 2009; Gallivan et al., 2011a), making a recruitment of this region on the basis of arbitrary stimulus–response mappings alone less likely.

Overlapping representations for reach direction and grip type

Our results show that both reach direction and grip type are represented in PMd, PMv, M1, S1, SPLa and aIPS. The reported directional selectivity in these regions is in line with directional tuning measured in monkey area M1 (Georgopoulos et al., 1982), area PMd (Caminiti et al., 1991), areas 2 and 5 (Kalaska et al., 1983), and in various fronto-
parietal areas in the human brain (Fabbri et al., 2010, 2012; Lingnau et al., 2014). Likewise, grip selectivity in these areas is consistent with similar findings in monkey area AIP (Murata et al., 2000; Taira et al., 1990), area F5 (Fluet et al., 2010; Rizzolatti et al., 1988; Umilta et al., 2007), PMd (Raos et al., 2004), and M1 (Muir and Lemon, 1983; Umilta et al., 2007) and in human aIPS, PMv (Binkofski et al., 1999; Cavina-Pratesi et al., 2010; Culham et al., 2003; Frey et al., 2005), as well as PMd, M1, and S1 (Ehrsson et al., 2000). Selectivity for grip type and reach direction in S1 is likely due to sensitivity to somatosensory feedback associated with the specific movement. Somatosensory feedback might also be reflected in the results in M1 and PMd, since both regions receive kinesthetic and proprioceptive information from S1 through short-loop and long-loop projections, respectively (Gardner et al., 2007).

Note that whereas previous studies investigated the reach and grip components separately, the novelty of our study consists in the manipulation of grip type and reach direction within the same paradigm, allowing us to measure the relation between the selectivity for the two components. Within some of the overlapping regions selective for grip type and reach direction (PMd, S1), we observed independent selectivity for the two components. Using a more liberal statistical threshold, we obtained weak interactions in PMv, M1, aIPS and SPLa. One should note that Stark et al. (2007) reported an interaction between selectivity for grip type and reach direction in only 1/4 of neurons in PMd and PMv.

We observed the strongest trend for an interaction between reach direction and grip type in SPLa, corresponding to monkey ventral intraparietal area (VIP) (Mars et al., 2011). This region has been reported to be sensitive to the direction of visual, tactile and auditory stimuli (Duhamel et al., 1998) and thus might be a candidate to be sensitive to the direction of visual, tactile and auditory stimuli (Duhamel et al., 1998) and thus might be a suitable candidate to combine information from the reach and grasp component.

Conclusions

We found overlapping representations for both the reach and grasp components in PMd, PMv, M1, S1, SPLa, and aIPS. These results provide further evidence against the view of a clear-cut distinction between a dorsomedial and a dorsolateral pathway specialized for the two components (Cavina-Pratesi et al., 2010; Fattori et al., 2010; Stark et al., 2007), leaving open the possibility of alternative accounts like a different temporal or spatial qualitative involvement of the two streams in the execution of the reach-to-grasp actions (Verhagen et al., 2013) or a different role in the degree of online control of the movement (Grol et al., 2007). Moreover, we observed trends for an interaction between the reach and grasp components in PMv, M1, and aIPS, and SPLa tentatively suggesting that these areas might be involved in the combination of the reach and grasp component (see also Stark et al., 2007). Further experiments are required to better understand how this combination of information is achieved. However, our data provide an interesting starting point for future investigations examining this question.

Conflict of interest

The authors declare no competing financial interests.

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Appendix A. Supplementary data

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References


