

INTRODUCTION

With everyday actions, individual objects are parsed from others in a busy and crowded environment by the ventral stream, and selected for potential action, while the dorsal stream then specifies particular motor outputs and governs online control (Goodale & Humphrey, 1998; Milner & Goodale, 2006, pp. 231-233). According to this account, the dorsal stream subserves actions carried out immediately. However, even when a short delay is required before the response, the ventral (perceptual) stream is recruited (James et al., 2002; Singhal et al., 2013).

Here, we used functional magnetic resonance imaging (fMRI) in healthy normal participants to investigate the contributions of the ventral and dorsal stream during haptically guided grasping without any visual feedback. Specifically, we assessed whether and how the tactile information about objects' geometry (shape) acquired just a few seconds ago is used for guidance of object-directed grasping.

Event related design allowed us to clearly distinguish activation related to tactile exploration/encoding, maintenance of this information during the delay period, and its use at the time of grasp execution, thus providing a richer characterization of dorsal- and ventral-stream brain regions in haptically guided actions.

METHODS

Participants: 10 neurologically intact right-handed volunteers (4 females, age range: 22–35 years). **Scanning:** performed on a Siemens (Erlangen, Germany) 3T Allegra MRI at LCNI (Lewis Center for NeuroImaging) at the University of Oregon.

IMAGING PARAMETERS

- Functional volumes were collected using a T2*-weighted gradient echo sequence.
- 32 contiguous slices of 3.5-mm thickness.
- TR = 2000 ms, TE = 30 ms.
- High-resolution T1-weighted structural images were also acquired, using the 3D MP-RAGE pulse sequence.

Structural and functional fMRI data were preprocessed and analyzed using fMRIB's Software Library [FSL v.5.0.6] (Smith et al., 2004).

For every participant, each of the five fMRI runs containing the Explore, Plan, and Grasp (as well as Reach or No Go) conditions were modeled separately at the first level. Orthogonal contrasts (one-tailed t-tests) were used to test for differences between each of the experimental conditions and resting baseline. Orthogonal contrasts were also used to test for differences between conditions.

The resulting first-level contrasts of parameter estimates (COPEs) then served as inputs to higher-level analyses carried out using FLAME Stage 1+2 to model and estimate random-effects components of mixed-effects variance. Z (Gaussianized T) statistic images were thresholded using a cluster-based threshold of $Z > 2.3$ and a whole-brain corrected cluster significance threshold of $p = 0.05$.

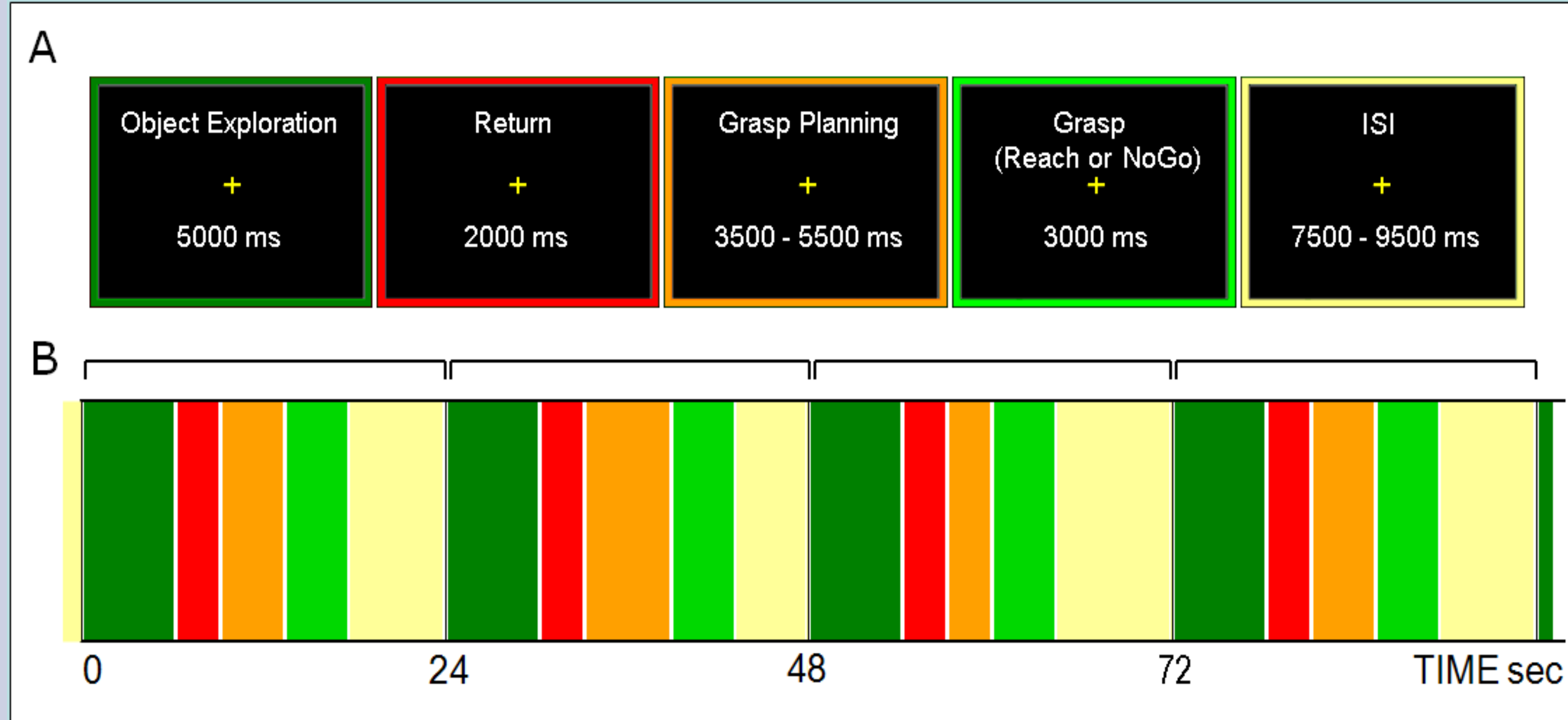


Figure 1. Experimental design and timing. Each trial consisted of an 5s exploration phase, a brief (2s) delay interval, a variable (3.5 to 5.5s) action planning phase, i.e. typically for grasp preparation, yet two other tasks such as Reach or No Go were also introduced for the purpose of localizing grasp- and planning-related areas, a 3s action execution stage, followed by a variable (7.5 to 9.5s) ISI.



Figure 2. Examples of differently shaped objects (mainly **complex**). Participants were asked first to explore them and after a delay period to grasp these objects with their dominant (right) hand. The last object on the right has a circular shape and such stimuli served as **simple** controls.

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RESULTS

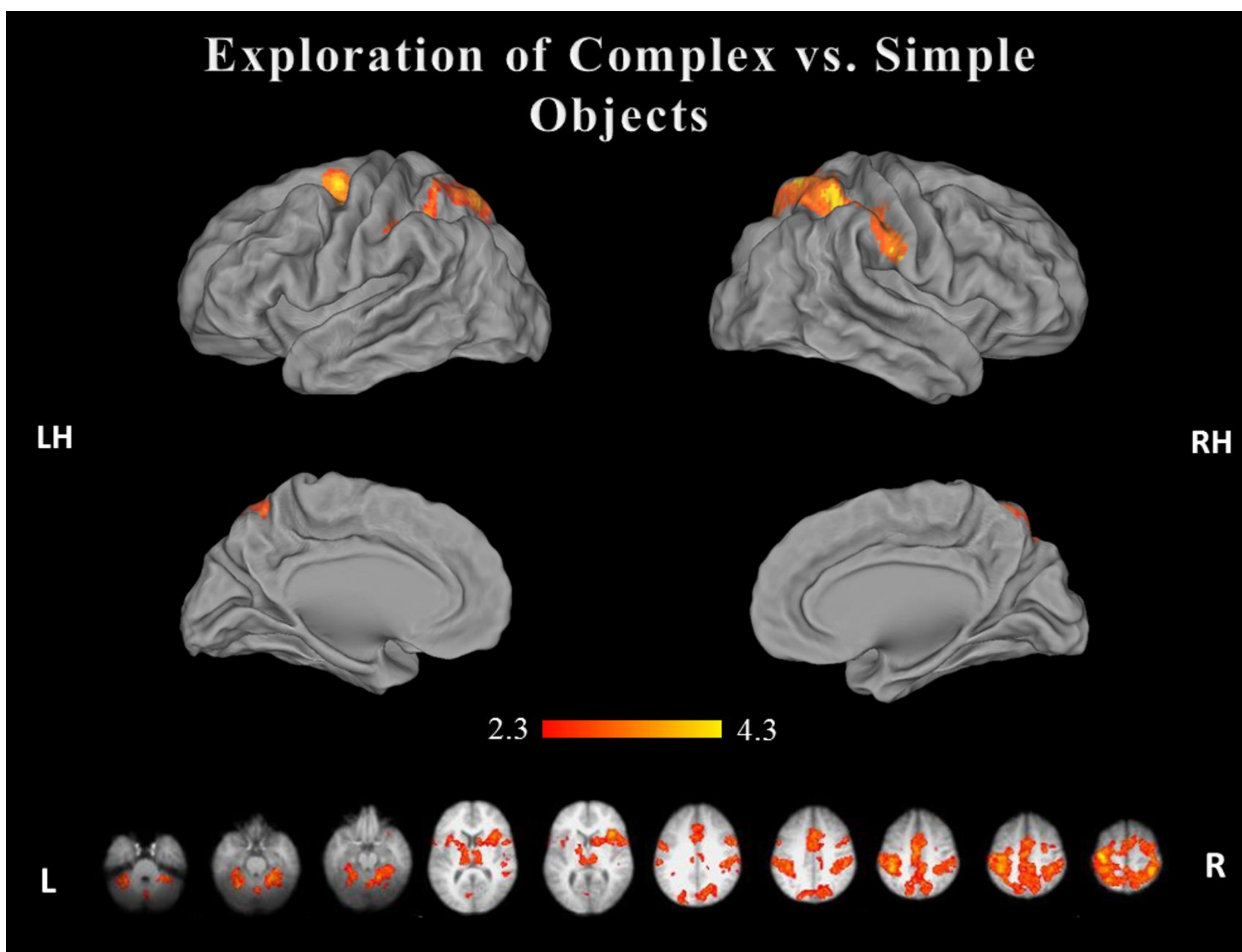


Figure 3. Statistical parametric maps representing areas of significantly increased activity ($Z > 2.3$, clusterwise corrected $P = 0.05$) associated with comparison of exploration of complex vs. simple objects, overlaid on PALS atlas.

We found increased bilateral signal modulations extending from the superior parietal gyrus, via anterior intraparietal sulcus, and through anterior supramarginal gyrus, with greater involvement on the right. The dorsal premotor cortex was engaged exclusively on the left.

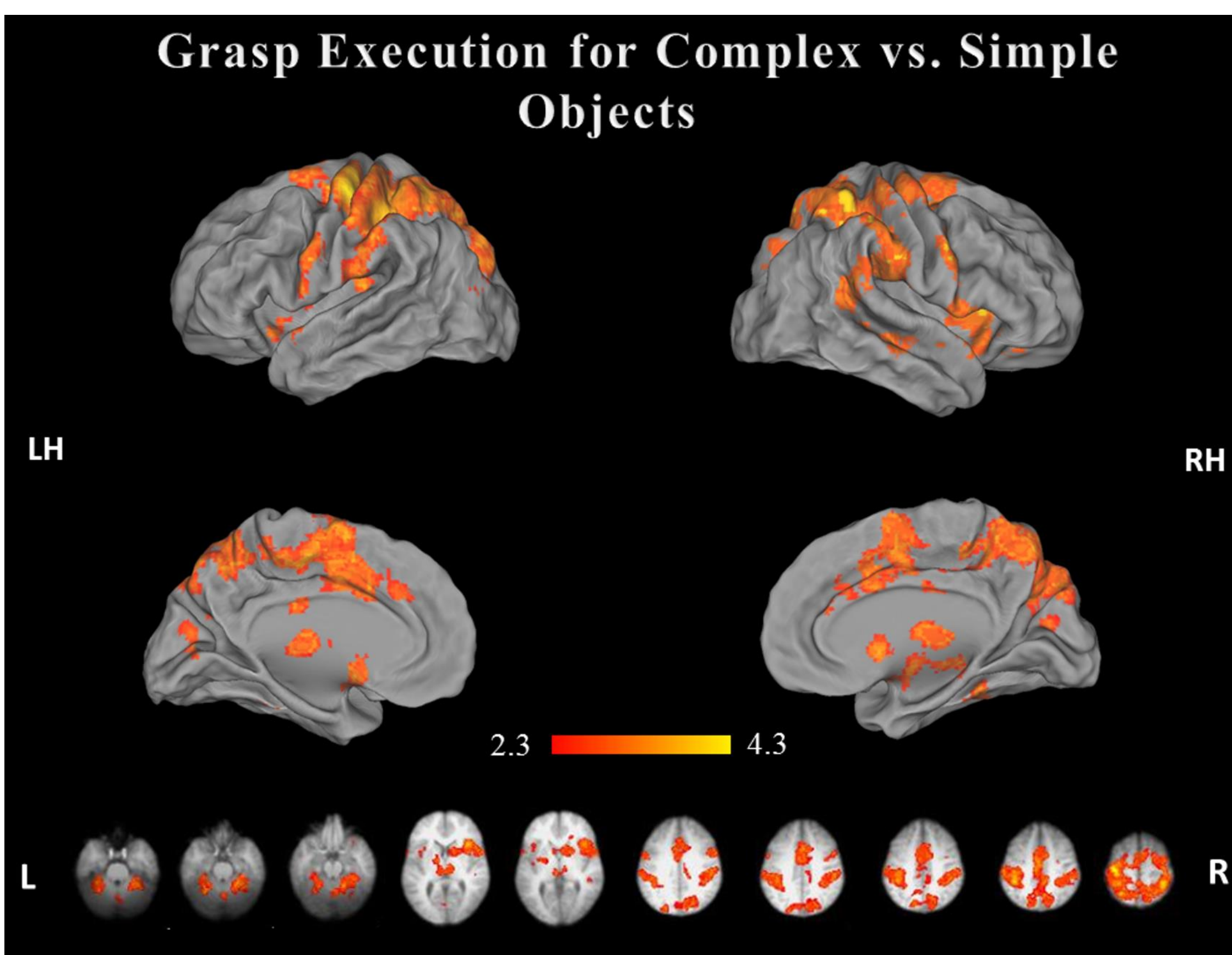
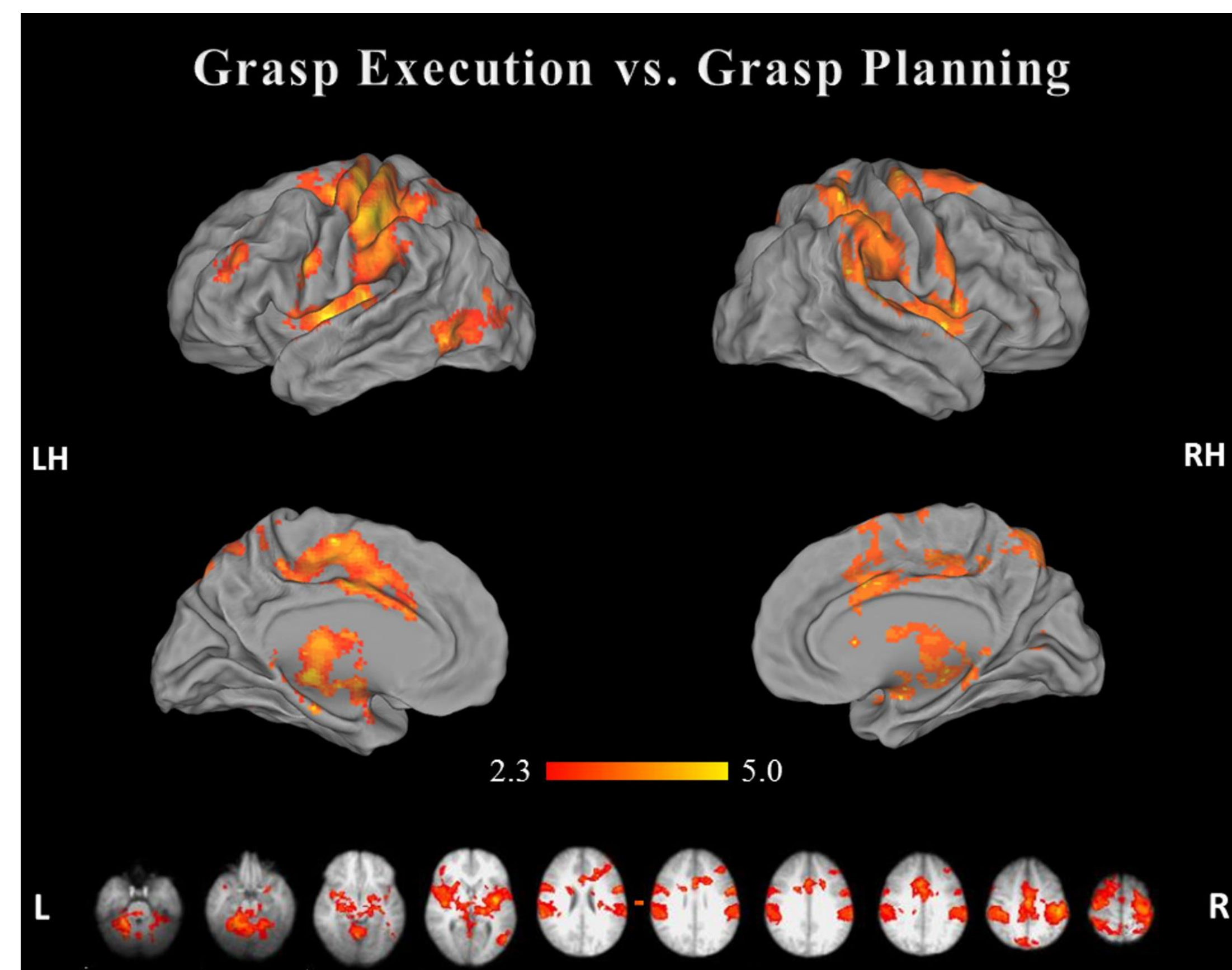


Figure 4. Statistical parametric maps showing increased activity along the frontoparietal dorso-dorsal pathways associated with online control of grasping.

The bilateral involvement of the sensorimotor cortex was accompanied by activity in the superior parietal lobule (SPL) areas, the dorsal and ventral premotor areas (PMd and PMv), and anterior divisions of the insulae.

Figure 5. Difference in neural activity between haptically-driven grasp execution and grasp planning based on the haptically acquired information. This contrast revealed the ventro-dorsal (SMG-PMv), as well as both lateral and medial prefrontal regions.

Unexpectedly, we found increased activity in the caudal divisions of the left middle temporal area (cMTG), and in the left middle frontal gyrus (MFG).



DISCUSSION

Our study provides new insights about the cerebral circuits underlying haptically-guided behavior. We demonstrated that a dorso-dorsal (SPL-dPMC) and ventro-dorsal (IPL-vPMC) pathways are engaged in motor planning in the absence of vision, including haptically-guided grasping after a short delay.

These findings support the involvement of an “object-directed action” network for haptic modality. Interestingly, the revealed engagement of the left cMTG/MT/LO and left MFG (see Figure 5) suggests that these areas are suppressed during the planning phase (cf. Lewis et al. 2006, Króliczak et al., 2007).

We furthermore provided evidence that might suggest an analogy between the role of left MFG in haptic modality to the one of vPMC in visual modality, suggesting its role in retention of haptically acquired information related to geometry of explored objects.

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