

Overlapping representations for grip type and reach direction



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ABSTRACT

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 (PMDs). Instead, we found selectivity for both grip type and reach direction in the inferior portion of dorsal premotor cortex (PMDi), 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 PMDi and S1 contain both grip- 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.

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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 grasping an object (Fogassi et al., 2001; Gallese et al., 1994). Human fMRI studies demonstrated that both aIPS and PMv

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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; Failletot 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 hand (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.

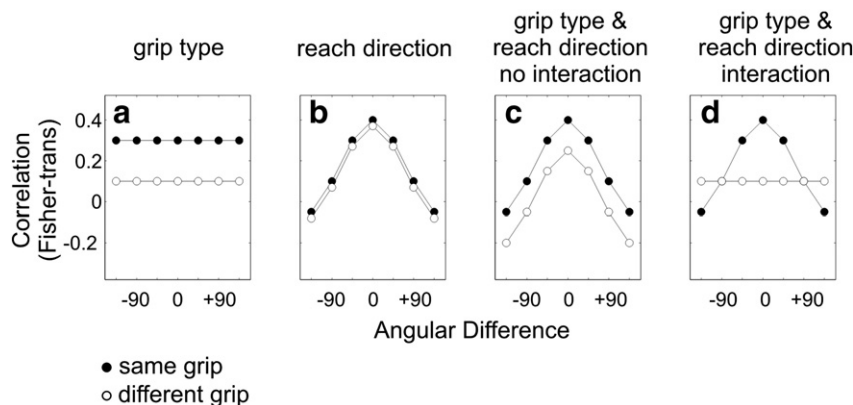


Fig. 1. Hypothetical Fisher-transformed correlations between odd and even runs as a function of angular difference in reach direction (x-axis) and combination of grip types (black circles: same grip type, white circles: different grip type). a–d: Hypothetical data from a ROI that contains neuronal populations 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.

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