

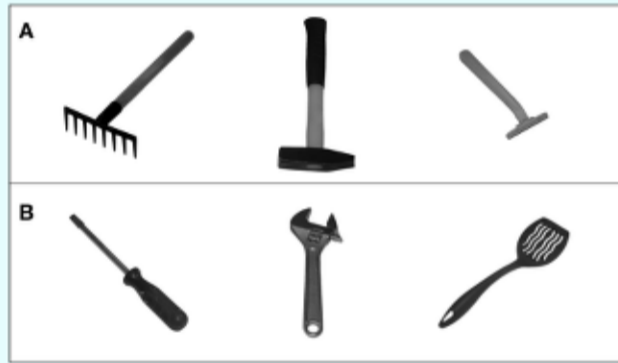
## INTRODUCTION

Adoption of an appropriate hand posture during interactions with manipulable objects depends on action goals. The intention to properly use, transmit, or displace a tool may engage different mechanisms in the brain. Yet, no study has directly compared activation patterns associated with the control of actions motivated by such distinct goals. Here, we used functional magnetic resonance imaging (fMRI) to establish the neural underpinnings of planning and execution of visually-guided grasps with different intentions in mind. We hypothesized that grasping an object in order to use it would more strongly engage the subdivisions of the praxis representation network (PRN).

## METHODS

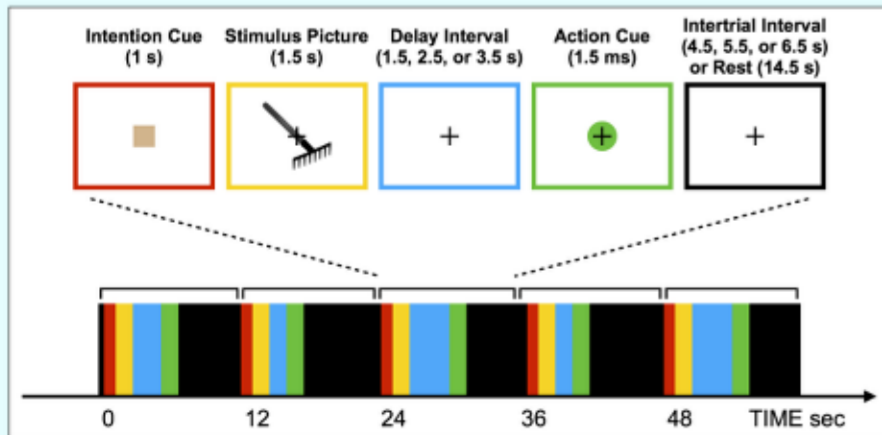
**Participants:** twenty healthy individuals (age range: 20-29, mean age = 24.7; 10 females), all right-handed (mean Edinburgh Handedness Inventory *Lateralality Quotient* = 96.6), none had a history of neurological or psychiatric disorders. They voluntarily participated in an event-related experiment in which BOLD fMRI signal associated with planning and execution of tool-directed actions was measured.

**Stimuli:** high-resolution pictures of graspable tools presented at six different orientations in their foreshortened views (see **Figure 1**).



**Figure 1.** Examples of stimuli used in our experiment: (A) Tools presented at 3 different orientations, i.e., 45, 0, or 315 degrees, in the experimental conditions: "Grasp to use", "Grasp to pass", and "Move". (B) Tools presented at another 3 different orientations, i.e., 135, 180, or 225 degrees, in the control, "Grasp to use" condition.

**Design and protocol:** standard neuroimaging parameters and an optimized event-related design were used (Kroliczak & Frey, 2009). Participants performed the following four tasks with their dominant right hands: (1) planning grasps of tools with an intention to (A) functionally use them, or (B) to pass them to a different person; (2) planning reaching movements directed at tools with an intention to move them with the backs of their hands, and (3) pantomimed execution of the planned actions (grasping/reaching movements). There were six (~6-min.) functional runs in this experiment. Trial structure and timing is shown in **Figure 2**.



**Figure 2.** Trial structure and timing. The 1-s Intention cue was followed by a 1.5-s Stimulus picture, and a variable (1.5, 2.5, or 3.5 s) Delay interval for action planning. Next, a 1.5-s "Go" cue for the execution of the planned action was presented. ITIs were 4.5, 5.5, or 6.5 s. Additional Rest intervals were introduced pseudo-randomly and their duration was 14.5 s.

## Imaging parameters

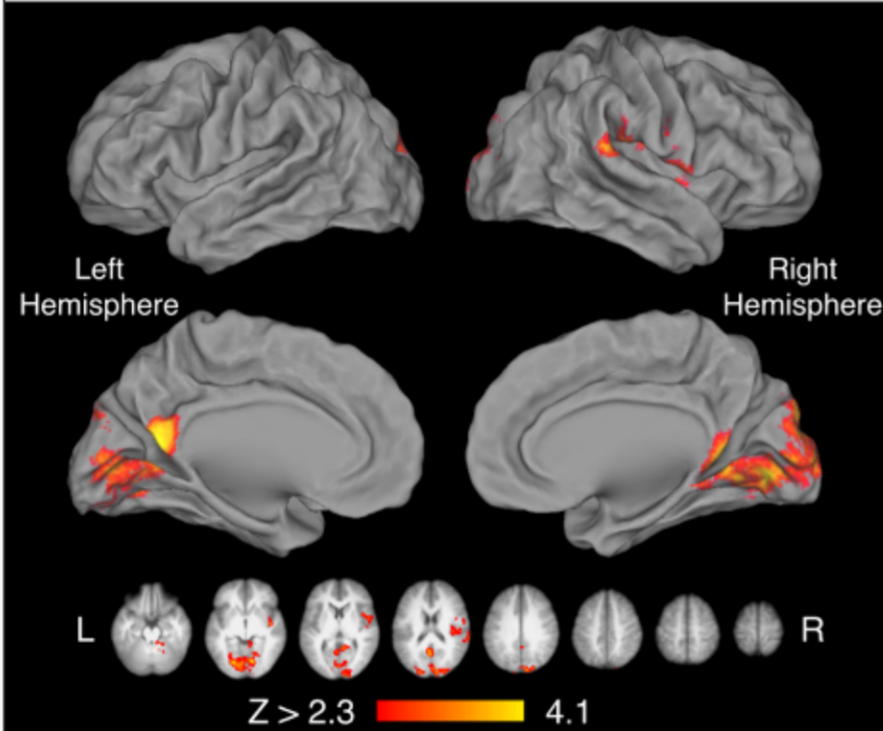
- 1) fMRI (BOLD) echoplanar images (T2\*-weighted)
  - 2) 16 channel head coil
  - 3) 35 contiguous axial slices of 3.1 mm thickness (3.1-mm isotropic voxels)
  - 4) Images sampled every 2 seconds (TR = 2000 ms)
  - 5) Session duration (with all additional localizers, structural and resting state runs) lasted ~95 minutes
- All scanning was performed in the Rehasport Clinic (Poznan, Poland) on a 3-Tesla Siemens MAGNETOM Spectra MRI scanner (Siemens Healthcare, Erlangen, Germany).

## IMAGE ANALYSES

FSL ver. 5.0.7 was used for data analyses. For a given participant, each fMRI run was modeled separately at the first level. Inter-session (Level 2) analyses used a fixed-effects model. Inter-subject (Level 3) random-effects components of mixed-effects variance were modeled and estimated using FLAME Stage 1 ( $Z > 2.3$ ,  $p = 0.05$ , corrected for cluster size).

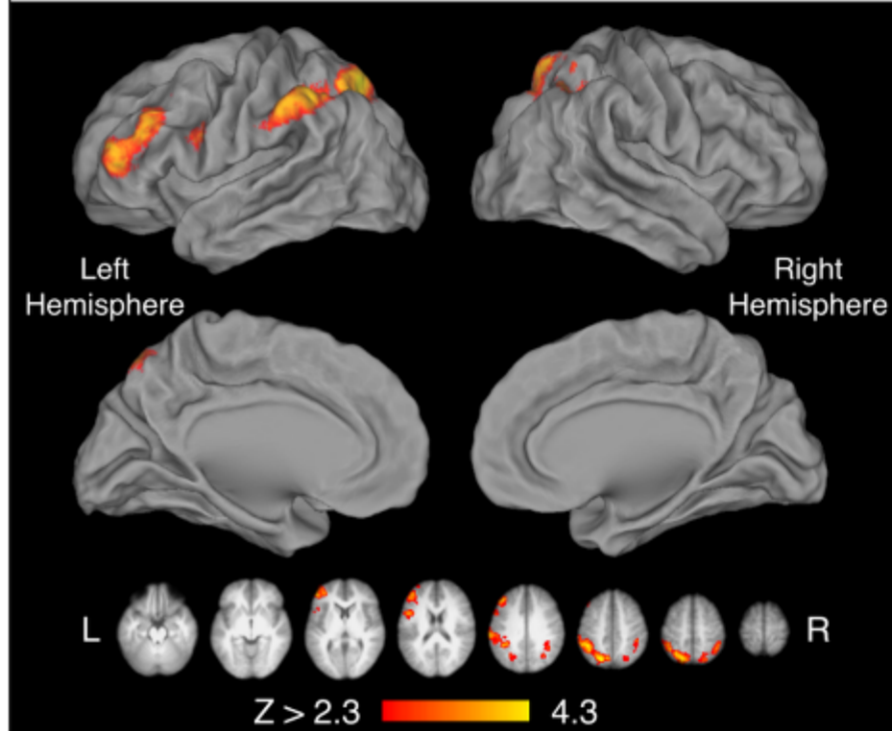
## RESULTS

### Planning grasping-to-use vs. grasping-to-pass



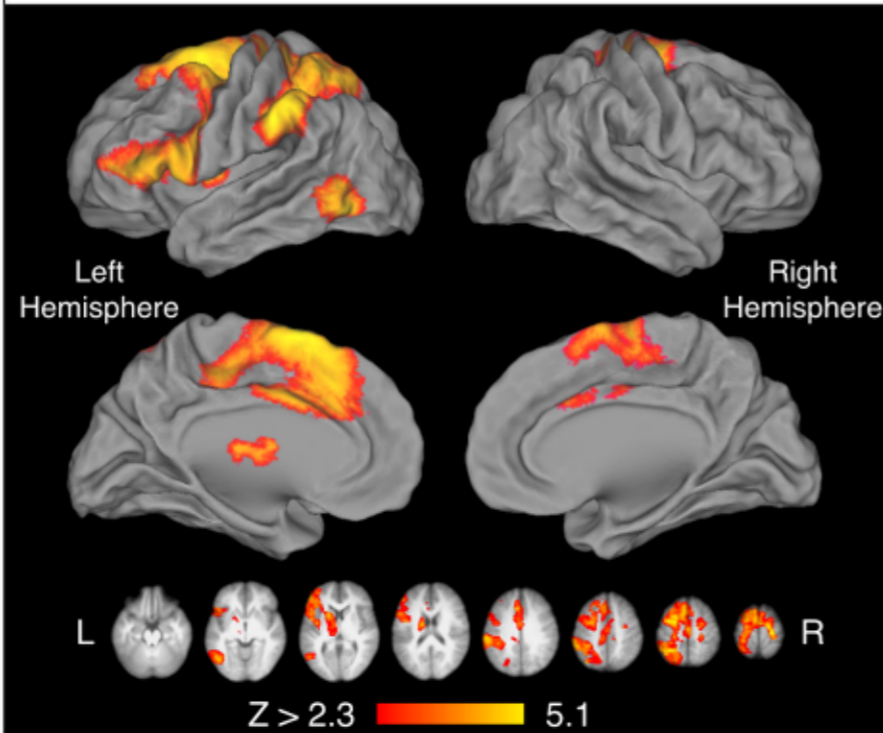
**Figure 3.** Planning to grasp a tool in order to use it vs. to pass it: grip kinematics and hand rotations were matched.

### Planning grasping-to-pass vs. grasping-to-use



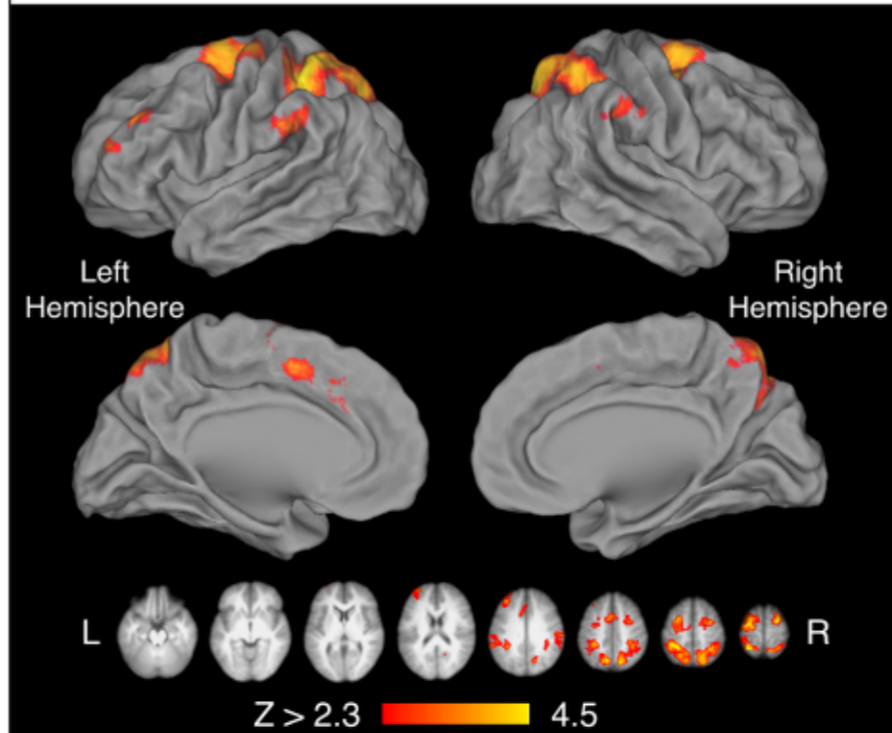
**Figure 4.** Planning to grasp a tool in order to pass it vs. to use it: grip kinematics and hand rotations were matched.

### Hand-Independent Praxis Representation Network (PRN)



**Figure 5.** Areas significantly involved during pantomimed tool use contrasted with repetitive abstract hand movements matched in kinematic complexity.

### The control of uncomfortable hand rotations



**Figure 6.** The planning of most demanding (uncomfortable) functional grasps of tools (cf. Fig. 1A) vs. relatively easy (comfortable) functional grasps (cf. Fig. 1B).

**Figure 3** shows significant BOLD signal increases associated with planning grasping to use a tool (vs. grasping to pass) with grasp kinematics and hand rotations accounted for (cf. **Figure 1**). The relevant activity was found in the right temporo-parietal junction (TPJ), parietal operculum, and the middle and posterior divisions of the insular cortex. On the medial surface, significant signal modulations were observed bilaterally in the calcarine sulci and lingual gyri, with a noticeable involvement of the retrosplenial cortex predominantly in the left hemisphere.

In the inverse contrast (see **Figure 4**), there was greater engagement of the left parieto-frontal network, with the involvement of the supramarginal gyrus (SMG, mainly its anterior division), ventral premotor cortex (PMv), and middle frontal gyrus (MFG). Additionally, bilateral activity with a clear left-sided bias was observed in the superior parietal gyri (SPG) and anterior parts of the intraparietal sulci (aIPS).

Noteworthy, most of the clusters of activity related to planning grasping-to-pass contrasted with grasping-to-use were located within the praxis representation network (PRN) identified independently in our localizer runs (cf. **Figure 5**).

As to the control of uncomfortable hand rotations during the planning of most demanding functional grasps (see **Figure 6**), the relevant activity was present bilaterally in the superior parietal gyri (SPG), anterior intraparietal sulci (aIPS), supramarginal gyri (SMG), and dorsal premotor cortices (PMd), as well as in the middle frontal gyrus (MFG) and supplementary motor complex (SMC) of the left hemisphere.

## DISCUSSION

While greater activity of the retrosplenial cortex during the planning to properly use a tool is consistent with its role in storing functional knowledge of manipulable objects (Canessa et al., 2008), this study demonstrates, for the first time, that the areas of significant signal modulations accompanying the planning to transmit a tool belong to the left-lateralized praxis representation network (PRN) mediating a wide range of visually-guided manual tasks (e.g., Jacobs et al., 2010; Kroliczak et al., 2008; Kroliczak & Frey, 2009).

The greater bilateral involvement of the ventral and dorsal divisions of superior parietal lobules and the left supplementary motor complex (SMA-preSMA) in controlling hand rotations for the most uncomfortable functional grasps is consistent with the reported contribution of these areas in the prospective planning of motor tasks, including substantial visuo-spatial processing (e.g., Van Elk et al., 2012; Makoshi et al., 2011).

All in all, our results provide convincing evidence for the intention-dependent engagement of the key subdivisions of praxis representation network that is not specific to tool-use actions.

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