Journal of the International Neuropsychological Society (2018), **24**, 1013–1025
Copyright © INS. Published by Cambridge University Press, 2018.
doi:10.1017/S1355617718000590

Decoding Brain States for Planning Functional Grasps of Tools: A Functional Magnetic Resonance Imaging Multivoxel Pattern Analysis Study

Mikolaj Buchwald,[1] Łukasz Przybylski,[2] AND Gregory Króliczak[1]
[1]Action & Cognition Laboratory, Institute of Psychology, Faculty of Social Sciences, Adam Mickiewicz University in Poznań, Poland
[2]Section of Logic and Cognitive Science, Institute of Psychology, Faculty of Social Sciences, Adam Mickiewicz University in Poznań, Poland

(RECEIVED January 2, 2018; FINAL REVISION May 22, 2018; ACCEPTED May 28, 2018; FIRST PUBLISHED ONLINE September 10, 2018)

Abstract

Objectives: We used multivoxel pattern analysis (MVPA) to investigate neural selectivity for grasp planning within the left-lateralized temporo-parieto-frontal network of areas (*praxis representation network*, PRN) typically associated with tool-related actions, as studied with traditional neuroimaging contrasts. **Methods:** We used data from 20 participants whose task was to plan functional grasps of tools, with either right or left hands. Region of interest and whole-brain searchlight analyses were performed to show task-related neural patterns. **Results:** MVPA revealed significant contributions to functional grasp planning from the anterior intraparietal sulcus (aIPS) and its immediate vicinities, supplemented by inputs from posterior subdivisions of IPS, and the ventral lateral occipital complex (vLOC). Moreover, greater local selectivity was demonstrated in areas near the superior parieto-occipital cortex and dorsal premotor cortex, putatively forming the *dorso-dorsal* stream. **Conclusions:** A contribution from aIPS, consistent with its role in prospective grasp formation and/or encoding of relevant tool properties (e.g., potential graspable parts), is likely to accompany the retrieval of manipulation and/or mechanical knowledge subserved by the supramarginal gyrus for achieving action goals. An involvement of vLOC indicates that MVPA is particularly sensitive to coding of object properties, their identities and even functions, for a support of grip formation. Finally, the engagement of the superior parieto-frontal regions as revealed by MVPA is consistent with their selectivity for transient features of tools (i.e., variable affordances) for anticipatory hand postures. These outcomes support the notion that, compared to traditional approaches, MVPA can reveal more fine-grained patterns of neural activity. (*JINS*, 2018, *24*, 1013–1025)

Keywords: MVPA, Tool use, Affordances, Motor control, Praxis, Functional neuroimaging

INTRODUCTION

Our daily activities comprise of numerous actions involving tools. For these actions to be appropriate for object functions, quite refined neural processing must be invoked, along with retrieval of abstract knowledge on tools and their proper handling (Frey, 2007; Vingerhoets, 2014; see also Orban, 2016; Reynaud, Lesourd, Navarro, & Osiurak, 2016). Indeed, the activation of relevant tool and action concepts, as well as all the necessary perceptual processing and visuomotor transformations preceding real activities with tools must be performed, or at least orchestrated, within a specialized network of brain regions, often referred to as the praxis representation network (PRN; see Frey, 2008; Kroliczak & Frey, 2009). The temporo-parieto-frontal subdivisions of this network are commonly associated, respectively, with processing of object functionality, its incorporation into action plans, and conversion of the assembled information into deliberate motor acts (Andersen & Buneo, 2002; Beurze, de Lange, Toni, & Medendorp, 2007; Vingerhoets & Clauwaert, 2015). Yet, an often-neglected prerequisite of successful actions with tools is a proper grasp. The latter requires that the functional part of an object be distinguished from the remaining subdivisions of its structure, particularly its handle, whose spatial relation to the acting hand must be also appropriately computed. Put differently, even such simple tasks as grasping tools may already require quite sophisticated neural machinery (Przybylski & Kroliczak, 2017; see also McDowell, Holmes, Sunderland, & Schurmann, 2018).

The majority of earlier studies concerning the role of networks underlying skilled actions with functional objects have

---

Correspondence and reprint requests to: Mikolaj Buchwald, Instytut Psychologii UAM, ul. Szamarzewskiego 89, 60-568 Poznań, Poland. E-mail: mikolaj.buchwald@amu.edu.pl

focused almost exclusively on applying whole-brain, voxelwise, that is, mass-univariate, analyses to investigating neural underpinnings of pantomimed and/or real actions with tools, with the grasp component typically missing (Hermsdorfer, Terlinden, Muhlau, Goldenberg, & Wohlschlager, 2007; Johnson-Frey, Newman-Norlund, & Grafton, 2005; Valyear, Gallivan, McLean, & Culham, 2012; Vingerhoets, Vandekerckhove, Honore, Vandemaele, & Achten, 2011; see also Brandi, Wohlschlager, Sorg, & Hermsdorfer, 2014; Kubiak & Kroliczak, 2016; Marangon, Kubiak, & Kroliczak, 2016; Mizelle, Kelly, & Wheaton, 2013).

Notably, even in studies using univariate approaches with their subtraction of neural signals from control conditions, region of interest (ROI) analyses of percent signal change capitalize on neural activity averaged across a vector of voxels. Nevertheless, an increasing trend has been recently observed for analyzing neuroimaging data and interpreting their results in terms of patterns of activity (Fabbri, Stubbs, Cusack, & Culham, 2016; Gallivan, McLean, Valyear, Pettypiece, & Culham, 2011; Gertz, Lingnau, & Fiehler, 2017; see also Shay, Chen, Garcea, & Mahon, 2018). Such approaches provide additional explanatory power (Quadflieg et al., 2011) and allow for characterizing neural representations as synchronized signal fluctuations (Haxby, Connolly, & Guntupalli, 2014; Norman, Polyn, Detre, & Haxby, 2006). Namely, while in univariate analyses each voxel is treated independently, multivariate analyses typically reveal information encoded in a distributed manner across many voxels.

Indeed, this technique is known as multivoxel pattern analysis (MVPA) because signals from multiple spatial locations serve as inputs to (multivariate) models, whereas in mass-univariate tests information is analyzed for each voxel separately, and often combined into clusters of activity at the latest stages of analyses. Therefore, here we tested potential advantages of MVPA on data from a recent study conducted in our lab (Przybylski & Kroliczak, 2017), with the latter based mainly on the outcomes from the univariate, subtraction method.

Przybylski and Kroliczak (2017) ran an fMRI study to investigate brain regions involved in processing visual and visuo-motor signals associated with preparation of functional grasps of tools. The stimuli were pictures of objects and the task was to plan and subsequently pantomime a proper grip. Planning functional grasps of tools was contrasted with planning grasps for control non-tool wooden objects (such as rods, sticks, etc.), with exemplars across both categories matched for their sizes and/or shape complexities.

The obtained results were such that regardless of the hand involved in planning functional grasps, the activity within the left-lateralized PRN complex was observed. This was rather surprising given that PRN is typically associated with the control of tool use gestures/actions, not the sole functional grip *per se*. Notably, such results are consistent with theoretical frameworks provided by ecological psychology (Gibson, 1977), wherein visuospatial processing of an object, affordances such as grasp, and action execution are largely inseparable (cf. Osiurak, Rossetti, & Badets, 2017).

Using Przybylski and Kroliczak's (2017) data and MVPA, here we tested where and how neural response patterns encode grasp planning information, and whether multivariate analyses corroborate outcomes from the univariate subtraction technique previously used. After all, it is often suggested that MVPA provides more "fine-grained" outcomes (Kriegeskorte, Goebel, & Bandettini, 2006). From a broader perspective, especially in the light of the forthcoming brain-machine interface possibilities, it is essential to study preparatory neural mechanisms preceding common intentional actions. In this fast-developing field of research and its applications, an advantage of decoding-based approaches over measuring differences between means seems indisputable (Andersen, Musallam, & Pesaran, 2004; Haynes & Rees, 2006).

METHODS

Participants

Data from 20 healthy participants identical to those from a study by Przybylski and Kroliczak (2017) were used in this report: they were all native Polish-speaking students (10 females; age 19 to 24 years; mean = 22.7; $SD = 1.6$), right-handed (Edinburgh Handedness Inventory index: $M = 92.9$; $SD = 13.9$; Oldfield, 1971), with normal or corrected to normal visual acuity. Written informed consent was obtained from each individual. After the study participants were compensated financially for their time and effort, and were debriefed. All protocols and procedures, which conformed to the principles of the 2013 WMA Helsinki Declaration, were approved by the Bio-Ethics Committee at Poznan University of Medical Sciences.

Stimuli

Photographs of 12 tools were used as stimuli. Each object was shown in the foreshortened perspective, that is, as if the viewer was standing in the front of the table on which an object was laid down. The experimental stimuli were chosen from kitchen, workshop and garden tools (see examples in Figure 1A, left panel). Control objects were pictures of 12 wooden pieces, such as parts of the branches or man-made wooden sticks (see Figure 1A, right panel). Although all the stimuli were well-known common objects, before the study participants were familiarized with them and with all the tasks to be performed during experiment proper. Graspable parts of tools and control stimuli were matched for size and/or complexity and were not expected to contribute to the observed variance as a confounding factor. Each object was presented in one of three different views (orientations), which within each category of objects assured no differences in task difficulty for the grasping hand (left or right). Because in their original report Przybylski and Kroliczak (2017) demonstrated that the greater engagement of the parieto-frontal networks for tools was observed regardless of object

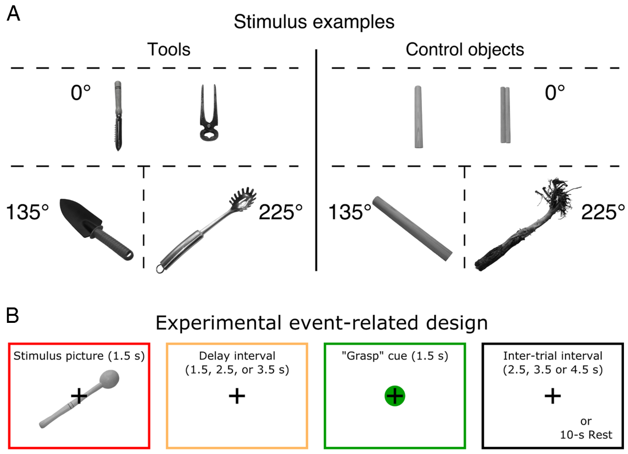

Fig. 1. Examples of stimuli and an experimental paradigm (adapted with permission of Cambridge University Press from Przybylski & Kroliczak, 2017). (A) The two classes of stimuli and their orientations. The functional items were simple tools (left panel) and control stimuli were wooden pieces and branches (right panel). Each object was presented at three different orientations: 0°, 125°, and 225°. (B) A schematic of an event-related paradigm used in this study. The grasp-planning phase started with stimulus onset and lasted for a variable interval of 3, 4, or 5 s. Subsequently, participants pantomimed the preplanned grasp for the duration of the "Grasp" cue (1.5 s). A trial was pseudo-randomly followed by either a variable inter-trial interval (ITI of 2.5, 3.5, or 4.5 s) or a period of 10-s rest.

orientation, the orientation factor was omitted in the current analyses.

Procedure

On two separate (typically consecutive) days, volunteers participated in two scanning sessions wherein they performed the task with their right (dominant) or left (non-dominant) hands, with the order of the tested hand counterbalanced. In an event-related paradigm, a varying ISI (0.0, 0.25, 0.5, or 0.75 s) was introduced at the beginning of each trial to jitter the stimulus onset with respect to the acquisition of a functional volume, therefore, artificially improving temporal resolution of the fMRI scans (Miezin, Maccotta, Ollinger, Petersen, & Buckner, 2000). Subsequently, the stimulus picture was displayed on the screen for 1.5 s, which coincided with the beginning of the grasp-planning phase, lasting for additional 1.5, 2.5, or 3.5 s following stimulus offset (3, 4, or 5 s in total).

Then, the "Grasp" cue (green circle) was shown for 1.5 s and participants' task was to pantomime the preplanned grasp, either functional or control, for tools or non-tools, respectively. A given trial concluded with an inter-trial interval of 2.5, 3.5, or 4.5 s, or a 10-s rest period. The protocol schematic is illustrated in Figure 1B. Grasp-planning activity in both conditions was modeled as the 3-s period beginning with the onset of the stimulus picture (displayed for 1.5 s) and lasting through the end of the shortest (1.5-s) delay interval (an approach inspired by Kroliczak & Frey, 2009).

Data Acquisition

Siemens 3 Tesla MAGNETOM Trio MRI scanner in the Laboratory of Brain Imaging (http://lobi.nencki.gov.pl) in Warsaw, Poland, was used to perform imaging with a 32-channel head coil. For better slice prescriptions, before functional runs, Auto Align Scout and True FISP sequences were applied. T_2^*-weighted gradient echo sequence was used to acquire blood-oxygen-level-dependent (BOLD) echo-planar images: time repetition (TR) = 2000 ms; time to echo (TE) = 30 ms; flip angle (FA) = 90°; 64 × 64 matrix; field of view (FOV) = 200 mm; 34 contiguous axial slices; 3.1-mm isotropic voxels (each run consisted of 145 such volumes).

We also acquired T_1-weighted structural images using magnetization prepared rapid gradient echo (MP-RAGE) pulse sequence: TR = 2540 ms; TE = 3.32 ms; inversion time (TI) = 1200 ms; FA = 7°; 256 × 256 voxel-matrix; FOV = 256 mm; 176 contiguous axial slices; 1.0-mm isotropic voxels. Additionally, to improve registration between native space (functional echo planar images) and anatomical T_1-weighted scans, T_2-weighted structural images were collected: TR = 3200 ms; TE = 402 ms; FA = 120°; 512 × 512 voxel-matrix; FOV = 256 mm; 176 contiguous axial slices; 0.5 × 0.5 × 1.0 mm non-isotropic voxels. We converted raw data to NIfTI-1 format using MRI-Convert software (http://lcni.uoregon.edu/downloads/mriconvert).

Preprocessing

Functional data were preprocessed using FSL (FMRIB's Software Library) (https://fsl.fmrib.ox.ac.uk/fsl/fslwiki), with the following procedures: brain extraction (BET), motion correction (MCFLIRT), and high-pass filtering ($\sigma = 50.0$ s). No spatial smoothing was used. Because the main task always consisted of five functional runs per hand, and the analysis was performed separately for each hand, as well as compared across subjects and/or hands, all runs were co-registered (using FLIRT) to common space, i.e., the middle volume of the first functional run. The very same reference (i.e., middle) volume was also spatially normalized (using matrices from the registration of the first run) to the MNI 152 2-mm standard space trough initial, high-resolution T_2-weighted and standard T_1-weighted structural images. All the operations were performed with either FSL FEAT (FMRI Expert Analysis Tool) v5.0.9 (Jenkinson, Beckmann, Behrens, Woolrich, & Smith, 2012) or its subcomponents and commands. The same anatomical data and processing procedures as in Przybylski and Kroliczak (2017) were used for spatial registration of the structural (T_2- and T_1-weighted) images.

MVPA

Because a fast event-related design was used in this experiment, parameter estimates (PEs) for each trial had to be calculated first. To this end, a general linear model (GLM) was created separately for each trial using the least squares-separate approach (LS-S, for details see: Mumford, Turner, Ashby, & Poldrack, 2012). Each GLM was created for every trial within each run, every time with two explanatory variables: the first for the trial of interest, and the second for all the remaining other trials within a given run. Specifically, as there were 12 trials per condition during one functional run (i.e., 24 trials in total per run) then 24 GLMs were created to obtain one PE for each trial (24 × 5 runs, which gives 120 matrices of *beta* values altogether). Motion parameters, cerebrospinal fluid, and white-matter time series were used as additional regressors. PEs were not normalized before the multivariate analysis. (We would have considered normalizing PEs if the outcomes just replicated the univariate results; cf. Misaki, Kim, Bandettini, & Kriegeskorte, 2010). The two classified conditions were: (1) planning functional grasps of tools; and (2) planning control grasps of non-tool objects. In other words, planning of tool-oriented grasps was always classified against planning grasps of non-tools.

Subsequently, the *n*-fold cross-validation method was used, where *n* was the number of runs (an approach often called *leave-one-run-out* method). We evaluated classifier performance using the accuracy metric. Because the number of trials per condition was equal, there was no risk of the accuracy paradox. As there were 12 trials per condition for one run, and five runs in total, each fold of the validation consisted of 96 PEs (12 × 2 × 4; trials × conditions × runs) for training the classifier and 24 (12 × 2 × 1; trials × conditions × run) PEs to test the accuracy of the classification. This operation was performed five times, and the classification accuracies were averaged (with arithmetic mean). This way the single accuracy score was obtained per each hand for each participant in a range of 0.0 to 1.0 (i.e., 0% to 100%). MVPA classification was performed with the support vector machine (SVM)-based classifier (linear kernel, *C* parameter fixed at 1.0) implemented in Python's package scikit-learn (Abraham et al., 2014; http://scikit-learn.org/stable), *via* the nilearn module (http://nilearn.github.io).

ROI Selection

Based on previous research, 12 left-hemispheric ROIs were selected: (1) human intraparietal area 1 (hIP1); (2) dorsal intraparietal sulcus, anterior division (DIPSA); (3) dorsal intraparietal sulcus, medial division (DIPSM); (4, 5, and 6) supramarginal gyrus (its cytoarchitectonic subdivisions: PF, PFm, and PFt); (7) putative human homologue of the anterior intraparietal area (phAIP/aIPS); (8) superior parieto-occipital cortex (SPOC); (9) ventral premotor cortex (PMv); (10) dorsal premotor cortex (PMd); (11) caudal middle temporal gyrus (cMTG), and (12) rostral middle frontal gyrus (rMFG). Additionally, one control (13th) region was included in the analysis, namely, the right lateral ventricle (rLV). For more detailed information on the sources of all ROIs, see Table 1. The borders of the ROIs mapped to the inflated and flat brain surfaces are shown in Figure 2.

Before MVPA, ROIs were transformed from standard space (MNI152 2mm) to individual subjects' native spaces using FLIRT (with transformation matrices obtained during a preprocessing step, from the middle volume of the first functional run, through T_2- and T_1-weighted images, see the *Preprocessing* section). The values from voxels (*beta weights*) within the range of respective masks were used for training and testing the classifier.

ROI *t* Tests

For the following *t* test statistical procedures classification scores were averaged (with arithmetic mean) across validation folds; hence there were 20 (number of participants)

Table 1. Regions of interest used in the analysis

No.	Region	Source	No. of voxels
1.	hIP1	Choi et al., 2006, Durand, Peeters, Norman, Todd, & Orban, 2009	93
2.	DIPSA	Orban, Van Essen, & Vanduffel, 2004	161
3.	DIPSM		203
4.	PF	Cytoarchitectonic subdivisions of SMG; see Caspers et al., 2006	399
5.	PFm		400
6.	PFt		236
7.	phAIP	Binkofski et al., 1998, and Orban et al., 2004	293
8.	SPOC	Hutchison, Culham, Flanagan, Everling, & Gallivan, 2015	1120
9.	PMd	Kroliczak & Frey, 2009	660
10.	PMv		135
11.	cMTG		239
12.	rMFG		530
13.	rLV	Harvard-Oxford Subcortical Atlas from FSL (95% prob. threshold)	50

Note. The number of voxels was calculated for ROIs in MNI 152 brain template. The sizes of the ROIs in individual subjects' native spaces varied depending on structural differences. See Figure 2 for the visualization on the brain surfaces.
hIP1 = human intraparietal area 1; DIPSA = dorsal intraparietal sulcus, anterior division; DIPSM = dorsal intraparietal sulcus, medial division; PF, PFm, PFt = supramarginal gyrus (SMG) subdivisions; phAIP = putative human homologue of the anterior intraparietal; SPOC = superior parieto-occipital cortex; PMv = ventral premotor cortex; PMd = dorsal premotor cortex; cMTG = caudal middle temporal gyrus; rMFG = rostral middle frontal gyrus; rLV = right lateral ventricle.

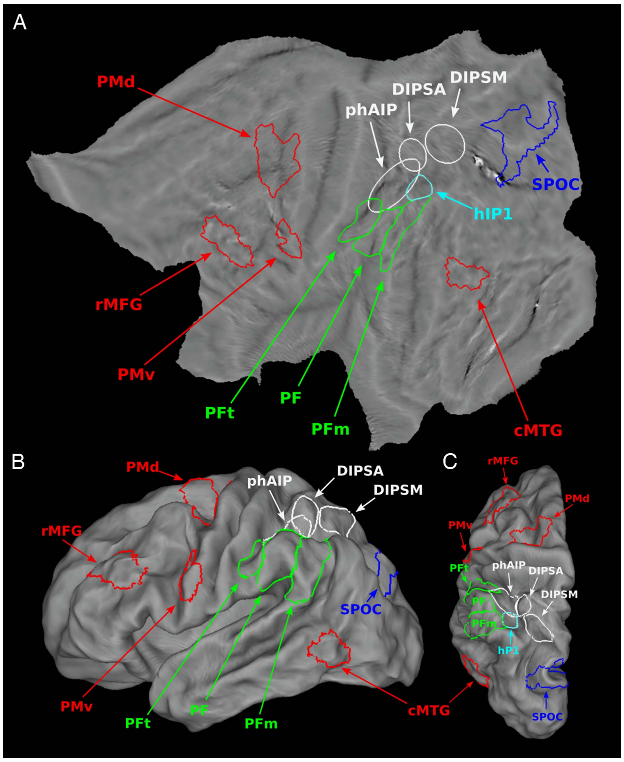

Fig. 2. ROIs shown on: (A) the flattened brain surface, (B) the partly inflated lateral, and (C) dorsal surface of the left hemisphere. hIP1, human intraparietal area 1; DIPSA, dorsal intraparietal sulcus, anterior division; DIPSM, dorsal intraparietal sulcus, medial division; PF, PFm, PFt, supramarginal gyrus subdivisions; phAIP, putative human (homologue of the) anterior intraparietal area; SPOC, superior parieto-occipital cortex; PMv, ventral premotor cortex; PMd, dorsal premotor cortex; cMTG, caudal middle temporal gyrus; rMFG, rostral middle frontal gyrus; rLV, right lateral ventricle. The sizes of the ROIs in individual subjects' native spaces varied depending on structural differences.

values per ROI. To assess statistical significance of the decoding within the functional ROIs, a one-sample *t* test was run across participants (separately for each hand) with respect to 50% chance level. This was followed by Bonferroni correction for multiple comparisons (25 tests in total, i.e., 2 tests per hand for 12 functional ROIs and 1 for the control site).

Furthermore, to provide more exact information about the actual contribution of the particular region, the performance of each hand within each ROI was contrasted with the corresponding results for our control ROI (rLV), whose classification accuracy was averaged across hands before the *t* tests. The comparison was achieved by running 24 Bonferroni-corrected paired *t* tests (12 for the dominant hand and 12 more for the left hand). Finally, we opted for determining which of the ROIs differed in terms of classification accuracies depending on whether the action was planned for the dominant or non-dominant hand. Since the accuracy scores within binary independent variable were tested, *p*-values were not adjusted for multiple comparisons in this case.

Before *t* tests, we conducted two-sigma outlier detection and normality assessment with Shapiro-Wilk test. All statistical procedures within this section were carried out with Python's SciPy module, v. 0.19.0 (Oliphant, 2007), with corrections for multiple tests performed with StatsModels, v. 0.6.1 (Seabold & Perktold, 2010).

Searchlight Analysis

In addition to ROI analyses, a whole-brain searchlight procedure was also applied to reveal further nodes of the network (brain areas specific to the planning of functional grasps of tools) and/or to validate the results obtained with the ROIs from earlier analyses. A radius of 5.6 mm around the voxel of interest was the spherical region for each searchlight classification (with SVM classifier and *C* parameter at 1.0). Cross-validation was the same as for ROI decoding (*n*-fold cross validation). The resulting five scores ($5 \times k$ matrix) per participant and per hand were averaged (arithmetic mean) to create a single vector of variables, of the length *k* (where *k* was the number of voxels in particular subject's native space). The resulting maps (one for each of the 20 participants) were then spatially transformed with registration matrices from the first functional run to the MNI152 2-mm standard atlas.

A second-level searchlight analysis was performed by: (1) combining the first-level brain maps (individual participant's results) with one sample *t* test (null hypothesis being that the classification is at 50% chance level), for the right and left hand separately; (2) a direct comparison between the right and left hand, with a paired *t* test. The outcomes of both contrasts were subsequently corrected for multiple comparisons with the Bonferroni method.

RESULTS

ROI *t* Test Results

Significant classifications against chance level for each ROI and for each hand separately are depicted in Figure 3 as red asterisks. Except for rLV, the results from all ROIs were significantly different from chance ($\alpha = 0.05$). Notably, significance levels achieved for the studied regions ranged from $1*10^{-3}$ to $5*10^{-10}$. The lowest *p*-values were obtained within PMd, DIPSM, and phAIP. The least probable effects were observed in the PMv, PFm, cMTG, rMFG, and hIP1. Using nonparametric permutation tests (Etzel, 2017) rather than *t* tests yielded qualitatively similar results.

When praxis-related ROIs were compared to the reference area, all but one (rMFG) showed statistically significant differences at least at $p < .05$ (regardless of the hand). These results are marked with blue asterisks on the graph in Figure 3. All *t* test comparisons within ROIs (between hands) turned out to be statistically non-significant.

Searchlight Analysis Results

This analysis revealed that the information required to decode planning functional grasps of tools is processed mainly in the

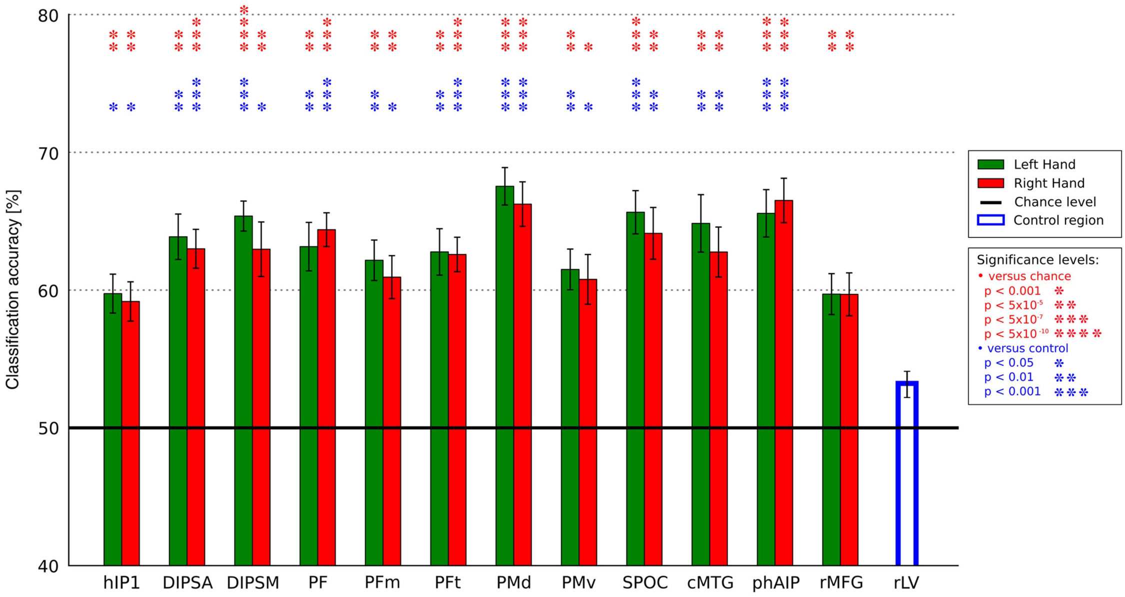

Fig. 3. The results of the ROI analyses. Green bars (left ones) represent mean accuracy scores for the left-hand, and red ones for the right hand (averaged, with arithmetic mean, across folds and subjects). Red asterisks (upper set) indicate statistically significant differences with respect to chance level (at 50%) as measured with two-tailed one-sample *t* tests. The significance against the control region (rLV, the last bar on the right with thick blue borders) is denoted by blue asterisks (lower set), the results of pairwise *t* test comparisons. Error bars are standard errors of measurement. Thick, solid, black horizontal line represents the chance level. Abbreviations as in Figure 2.

left cerebral hemisphere (regardless of the hand). Yet, when participants were asked to plan grasps with their dominant hand, the pattern of statistically significant voxels included: (1) PMd, extending to the superior frontal gyrus (SFG); (2) SPOC vicinity, extending to the dorsal IPS; (3) small clusters within SMG (PFt, PF); as well as additional locations in (4) area V3, LO1 and the ventral lateral occipital complex (vLOC), and (5) the supplementary motor area (SMA). These effects are visualized in Figure 4A. Right-hemispheric voxels were located mainly in: (1) vLOC; (2) antero-dorsal precuneus; (3) dorsal IPS (including DIPSA/DIPSM); (4) PF; and (5) three small clusters in superior frontal cortices (Figure 4B).

For functional grasp planning with the left-hand, the left-hemisphere statistically significant patterns were found in: (1) PMd; (2) phAIP/aIPS; (3) DIPSA, DIPSM; (4) small clusters in PFt and PFm; and (5) vLOC. For activity patterns see Figure 5A. In the right hemisphere, the most important clusters were located in: (1) DIPSA and DIPSM; (2) PMd; (3) PFt; and (4) vLOC (see Figure 5B). A direct comparison between maps for the two hands (treated as dependent groups) with paired *t* test revealed no statistically significant results.

Figure 2, Figure 4, as well as Figure 5 were generated using the Caret software (https://www.nitrc.org/projects/caret/; Van Essen et al., 2001). To enable comparisons of our results with future studies that will use the Connectome Workbench (a potential standard) in data visualization (https://www.humanconnectome.org/software/connectome-workbench; Marcus et al., 2011), in Figure 6, we also mapped our searchlight patterns onto its inflated (midthickness) and flat surfaces, emphasizing the associated areas (of the 180 identified and delineated parcellations; Glasser et al., 2016). Only the surfaces of the left hemisphere, typically associated with praxis skills, were used to map these results.

DISCUSSION

The outcomes obtained with MVPA are in substantial agreement with earlier studies demonstrating that the control of praxic skills is primarily left lateralized and involves the occipito-temporal, as well as parieto-frontal subdivisions of PRN (Frey, 2008; see also Kristensen, Garcea, Mahon, & Almeida, 2016; Przybylski & Kroliczak, 2017; Vingerhoets & Clauwaert, 2015). This network of areas, with SMG as its central node, is typically associated with representing manipulation knowledge (Buxbaum, 2001; Buxbaum & Kalenine, 2010; cf. Goldenberg, 2017; Lesourd, Osiurak, Navarro, & Reynaud, 2017) or mechanical knowledge (Goldenberg & Hagmann, 1998; Osiurak et al., 2009; Osiurak, Jarry, Lesourd, Baumard, & Le Gall, 2013; see also Lesourd, Budriesi, Osiurak, Nichelli, & Bartolo, 2017) linked to object functionality, and its integration into action plans for programming of deliberate motor responses (Bernier, Cieslak, & Grafton, 2012; Fabbri et al., 2016; Gallivan et al., 2011).

The observed left-brain bias, revealed regardless of the used hand, indicates that PRN contains hand-independent representations of praxis skills (Kroliczak, Piper, & Frey, 2016). Nevertheless, MVPA exposed greater contributions from aIPS, an area linked to the control of grasping movements (e.g., Cavina-Pratesi, Goodale, & Culham, 2007; Kroliczak, McAdam, Quinlan, & Culham, 2008), and vLOC, associated with encoding visual characteristics of tools, their concepts, and the retrieval of their function-relevant features

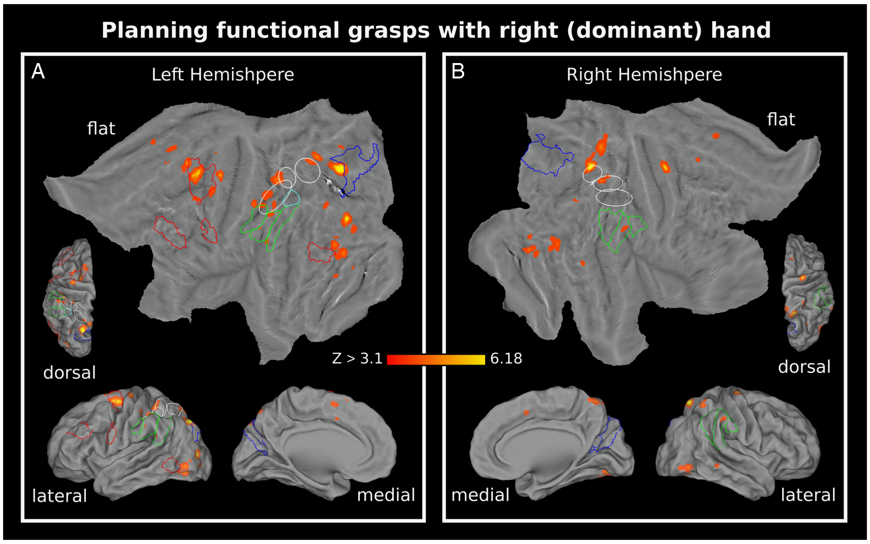

Fig. 4. The results of searchlight analysis for functional grasp planning with the right hand. Specifically, this figure depicts statistically significant decoding accuracies of planning functional grasps of tools *versus* non-tools. The unit with the red-yellow bar is a *Z*-score (standardized t-score, from one-sample *t* test across subjects against 50% prior chance decoding accuracy, corrected for multiple comparisons with Bonferroni method at $p < .05$) and thresholded at 3.1 value. Names of the ROI borders mapped to the left hemisphere surface can be found in Figure 2. Right-hemisphere ROIs are shown here for convenience. These are as follows: SPOC (blue; left upmost), DIPSM, DIPSA, phAIP (white, top to bottom; between SPOC and PF complex); PFm, PF and PFt (green, left to right; bottom cluster of borders).

(e.g., Bracci, Cavina-Pratesi, Ietswaart, Caramazza, & Peelen, 2012; Garcea & Mahon, 2014; Nastase et al., 2017; Oosterhof, Wiggett, Diedrichsen, Tipper, & Downing, 2010; see also Peelen et al., 2013; Wurm & Lingnau, 2015).

Core Areas for Planning Functional Grasps

Praxis-related literature emphasizes the importance of left aSMG as the core region responsible for the integration of signals from posterior SMG, IPS, as well as from the tempo-occipital cortices (e.g., Orban & Caruana, 2014; Peeters, Rizzolatti, & Orban, 2013), thus playing a critical role in motor cognition. However, MVPA results obtained here for functional grasp planning highlight the role of aIPS and vLOC, the two areas that likely provide prerequisite inputs to SMG for performing actions with tools. Indeed, these outcomes are consistent with a notion that manipulation knowledge is supported by perceptual representations in the

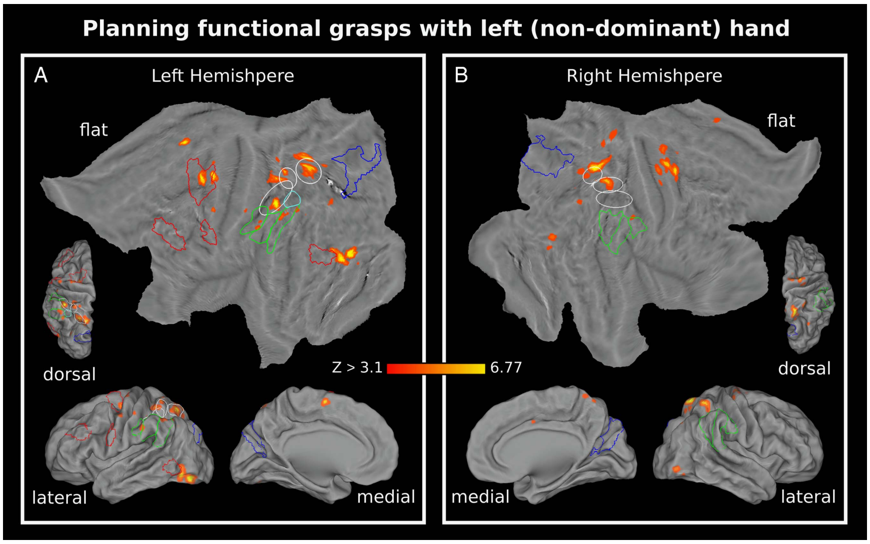

Fig. 5. The results of searchlight analysis for functional grasp planning with the left hand. As before (Figure 4), this figure depicts statistically significant decoding accuracies of planning functional grasps of tools *versus* non-tools. The units are *Z*-scores from one-sample *t* test against 50% chance level, corrected for multiple comparisons with Bonferroni method at $p < .05$ and thresholded at 3.1 value. For ROI names see Figure 2 (left hemisphere) and Figure 4 (right hemisphere).

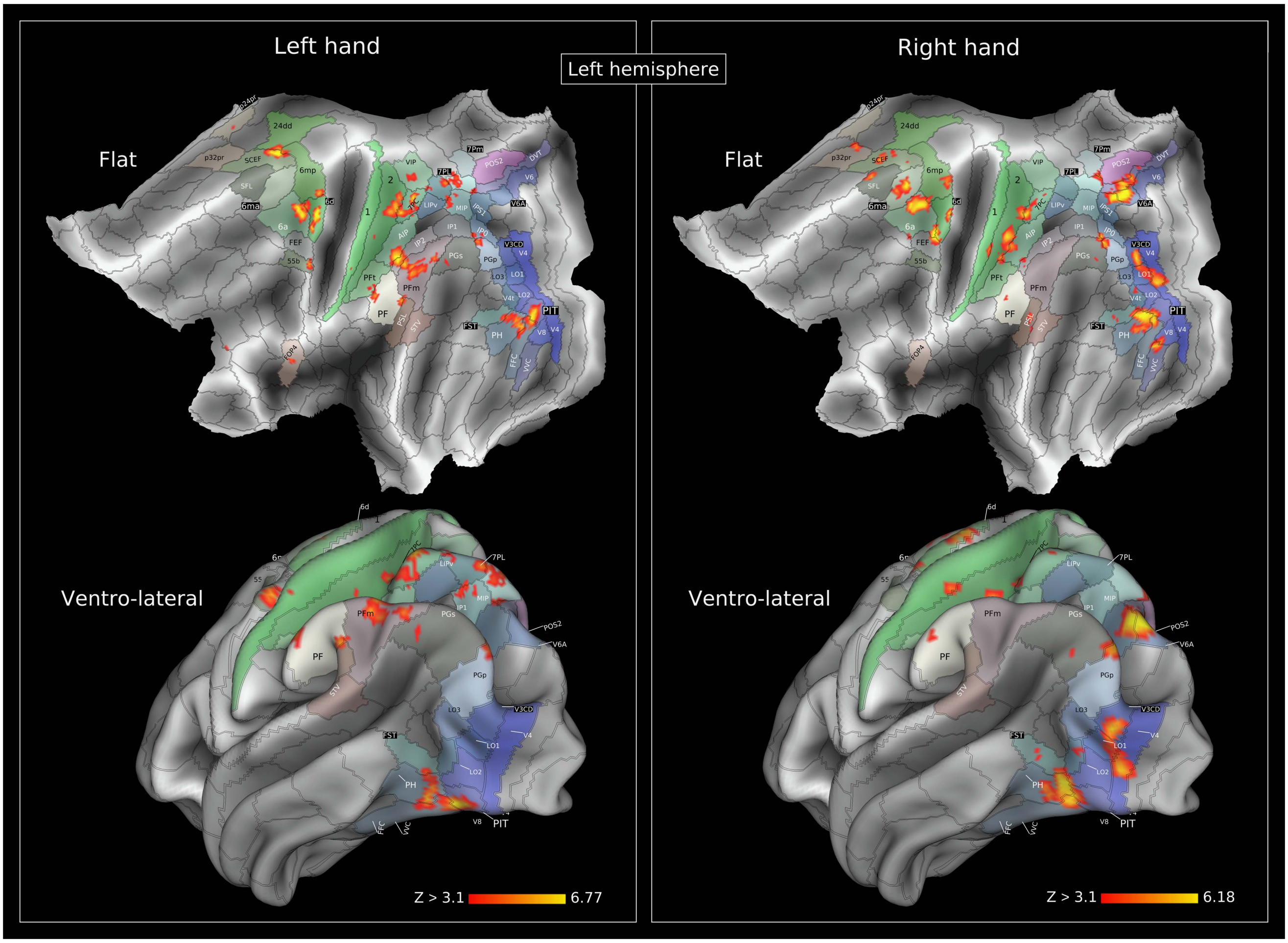

Fig. 6. MVPA results displayed on flat and inflated (midthickness) surfaces from the Connectome Workbench (v. 1.2.3.) visualization software (Glasser et al., 2016) of the Human Connectome Project (HCP). The borders of 180 areas from the HCP's parcellation are also shown, and the critical ones provided with their labels (which are described in details in Supplemental Materials for Glasser et al., 2016).

ventral stream (e.g., Almeida, Fintzi, & Mahon, 2013; Mahon, Kumar, & Almeida, 2013; see also Gallivan, Cant, Goodale, & Flanagan, 2014), and their projections to SMG interact with manipulation-based action representations stored or elaborated there (Buxbaum, 2017; cf. Osiurak & Badets, 2016; Reynaud et al., 2016). In this framework, vLOC would also contribute to object *parsing*, including identification of functional and graspable subdivisions, thus allowing aIPS to concentrate almost exclusively on processing object handle(s)/graspable part(s).

It is of note, however, that both our earlier study (Przybylski & Kroliczak, 2017) and the current outcomes indicate that the traditionally defined cMTG (e.g., Kroliczak & Frey, 2009; see also Garcea, Kristensen, Almeida, & Mahon, 2016; Vingerhoets, Nys, Honore, Vandekerckhove, & Vandemaele, 2013) was barely involved in the planning of functional grasps. Indeed, regardless of the hand, the multivoxel patterns of brain activity were observed only in the nearby occipital cortex. Yet, overlapping clusters in very similar locations have been shown to respond both to tools and hands (Bracci, Ritchie, & de Beeck, 2017; Striem-Amit, Vannuscorps, & Caramazza, 2017) and were also reported engaged in some aspects of matching of hand posture to object orientation (Vingerhoets et al., 2013), a kind of processing that could be considered a prerequisite of further interactions with tools. All things considered, planning functional grasps of tools requires the reasoning about object properties associated with activity within vLOC and SMG subdivisions putatively interacting with it, as well as integrating signals from aIPS (Chao & Martin, 1999; Grill-Spector & Weiner, 2014; Orban & Caruana, 2014).

Although MVPA reveals some local differences in activity patterns observed in areas PFt, PF, and PFm between hands (see Figure 7A–D), a direct between-hands contrast convincingly demonstrates that the neural underpinnings of higher-order actions should be virtually identical. The results of ROI analyses (e.g., PFt, PF, and PFm ROIs in Figure 3) are consistent with this notion. Nevertheless, in individuals with somewhat atypically represented praxic functions this relationship may change and the extent of neural activity accompanying the use of the better-trained or the dominant hand may show closer affinity to the degree and direction of handedness (e.g., Dassonville, Zhu, Uurbil, Kim, & Ashe, 1997; cf. Drager et al., 2004; Biduła, Przybylski, Pawlak, &

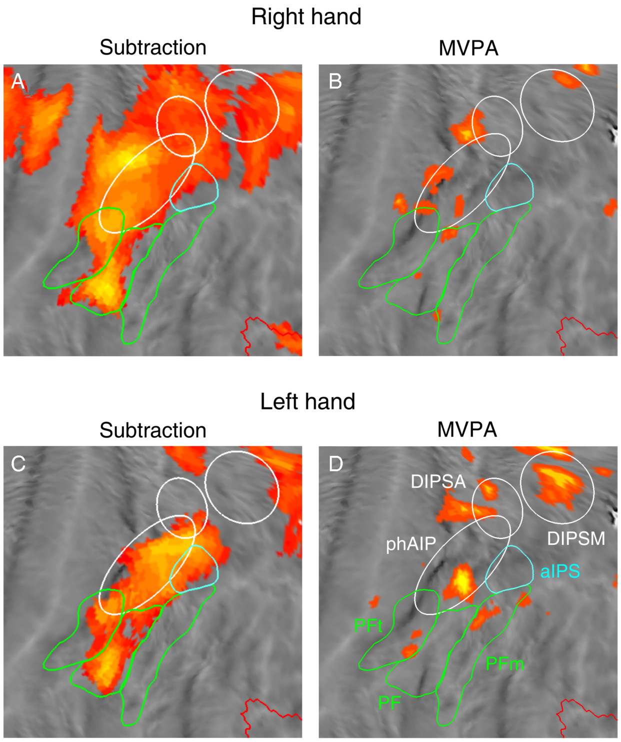

Fig. 7. Subdivisions of left inferior parietal lobule and their involvement in planning functional grasps as revealed by traditional (contrast) analyses and MVPA. The outcomes are shown on flat brain surfaces using Caret software. The outcomes for the right hand: (A) activity patterns adopted from a study by Przybylski and Kroliczak (2017) and (B) the multivoxel patterns of brain activity from the searchlight analysis (MVPA). The outcomes for the left hand: (C) activity patterns from a study by Przybylski and Kroliczak (2017) and (D) the multivoxel patterns of brain activity from the current analysis (MVPA).

Kroliczak, 2017; see also Kroliczak, Buchwald, Potok, & Przybylski, 2018).

In sum, the current outcomes obtained with MVPA are consistent with the notion that transformations of object-related information into goal-directed actions are computed across a much broader range of brain areas or regions (Gallivan & Culham, 2015), even if actions are limited to planning functional grasps. Nevertheless, it should be mentioned that the task used here, that is, participants planned and executed pantomimed functional grasps, does not necessarily invoke typical visuomotor (i.e., dorsal stream; Goodale & Milner, 1992) mechanisms for reach-to-grasp actions directed at objects under guidance of visual feedback in real time (Kroliczak, Cavina-Pratesi, Goodman, & Culham, 2007; Gallivan, McLean, Valyear, & Culham, 2013; Freud et al., 2018).

Instead, a greater contribution from the ventral stream would be expected (Goodale, Jakobson, & Keillor, 1994; Rossit et al., 2011), particularly because pantomimed grasps resembled manual estimations (Kroliczak, Westwood, & Goodale, 2006), although taking into account the requisite hand rotations. Yet, the stimuli were functional objects, and adaptive behavior in their presence requires contributions of the dorsal and ventral streams (Goodale, Kroliczak, & Westwood, 2005), with numerous functional subdivisions of the former. The remaining clusters will be discussed next.

Remaining regions

MVPA also revealed the involvement of several further regions in transforming visual information into plans for functional grasps of tools. Although the greater engagement of these auxiliary areas in the more demanding actions incorporating tools is not surprising, it is unlikely that their contribution to task performance is tool specific.

Neural activity within IPS (namely phAIP, DIPSA, and/or DIPSM) is consistent with an idea that IPS does not code the detailed movement kinematics but rather the to-be-obtained action goals (Hamilton & Grafton, 2008). Yet another reason for its involvement is the fact that a tool's handle affords "a grasp" more noticeably than a corresponding part in the control (non-tool) object (Vingerhoets, 2014).

Another vicinity revealed with MVPA was PMd, which is often associated with neural underpinnings of the preparation and control of visuomotor processes involving task-response associations and action sequencing (Cross, Hamilton, Cohen, & Grafton, 2017). PMd also belongs to the *dorso-dorsal* stream, composed of the V6/V6A–dorso-medial intraparietal–PMd circuit (Rizzolatti & Matelli, 2003). A contribution from all these nodes was revealed by our analysis. Although it has been speculated that this circuit is involved in on-line control of actions (Binkofski & Buxbaum, 2013; see also Milner & Goodale, 2008), the on-line component does not extend here to the actually performed manual tasks but a mere preparation for them. This outcome is consistent with the postulated contribution of the *dorso-dorsal* stream in processing *variable affordances*, that is temporary and/or transient object characteristics such as changes in their orientation, size or shape, and the required adjustments of grip/arm rotation for the task at hand (Kroliczak et al., 2008; Sakreida et al., 2016).

Notably, while the PMd contribution was substantial, the SPOC vicinity was underrepresented here. Yet, the stimuli were not within reach (they were pictures on the screen) and, again, the mechanisms involved in pantomimed grasp planning (whether functional or not) can be different from preparation for real reaching and grasping (Gallivan, Cavina-Pratesi, & Culham, 2009). Furthermore, these objects were not presented in lower visual fields, which are preferentially processed for hand actions by SPOC (Rossit, McAdam, McLean, Goodale, & Culham, 2013). Nevertheless, our results are quite consistent with recent outcomes revealing grater connectivity between cMTG/LOC and aIPS (Chen, Snow, Culham, & Goodale, 2018), with some contribution from the superior parietal lobule (SPL) in a contrast of tools *versus* non-tools (whether elongated or stubby). As in their study, the SPL activity we observed here, regardless of the hand used, extended toward SPOC.

SMA, typically associated with the control of visually guided movements (Picard & Strick, 2003) also contributed to planning functional grasps of tools. The patterns of neural activity elicited by such skilled motor acts (including finger sequencing) are often decoded most accurately within this area (Wiestler & Diedrichsen, 2013). Although grasp performance was pantomimed (with no further tool-use actions), the task nevertheless involved internally generated movement plans which also require SMA (Elsinger, Harrington, & Rao, 2006), whose inputs are critical in the process of predictive motor planning (cf. Makoshi, Kroliczak, & van Donkelaar, 2011).

Conclusions

The engagement of the temporo/occipital-parieto-frontal cortices in processing functional grasps of tools revealed by MVPA is largely consistent with the outcomes from traditional subtraction analyses. Nevertheless, the multivoxel patterns of brain activity, which are obtained with different theoretical and algorithmic framework from these that underlie subtraction contrasts, put greater emphasis on grasp coding in aIPS, the occipito-temporal encoding of visual/structural and functional features of tools, as well as on sensorimotor, *dorso-dorsal* preparatory processes, rather than on the integrative role of aSMG.

The ventral occipital regions may provide auxiliary inputs for grip formation and the retrieval of critical, tool-related knowledge on their invariant features, that is, stable affordances, that underlie reasoning about tool properties based on manipulation and mechanical knowledge most likely stored in left SMG. All in all, MVPA is a reliable technique that may greatly enrich our understanding of information processing preceding any functional interactions with tools.

ACKNOWLEDGMENTS

The authors declare no conflict of interest. This work was supported by National Science Centre (Narodowe Centrum Nauki, NCN) grant *Maestro* 2011/02/A/HS6/00174 to Gregory Kroliczak. During all stages of this work M.B., Ł.P., and G.K. were also supported by the *Maestro* grant. The equipment used for data acquisition and analyses was funded by the Ministry of Science and Higher Education (Ministerstwo Nauki i Szkolnictwa Wyższego, MNiSW) grant 6168/IA/128/2012 to Gregory Króliczak. The CePT research infrastructure was purchased with funds from the European Regional Development Fund as part of the Innovative Economy Operational Programme, 2007–2013. Author contributions: This project was conceptualized by G.K., Ł.P., and M.B. Data were collected by Ł.P. and G.K., analyzed by M.B., and interpreted by M.B, G.K., and Ł.P. The manuscript was written by M.B. and G.K. The authors thank Guy Orban and David Van Essen for introducing us to new methods of parcellation and visualization of neuroimaging data.

REFERENCES

Abraham, A., Pedregosa, F., Eickenberg, M., Gervais, P., Mueller, A., Kossaifi, J., … Varoquaux, G. (2014). Machine learning for neuroimaging with scikit-learn. *Frontiers in Neuroinformatics*, *8*, 14. doi: 10.3389/fninf.2014.00014

Almeida, J., Fintzi, A.R., & Mahon, B.Z. (2013). Tool manipulation knowledge is retrieved by way of the ventral visual object processing pathway. *Cortex*, *49*(9), 2334–2344. doi: 10.1016/j.cortex.2013.05.004

Andersen, R.A., & Buneo, C.A. (2002). Intentional maps in posterior parietal cortex. *Annual Review of Neuroscience*, *25*, 189–220. doi: 10.1146/annurev.neuro.25.112701.142922

Andersen, R.A., Musallam, S., & Pesaran, B. (2004). Selecting the signals for a brain-machine interface. *Current Opinion in Neurobiology*, *14*(6), 720–726. doi: 10.1016/j.conb.2004.10.005

Bernier, P.M., Cieslak, M., & Grafton, S.T. (2012). Effector selection precedes reach planning in the dorsal parietofrontal cortex. *Journal of Neurophysiology*, *108*(1), 57–68. doi: 10.1152/jn.00011.2012

Beurze, S.M., de Lange, F.P., Toni, I., & Medendorp, W.P. (2007). Integration of target and effector information in the human brain during reach planning. *Journal of Neurophysiology*, *97*(1), 188–199. doi: 10.1152/jn.00456.2006

Biduła, S.P., Przybylski, L., Pawlak, M.A., & Kroliczak, G. (2017). Unique neural characteristics of atypical lateralization of language in healthy individuals. *Frontiers in Neuroscience*, *11*(525), 1–21. doi: 10.3389/fnins.2017.00525

Binkofski, F., & Buxbaum, L.J. (2013). Two action systems in the human brain. *Brain and Language*, *127*(2), 222–229. doi: 10.1016/j.bandl.2012.07.007

Binkofski, F., Dohle, C., Posse, S., Stephan, K.M., Hefter, H., Seitz, R.J., … Freund, H.J. (1998). Human anterior intraparietal area subserves prehension: A combined lesion and functional MRI activation study. *Neurology*, *50*(5), 1253–1259. doi: 10.1212/WNL.50.5.1253

Bracci, S., Cavina-Pratesi, C., Ietswaart, M., Caramazza, A., & Peelen, M.V. (2012). Closely overlapping responses to tools and hands in left lateral occipitotemporal cortex. *Journal of Neurophysiology*, *107*(5), 1443–1456. doi: 10.1152/jn.00619.2011

Bracci, S., Ritchie, J.B., & de Beeck, H.O. (2017). On the partnership between neural representations of object categories and visual features in the ventral visual pathway. *Neuropsychologia*, *105*, 153–164. doi: 10.1016/j.neuropsychologia.2017.06.010

Brandi, M.L., Wohlschlager, A., Sorg, C., & Hermsdorfer, J. (2014). The neural correlates of planning and executing actual tool use. *The Journal of Neuroscience*, *34*(39), 13183–13194. doi: 10.1523/JNEUROSCI.0597-14.2014

Buxbaum, L.J. (2001). Ideomotor apraxia: A call to action. *Neurocase*, *7*(6), 445–458.

Buxbaum, L.J. (2017). Learning, remembering, and predicting how to use tools: Distributed neurocognitive mechanisms: Comment on Osiurak and Badets (2016). *Psychological Review*, *124*(3), 346–360.

Buxbaum, L.J., & Kalenine, S. (2010). Action knowledge, visuomotor activation, and embodiment in the two action systems. *Annals of the New York Academy of Sciences*, *1191*, 201–218. doi: 10.1111/j.1749-6632.2010.05447.x

Caspers, S., Geyer, S., Schleicher, A., Mohlberg, H., Amunts, K., & Zilles, K. (2006). The human inferior parietal cortex: Cytoarchitectonic parcellation and interindividual variability. *NeuroImage*, *33*(2), 430–448. doi: 10.1016/j.neuroimage.2006.06.054

Cavina-Pratesi, C., Goodale, M.A., & Culham, J.C. (2007). FMRI reveals a dissociation between grasping and perceiving the size of real 3D objects. *PLoS One*, *2*, e424. doi: 10.1371/journal.pone.0000424

Chao, L.L., & Martin, A. (1999). Cortical regions associated with perceiving, naming, and knowing about colors. *Journal of Cognitive Neuroscience*, *11*(1), 25–35.

Chen, J., Snow, J.C., Culham, J.C., & Goodale, M.A. (2018). What role does "elongation" play in "tool-specific" activation and connectivity in the dorsal and ventral visual streams? *Cerebral Cortex*, *28*(4), 1117–1131. doi: 10.1093/cercor/bhx017

Choi, H.J., Zilles, K., Mohlberg, H., Schleicher, A., Fink, G.R., Armstrong, E., … Amunts, K. (2006). Cytoarchitectonic identification and probabilistic mapping of two distinct areas within the anterior ventral bank of the human intraparietal sulcus. *Journal of Comparative Neurology*, *495*(1), 53–69. doi: 10.1002/cne.20849

Cross, E.S., Hamilton, A.F.C., Cohen, N.R., & Grafton, S.T. (2017). Learning to tie the knot: The acquisition of functional object representations by physical and observational experience. *PLoS One*, *12*(10), e0185044. doi: 10.1371/journal.pone.0185044

Dassonville, P., Zhu, X.H., Uurbil, K., Kim, S.G., & Ashe, J. (1997). Functional activation in motor cortex reflects the direction and the degree of handedness. *Proceedings of the National Academy of Sciences of the United States of America*, *94*(25), 14015–14018.

Drager, B., Jansen, A., Bruchmann, S., Forster, A.F., Pleger, B., Zwitserlood, P., … Knecht, S. (2004). How does the brain accommodate to increased task difficulty in word finding? A functional MRI study. *NeuroImage*, *23*(3), 1152–1160. doi: 10.1016/j.neuroimage.2004.07.005

Durand, J.B., Peeters, R., Norman, J.F., Todd, J.T., & Orban, G.A. (2009). Parietal regions processing visual 3D shape extracted from disparity. *NeuroImage*, *46*(4), 1114–1126. doi: 10.1016/j.neuroimage.2009.03.023

Elsinger, C.L., Harrington, D.L., & Rao, S.M. (2006). From preparation to online control: Reappraisal of neural circuitry mediating internally generated and externally guided actions. *NeuroImage*, *31*(3), 1177–1187. doi: 10.1016/j.neuroimage.2006.01.041

Etzel, J.A. (2017). MVPA significance testing when just above chance, and related properties of permutation tests. *2017 International Workshop on Pattern Recognition in Neuroimaging*. *PRNI 2017*, *49*, 1–4. doi: 10.1109/PRNI.2017.7981498

Fabbri, S., Stubbs, K.M., Cusack, R., & Culham, J.C. (2016). Disentangling representations of object and grasp properties in the human brain. *The Journal of Neuroscience*, *36*(29), 7648–7662. doi: 10.1523/JNEUROSCI.0313-16.2016

Freud, E., Macdonald, S.N., Chen, J., Quinlan, D.J., Goodale, M.A., & Culham, J.C. (2018). Getting a grip on reality: Grasping movements directed to real objects and images rely on dissociable neural representations. *Cortex*, *98*, 34–48. doi: 10.1016/j.cortex.2017.02.020

Frey, S.H. (2007). What puts the how in where? Tool use and the divided visual streams hypothesis. *Cortex*, *43*(3), 368–375. doi: 10.1016/S0010-9452(08)70462-3

Frey, S.H. (2008). Tool use, communicative gesture and cerebral asymmetries in the modern human brain. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *363*(1499), 1951–1957. doi: 10.1098/rstb.2008.0008

Gallivan, J.P., Cant, J.S., Goodale, M.A., & Flanagan, J.R. (2014). Representation of object weight in human ventral visual cortex. *Current Biology*, *24*(16), 1866–1873. doi: 10.1016/j.cub.2014.06.046

Gallivan, J.P., Cavina-Pratesi, C., & Culham, J.C. (2009). Is that within reach? fMRI reveals that the human superior parieto-occipital cortex encodes objects reachable by the hand. *The Journal of Neuroscience*, *29*(14), 4381–4391. doi: 10.1523/JNEUROSCI.0377-09.2009

Gallivan, J.P., & Culham, J.C. (2015). Neural coding within human brain areas involved in actions. *Current Opinion in Neurobiology*, *33*, 141–149. doi: 10.1016/j.conb.2015.03.012

Gallivan, J.P., McLean, D.A., Valyear, K.F., & Culham, J.C. (2013). Decoding the neural mechanisms of human tool use. *Elife*, *2*, e00425. doi: 10.7554/eLife.00425

Gallivan, J.P., McLean, D.A., Valyear, K.F., Pettypiece, C.E., & Culham, J.C. (2011). Decoding action intentions from preparatory brain activity in human parieto-frontal networks. *The Journal of Neuroscience*, *31*(26), 9599–9610. doi: 10.1523/JNEUROSCI.0080-11.2011

Garcea, F.E., Kristensen, S., Almeida, J., & Mahon, B.Z. (2016). Resilience to the contralateral visual field bias as a window into object representations. *Cortex*, *81*, 14–23. doi: 10.1016/j.cortex.2016.04.006

Garcea, F.E., & Mahon, B.Z. (2014). Parcellation of left parietal tool representations by functional connectivity. *Neuropsychologia*, *60*, 131–143. doi: 10.1016/j.neuropsychologia.2014.05.018

Gertz, H., Lingnau, A., & Fiehler, K. (2017). Decoding movement goals from the fronto-parietal reach network. *Frontiers in Human Neuroscience*, *11*, 84. doi: 10.3389/fnhum.2017.00084

Gibson, J.J. (1977). The theory of affordances. In R. Shaw & J. Bransford (Eds.), *Perceiving, acting, and knowing. Toward an ecological psychology* (pp. 67–82). Hillsdale, NJ: Lawrence Erlbaum Associates.

Glasser, M.F., Coalson, T.S., Robinson, E.C., Hacker, C.D., Harwell, J., Yacoub, E., … Van Essen, D.C. (2016). A multimodal parcellation of human cerebral cortex. *Nature*, *536*(7615), 171–178. doi: 10.1038/nature18933

Goldenberg, G. (2017). Facets of pantomime. *Journal of the International Neuropsychological Society*, *23*(2), 121–127. doi: 10.1017/S1355617716000989

Goldenberg, G., & Hagmann, S. (1998). Tool use and mechanical problem solving in apraxia. *Neuropsychologia*, *36*(7), 581–589.

Goodale, M.A., Jakobson, L.S., & Keillor, J.M. (1994). Differences in the visual control of pantomimed and natural grasping movements. *Neuropsychologia*, *32*(10), 1159–1178. doi: 10.1016/0028-3932(94)90100-7

Goodale, M.A., Kroliczak, G., & Westwood, D.A. (2005). Dual routes to action: Contributions of the dorsal and ventral streams to adaptive behavior. *Progress in Brain Research*, *149*, 269–283. doi: 10.1016/S0079-6123(05)49019-6

Goodale, M.A., & Milner, A.D. (1992). Separate visual pathways for perception and action. *Trends in Neuroscience*, *15*(1), 20–25. doi: 10.1016/0166-2236(92)90344-8

Grill-Spector, K., & Weiner, K.S. (2014). The functional architecture of the ventral temporal cortex and its role in categorization. *Nature Reviews. Neuroscience*, *15*(8), 536–548. doi: 10.1038/nrn3747

Hamilton, A.F., & Grafton, S.T. (2008). Action outcomes are represented in human inferior frontoparietal cortex. *Cerebral Cortex*, *18*(5), 1160–1168.

Haxby, J.V., Connolly, A.C., & Guntupalli, J.S. (2014). Decoding neural representational spaces using multivariate pattern analysis. *Annual Review of Neuroscience*, *37*, 435–456. doi: 10.1146/annurev-neuro-062012-170325

Haynes, J.D., & Rees, G. (2006). Decoding mental states from brain activity in humans. *Nature Reviews. Neuroscience*, *7*(7), 523–534. doi: 10.1038/nrn1931

Hermsdorfer, J., Terlinden, G., Muhlau, M., Goldenberg, G., & Wohlschlager, A.M. (2007). Neural representations of pantomimed and actual tool use: Evidence from an event-related fMRI study. *NeuroImage*, *36*(Suppl. 2), T109–T118. doi: 10.1016/j.neuroimage.2007.03.037

Hutchison, R.M., Culham, J.C., Flanagan, J.R., Everling, S., & Gallivan, J.P. (2015). Functional subdivisions of medial parieto-occipital cortex in humans and nonhuman primates using resting-state fMRI. *NeuroImage*, *116*, 10–29. doi: 10.1016/j.neuroimage.2015.04.068

Jenkinson, M., Beckmann, C.F., Behrens, T.E., Woolrich, M.W., & Smith, S.M. (2012). Fsl. *NeuroImage*, *62*(2), 782–790. doi: 10.1016/j.neuroimage.2011.09.015

Johnson-Frey, S.H., Newman-Norlund, R., & Grafton, S.T. (2005). A distributed left hemisphere network active during planning of everyday tool use skills. *Cerebral Cortex*, *15*(6), 681–695. doi: 10.1093/cercor/bhh169

Kriegeskorte, N., Goebel, R., & Bandettini, P. (2006). Information-based functional brain mapping. *Proceedings of the National Academy of Sciences of the United States of America*, *103*(10), 3863–3868. doi: 10.1073/pnas.0600244103

Kristensen, S., Garcea, F.E., Mahon, B.Z., & Almeida, J. (2016). Temporal frequency tuning reveals interactions between the dorsal and ventral visual streams. *Journal of Cognitive Neuroscience*, *28*(9), 1295–1302. doi: 10.1162/jocn_a_00969

Kroliczak, G., Buchwald, M., Potok, W., & Przybylski, L. (2018). Handedness, praxis and language: A tricky triad revisited. *Polish Psychological Forum [Polskie Forum Psychologiczne]*, *23*(1), 22–34. doi: 10.14656/PFP20180102

Kroliczak, G., Cavina-Pratesi, C., Goodman, D.A., & Culham, J.C. (2007). What does the brain do when you fake it? An FMRI study of pantomimed and real grasping. *Journal of Neurophysiology*, *97*(3), 2410–2422. doi: 10.1152/jn.00778.2006

Kroliczak, G., & Frey, S.H. (2009). A common network in the left cerebral hemisphere represents planning of tool use pantomimes and familiar intransitive gestures at the hand-independent level. *Cerebral Cortex*, *19*(10), 2396–2410. doi: 10.1093/cercor/bhn261

Kroliczak, G., McAdam, T.D., Quinlan, D.J., & Culham, J.C. (2008). The human dorsal stream adapts to real actions and 3D shape processing: A functional magnetic resonance imaging study. *Journal of Neurophysiology*, *100*(5), 2627–2639. doi: 10.1152/jn.01376.2007

Kroliczak, G., Piper, B.J., & Frey, S.H. (2016). Specialization of the left supramarginal gyrus for hand-independent praxis representation is not related to hand dominance. *Neuropsychologia*, *93*, 501–512. doi: 10.1016/j.neuropsychologia.2016.03.023

Kroliczak, G., Westwood, D.A., & Goodale, M.A. (2006). Differential effects of advance semantic cues on grasping, naming, and manual estimation. *Experimental Brain Research*, *175*(1), 139–152. doi: 10.1007/s00221-006-0524-5

Kubiak, A., & Kroliczak, G. (2016). Left extrastriate body area is sensitive to the meaning of symbolic gesture: Evidence from fMRI repetition suppression. *Scientific Reports*, *6*, 31064. doi: 10.1038/srep31064

Lesourd, M., Budriesi, C., Osiurak, F., Nichelli, P.F., & Bartolo, A. (2017). Mechanical knowledge does matter to tool use even when assessed with a non-production task: Evidence from left brain-damaged patients. *Journal of Neuropsychology* (doi: 10.1111/jnp.12140

Lesourd, M., Osiurak, F., Navarro, J., & Reynaud, E. (2017). Involvement of the left supramarginal gyrus in manipulation judgment tasks: Contributions to theories of tool use. *Journal of the International Neuropsychological Society*, *23*(8), 685–691. doi: 10.1017/S1355617717000455

Mahon, B.Z., Kumar, N., & Almeida, J. (2013). Spatial frequency tuning reveals interactions between the dorsal and ventral visual systems. *Journal of Cognitive Neuroscience*, *25*(6), 862–871.

Makoshi, Z., Kroliczak, G., & van Donkelaar, P. (2011). Human supplementary motor area contribution to predictive motor planning. *Journal of Motor Behavior*, *43*(4), 303–309. doi: 10.1080/00222895.2011.584085

Marangon, M., Kubiak, A., & Kroliczak, G. (2016). Haptically guided grasping. fMRI shows right-hemisphere parietal stimulus encoding, and bilateral dorso-ventral parietal gradients of object- and action-related processing during grasp execution. *Frontiers in Human Neuroscience*, *9*, 691. doi: 10.3389/fnhum.2015.00691

Marcus, D.S., Harwell, J., Olsen, T., Hodge, M., Glasser, M.F., Prior, F., … Van Essen, D.C. (2011). Informatics and data mining tools and strategies for the human connectome project. *Frontiers in Neuroinformatics*, *5*, 4. doi: 10.3389/fninf.2011.00004

McDowell, T., Holmes, N.P., Sunderland, A., & Schurmann, M. (2018). TMS over the supramarginal gyrus delays selection of appropriate grasp orientation during reaching and grasping tools for use. *Cortex*, *103*, 117–129. doi: 10.1016/j.cortex.2018.03.002

Miezin, F.M., Maccotta, L., Ollinger, J.M., Petersen, S.E., & Buckner, R.L. (2000). Characterizing the hemodynamic response: Effects of presentation rate, sampling procedure, and the possibility of ordering brain activity based on relative timing. *NeuroImage*, *11*(6), 735–759. doi: 10.1006/nimg.2000.0568

Milner, A.D., & Goodale, M.A. (2008). Two visual systems re-viewed. *Neuropsychologia*, *46*(3), 774–785. doi: 10.1016/j.neuropsychologia.2007.10.005

Misaki, M., Kim, Y., Bandettini, P.A., & Kriegeskorte, N. (2010). Comparison of multivariate classifiers and response normalizations for pattern-information fMRI. *Neuroimage*, *53*(1), 103–118. doi: 10.1016/j.neuroimage.2010.05.051

Mizelle, J.C., Kelly, R.L., & Wheaton, L.A. (2013). Ventral encoding of functional affordances: A neural pathway for identifying errors in action. *Brain and Cognition*, *82*(3), 274–282. doi: 10.1016/j.bandc.2013.05.002

Mumford, J.A., Turner, B.O., Ashby, F.G., & Poldrack, R.A. (2012). Deconvolving BOLD activation in event-related designs for multivoxel pattern classification analyses. *NeuroImage*, *59*(3), 2636–2643. doi: 10.1016/j.neuroimage.2011.08.076

Nastase, S.A., Connolly, A.C., Oosterhof, N.N., Halchenko, Y.O., Guntupalli, J.S., Visconti di Oleggio Castello, M., … Haxby, J.V. (2017). Attention selectively reshapes the geometry of distributed semantic representation. *Cerebral Cortex*, *27*(8), 4277–4291. doi: 10.1093/cercor/bhx138

Norman, K.A., Polyn, S.M., Detre, G.J., & Haxby, J.V. (2006). Beyond mind-reading: Multi-voxel pattern analysis of fMRI data. *Trends in Cognitive Science*, *10*(9), 424–430. doi: 10.1016/j.tics.2006.07.005

Oldfield, R.C. (1971). The assessment and analysis of handedness: The Edinburgh inventory. *Neuropsychologia*, *9*, 97–113. doi: 10.1016/0028-3932(71)90067-4

Oliphant, T.E. (2007). Python for scientific computing. *Computing in Science & Engineering*, *9*(3), 10–20. doi: 10.1109/MCSE.2007.58

Oosterhof, N.N., Wiggett, A.J., Diedrichsen, J., Tipper, S.P., & Downing, P.E. (2010). Surface-based information mapping reveals crossmodal vision-action representations in human parietal and occipitotemporal cortex. *Journal of Neurophysiology*, *104*(2), 1077–1089. doi: 10.1152/jn.00326.2010

Orban, G.A. (2016). Functional definitions of parietal areas in human and non-human primates. *Proceedings Biological Sciences*, *283*(1828 doi: 10.1098/rspb.2016.0118

Orban, G.A., & Caruana, F. (2014). The neural basis of human tool use. *Frontiers in Psychology*, *5*, 310. doi: 10.3389/fpsyg.2014.00310

Orban, G.A., Van Essen, D., & Vanduffel, W. (2004). Comparative mapping of higher visual areas in monkeys and humans. *Trends in Cognitive Sciences*, *8*(7), 315–324. doi: 10.1016/j.tics.2004.05.009

Osiurak, F., & Badets, A. (2016). Tool use and affordance: Manipulation-based versus reasoning-based approaches. *Psychological Review*, *123*(5), 534–568. doi: 10.1037/rev0000027

Osiurak, F., Jarry, C., Allain, P., Aubin, G., Etcharry-Bouyx, F., Richard, I., … Le Gall, D. (2009). Unusual use of objects after unilateral brain damage: The technical reasoning model. *Cortex*, *45*(6), 769–783. doi: 10.1016/j.cortex.2008.06.013

Osiurak, F., Jarry, C., Lesourd, M., Baumard, J., & Le Gall, D. (2013). Mechanical problem-solving strategies in left-brain damaged patients and apraxia of tool use. *Neuropsychologia*, *51*(10), 1964–1972. doi: 10.1016/j.neuropsychologia.2013.06.017

Osiurak, F., Rossetti, Y., & Badets, A. (2017). What is an affordance? 40 years later. *Neuroscience and Biobehavioral Reviews*, *77*, 403–417. doi: 10.1016/j.neubiorev.2017.04.014

Peelen, M.V., Bracci, S., Lu, X., He, C., Caramazza, A., & Bi, Y. (2013). Tool selectivity in left occipitotemporal cortex develops without vision. *Journal of Cognitive Neuroscience*, *25*(8), 1225–1234. doi: 10.1162/jocn_a_00411

Peeters, R.R., Rizzolatti, G., & Orban, G.A. (2013). Functional properties of the left parietal tool use region. *NeuroImage*, *78*, 83–93. doi: 10.1016/j.neuroimage.2013.04.023

Picard, N., & Strick, P.L. (2003). Activation of the supplementary motor area (SMA) during performance of visually guided movements. *Cerebral Cortex*, *13*(9), 977–986.

Przybylski, L., & Kroliczak, G. (2017). Planning functional grasps of simple tools invokes the hand-independent praxis representation network: An fMRI study. *Journal of the International Neuropsychological Society*, *23*(2), 108–120. doi: 10.1017/S1355617716001120

Quadflieg, S., Etzel, J.A., Gazzola, V., Keysers, C., Schubert, T.W., Waiter, G.D., … Macrae, C.N. (2011). Puddles, parties, and professors: Linking word categorization to neural patterns of visuospatial coding. *Journal of Cognitive Neuroscience*, *23*(10), 2636–2649. doi: 10.1162/jocn.2011.21628

Reynaud, E., Lesourd, M., Navarro, J., & Osiurak, F. (2016). On the neurocognitive origins of human tool use: A critical review of neuroimaging data. *Neuroscience and Biobehavioral Reviews*, *64*, 421–437. doi: 10.1016/j.neubiorev.2016.03.009

Rizzolatti, G., & Matelli, M. (2003). Two different streams form the dorsal visual system: Anatomy and functions. *Experimental Brain Research*, *153*(2), 146–157. doi: 10.1007/s00221-003-1588-0

Rossit, S., Malhotra, P., Muir, K., Reeves, I., Duncan, G., & Harvey, M. (2011). The role of right temporal lobe structures in off-line action: Evidence from lesion-behavior mapping in stroke patients. *Cerebral Cortex*, *21*(12), 2751–2761. doi: 10.1093/cercor/bhr073

Rossit, S., McAdam, T., McLean, D.A., Goodale, M.A., & Culham, J.C. (2013). fMRI reveals a lower visual field preference for hand actions in human superior parieto-occipital cortex (SPOC) and precuneus. *Cortex*, *49*(9), 2525–2541. doi: 10.1016/j.cortex.2012.12.014

Sakreida, K., Effnert, I., Thill, S., Menz, M.M., Jirak, D., Eickhoff, C.R., … Binkofski, F. (2016). Affordance processing in segregated parieto-frontal dorsal stream sub-pathways. *Neuroscience and Biobehavioral Reviews*, *69*, 89–112. doi: 10.1016/j.neubiorev.2016.07.032

Seabold, S., & Perktold, J. (2010). Statsmodels: Econometric and Statistical Modeling with Python. *Proceedings of the 9th Python in Science Conference*, *(Scipy)*, 57–61. Retrieved from http://conference.scipy.org/proceedings/scipy2010/seabold.html.

Shay, E.A., Chen, Q., Garcea, F.E., & Mahon, B.Z. (2018). Decoding intransitive actions in primary motor cortex using fMRI: Toward a componential theory of ‘action primitives’ in motor cortex. *Cognitive Neuroscience*, 1–7. doi: 10.1080/17588928.2018.1453491

Striem-Amit, E., Vannuscorps, G., & Caramazza, A. (2017). Sensorimotor-independent development of hands and tools selectivity in the visual cortex. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(18), 4787–4792. doi: 10.1073/pnas.1620289114

Valyear, K.F., Gallivan, J.P., McLean, D.A., & Culham, J.C. (2012). fMRI repetition suppression for familiar but not arbitrary actions with tools. *Journal of Neuroscience*, *32*(12), 4247–4259. doi: 10.1523/JNEUROSCI.5270-11.2012

Van Essen, D.C., Drury, H.A., Dickson, J., Harwell, J., Hanlon, D., & Anderson, C.H. (2001). An integrated software suite for surface-based analyses of cerebral cortex. *Journal of the American Medical Informatics Association*, *8*(5), 443–459. doi: 10.1136/jamia.2001.0080443

Vingerhoets, G. (2014). Contribution of the posterior parietal cortex in reaching, grasping, and using objects and tools. *Frontiers in Psychology*, *5*, 151. doi: 10.3389/fpsyg.2014.00151

Vingerhoets, G., & Clauwaert, A. (2015). Functional connectivity associated with hand shape generation: Imitating novel hand postures and pantomiming tool grips challenge different nodes of a shared neural network. *Human Brain Mapping*, *36*(9), 3426–3440. doi: 10.1002/hbm.22853

Vingerhoets, G., Nys, J., Honore, P., Vandekerckhove, E., & Vandemaele, P. (2013). Human left ventral premotor cortex mediates matching of hand posture to object use. *PLoS One*, *8*(7), e70480. doi: 10.1371/journal.pone.0070480

Vingerhoets, G., Vandekerckhove, E., Honore, P., Vandemaele, P., & Achten, E. (2011). Neural correlates of pantomiming familiar and unfamiliar tools: Action semantics versus mechanical problem solving? *Human Brain Mapping*, *32*(6), 905–918. doi: 10.1002/hbm.21078

Wiestler, T., & Diedrichsen, J. (2013). Skill learning strengthens cortical representations of motor sequences. *Elife*, *2*, e00801. doi: 10.7554/eLife.00801

Wurm, M.F., & Lingnau, A. (2015). Decoding actions at different levels of abstraction. *The Journal of Neuroscience*, *35*(20), 7727–7735. doi: 10.1523/JNEUROSCI.0188-15.2015