



Research report

Resilience to the contralateral visual field bias as a window into object representations



Frank E. Garcea^{a,b}, Stephanie Kristensen^{c,d}, Jorge Almeida^{c,d,**} and Bradford Z. Mahon^{a,b,e,*}

^a Department of Brain and Cognitive Sciences, University of Rochester, USA

^b Center for Visual Science, University of Rochester, USA

^c Faculty of Psychology and Educational Sciences, University of Coimbra, Portugal

^d Proaction Laboratory, Faculty of Psychology and Educational Sciences, University of Coimbra, Portugal

^e Department of Neurosurgery, University of Rochester, USA

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ABSTRACT

Viewing images of manipulable objects elicits differential blood oxygen level-dependent (BOLD) contrast across parietal and dorsal occipital areas of the human brain that support object-directed reaching, grasping, and complex object manipulation. However, it is unknown which object-selective regions of parietal cortex receive their principal inputs from the ventral object-processing pathway and which receive their inputs from the dorsal object-processing pathway. Parietal areas that receive their inputs from the ventral visual pathway, rather than from the dorsal stream, will have inputs that are already filtered through object categorization and identification processes. This predicts that parietal regions that receive inputs from the ventral visual pathway should exhibit object-selective responses that are resilient to contralateral visual field biases. To test this hypothesis, adult participants viewed images of tools and animals that were presented to the left or right visual fields during functional magnetic resonance imaging (fMRI). We found that the left inferior parietal lobule showed robust tool preferences independently of the visual field in which tool stimuli were presented. In contrast, a region in posterior parietal/dorsal occipital cortex in the right hemisphere exhibited an interaction between visual field and category: tool-preferences were strongest contralateral to the stimulus. These findings suggest that action knowledge accessed in the left inferior parietal lobule operates over inputs that are abstracted from the visual input and is contingent on analysis by the ventral visual pathway, consistent with its putative role in supporting object manipulation knowledge.

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* Corresponding author. Meliora Hall, University of Rochester, Rochester, NY 14627-0268, USA.

** Corresponding author. Faculty of Psychology and Educational Sciences, University of Coimbra, 3001-802 Coimbra, Portugal.

E-mail addresses: jorgealmeida@fpce.uc.pt (J. Almeida), mahon@rcbi.rochester.edu (B.Z. Mahon).

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1. Introduction

One overarching feature of the human visual system is the contralateral representation of the visual fields across the two hemispheres. Another feature is that subregions of high level visual processing areas in the brain exhibit category preferences for a limited number of distinct categories (e.g., faces, places, animals, body parts, tools; Allison, McCarthy, Nobre, Puce, & Belger, 1994; Chao, Haxby, & Martin, 1999; Downing, Jiang, Shuman, & Kanwisher, 2001; Epstein, Harris, Stanley, & Kanwisher, 1999; Ishai, Ungerleider, Martin, Schouten, & Haxby, 1999; Kanwisher, McDermott, & Chun, 1997; for reviews, see Grill-Spector & Malach, 2004; Mahon & Caramazza, 2009; Martin, 2007, 2009; Op de Beeck, Haushofer, & Kanwisher, 2008; Peelen & Downing, 2007). A third broad characteristic of high-level vision is the distinction between a ventral and a dorsal visual object-processing pathway: the ventral pathway supports object identification while the dorsal pathway supports online control of object-directed actions (Goodale & Milner, 1992; Goodale, Milner, Jakobson, & Carey, 1991; Milner & Goodale, 2008; Ungerleider & Mishkin, 1982). Here we study the confluence of these three macroscopic properties of the visual system.

The ability to identify, grasp and then use objects correctly according to their function requires coordinated processing across the dorsal and ventral visual pathways, and in reference frames that are both invariant to the location of the target object (identification) and highly dependent on the object's location (grasping). A key issue is how and where information from the dorsal and ventral streams is integrated (e.g., see Gallivan, Cant, Goodale, & Flanagan, 2014; Garcea, Almeida, & Mahon, 2012; Garcea & Mahon, 2014). While such integration likely occurs in multiple areas, one candidate structure well suited to integrate information from the two visual pathways is the left inferior parietal lobule. Prior work has shown that the left parietal lobule exhibits neural specificity for manipulable objects (Chao & Martin, 2000; Mahon et al., 2007; Mruczek, von Loga, & Kastner, 2013; Noppeney, Price, Penny, & Friston, 2006; Peeters, Rizzolatti, & Orban, 2013; for reviews, see Lewis, 2006; Martin, 2007), supports complex object manipulation (Johnson-Frey, 2004; Liepmann, 1905; Rumiati et al., 2004), and has the requisite functional and anatomical connectivity that could, in principle, support the integration of multiple streams of information (Garcea & Mahon, 2014; Hutchison, Culham, Everling, Flanagan, & Gallivan, 2014; Kravitz, Saleem, Baker, & Mishkin, 2011; Rizzolatti & Matelli, 2003; Rushworth, Behrens, & Johansen-Berg, 2006; Stevens, Tessler, Peng, & Martin, 2015; for discussion, see Binkofski & Buxbaum, 2013).

Here we sought to test which regions of tool-selective parietal cortex receive functional inputs from the ventral visual pathway, and which receive inputs from the dorsal object-processing pathway. We reasoned that parietal regions that receive inputs from the ventral visual pathway should exhibit object-selectivity that largely abstracts away from the visual field location in which the stimuli were presented. The motivation for this prediction is that inputs that come via a ventral visual analysis of the input will have already been filtered through object categorization and identification processes. In

contrast, regions of parietal cortex or dorsal occipital cortex in which stimulus processing is not mediated by analysis in the ventral visual pathway, and which support volumetric analysis in the service of visuomotor actions, would be predicted to show preferences for tools with a strong bias toward the contralateral visual field (e.g., Handy, Grafton, Shroff, Ketay, & Gazzaniga, 2003). To test these hypotheses, we designed a functional magnetic resonance imaging (fMRI) experiment in which tool and animal stimuli were presented in the right and left visual fields while participants were required to maintain fixation on a central fixation point. This design allows us to determine brain regions that exhibit tool preferences regardless of whether the stimuli were presented in the left or right visual fields, as well as regions that exhibit tool preferences that are strongly modulated by the side of presentation.

2. Methods

2.1. Participants

Sixteen University of Rochester students (9 females; mean age = 22.4 years, SD = 2.7 years) participated in the study in exchange for payment. All participants were strongly right-handed (as established with the Edinburgh Handedness Questionnaire), had normal or corrected-to normal vision, were native English speakers, and had no history of neurological disorders. All participants gave written informed consent in accordance with the University of Rochester Research Subjects Review Board.

2.2. General procedure

Stimulus presentation was controlled with 'A Simple Framework' (ASF; Schwarzbach, 2011) using the Psychophysics Toolbox (Pelli, 1997) in MATLAB running on a MacPro. All participants viewed the stimuli binocularly through a mirror attached to the head coil adjusted to allow foveal viewing of a back-projected monitor (temporal resolution = 120 Hz). Each participant took part in two scanning sessions. The first scanning session included a T1 anatomical scan (6 min), and 8 three-minute runs of a category localizer (91 volumes per run; see below for materials and design). The second session included 6 seven-minute runs of the lateralized picture viewing experiment (204 volumes per run; see below for materials and design).

2.3. Experiment 1: tool, animal, face, place (TAFP) localizer. Materials and design

Twelve grayscale photographs of tools, animals, famous faces, and famous places were used; each item had 8 exemplars (for a total of 96 images per category; 384 images total). Phase-scrambled versions of the stimuli were created to serve as a baseline condition (for details on materials, see Fintzi & Mahon, 2014). Participants passively viewed images of tools, animals, faces, and places in a miniblock design. Within each 6-sec miniblock, 12 stimuli were presented for 500 msec each (ISI = 0 msec), and 6-sec fixation periods were presented between miniblocks; within each run, 8 miniblocks of intact

images and 4 miniblocks of phase-scrambled versions of the stimuli were presented. The order of stimulus presentation was balanced such that upon completion of 8 runs the participants had viewed all stimuli from the four categories (i.e., a different exemplar was used in each run). All participants completed 8 runs of the TAFP experiment (91 volumes per run).

2.4. Experiment 2: lateralized picture viewing materials and design

Sixteen pictures of tools and 16 pictures of animals were used. Scrambled versions of the items were created to serve as a baseline condition (groups of pixels were randomly displaced). Participants maintained fixation on a centrally-presented black dot while tool and animal stimuli were presented in a miniblock design (the participants' gaze was monitored online with a video feed inside the bore to ensure task compliance). Within each 8-sec miniblock, 16 intact or scrambled tools or animals were presented for 500 msec each (ISI = 0 msec), in either the left or right visual field (the center of the lateralized stimuli subtended ~ 5 degrees of the visual angle). Miniblocks were separated by 8 sec of fixation in which a black cross was presented in the center of the screen.

There were 3 factors in the experiment – Visual Field (2 levels; right, left), Category (2 levels; animals, tools), and Stimulus Identity (2 levels; intact, scrambled). Within a run, all intact images were presented eight times (four times within each visual field), and all scrambled images were presented four times (two times within each visual field); condition order was random with the caveat that the same cell of the design did not repeat across two successive miniblocks within a run. Fifteen of the 16 participants completed 6 runs of the lateralized picture viewing experiment; due to technical errors with the experiment, 1 participant completed 4 runs of the lateralized picture viewing experiment (always 204 volumes per run). As part of a separate research question, the tool and animal images were bathed in a red or green background color during stimulus presentation; as this factor of the experiment is not germane to the goals of the current report, it is not analyzed.

2.5. MRI acquisition and preprocessing

Whole brain blood oxygen level-dependent (BOLD) imaging was conducted on a 3-T Siemens MAGNETOM Trio scanner with a 32-channel head coil located at the Rochester Center for Brain Imaging. High-resolution structural T1 contrast images were acquired using a magnetization prepared rapid gradient echo (MP-RAGE) pulse sequence at the start of each session (TR = 2530, TE = 3.44 msec, flip angle = 7°, FOV = 256 mm, matrix = 256 × 256, 1 × 1 × 1 mm sagittal left-to-right slices). An echo-planar imaging pulse sequence was used for T2* contrast (TR = 2000 msec, TE = 30 msec, flip angle = 90°, FOV = 256 × 256 mm, matrix = 64 × 64, 30 sagittal left-to-right slices, voxel size = 4 × 4 × 4 mm). The first two volumes of each run were discarded to allow for signal equilibration.

MRI data were analyzed with the BrainVoyager software package (Version 2.8) and in-house scripts drawing on the BVQX toolbox written in MATLAB (<http://support.brainvoyager.com/available-tools/52-matlab-tools-bvqxtools>).

(html). Preprocessing of the functional data included, in the following order, slice scan time correction (sinc interpolation), motion correction with respect to the first volume of the first functional run, and linear trend removal in the temporal domain (cutoff: 2 cycles within the run). Functional data were registered (after contrast inversion of the first volume) to high-resolution deskulled anatomy on a participant-by-participant basis in native space. For each participant, echo-planar and anatomical volumes were transformed into standardized space (Talairach & Tournoux, 1988). All functional data were smoothed at 6 mm FWHM (1.5 voxels), and interpolated to 3 mm³ voxels.

3. Results

3.1. Independent definition of tool preferring regions

Tool preferring voxels were identified in a whole-brain analysis (random effects general linear model; $p < .005$, cluster corrected) with the contrast of Tools > Animals using the independent category-localizer experiment (for details, see Experiment 1 in Methods). Replicating previous studies (Chao et al., 1999; Chao & Martin, 2000; Garcea & Mahon, 2014; Mahon et al., 2007; Mahon, Kumar, & Almeida, 2013; Noppeney et al., 2006), viewing images of tools led to increased BOLD contrast in the left inferior and superior parietal lobule, the left posterior/inferior middle temporal gyrus, the left posterior parietal/dorsal occipital cortex, and bilateral medial fusiform gyrus. In addition, there was a significant increase in BOLD contrast for tool stimuli in the right superior parietal lobule, and the right posterior parietal/dorsal occipital cortex. The effect in the right posterior parietal/dorsal occipital tool preferring area was weaker than in the other areas, and was defined with a more lenient threshold, $p < .01$, cluster corrected. We note however that the location of this tool-preferring region is in very good agreement with prior work from our lab (e.g., Garcea & Mahon, 2014) and others (e.g., Fang & He, 2005). Fig. 1 shows all voxels in the brain that exhibited increased BOLD contrast for tool compared to animal stimuli, and Table 1 lists the coordinates and statistical values associated with the peak voxels for each region of interest (ROI).

3.2. Tool preferences robust to lateralized presentation

We next evaluated in which regions tool preferences were robust to the visual field in which the stimuli were presented. The most stringent test would be to run a whole brain analysis identifying all voxels that survive the conjunction analysis of [right tools] > [right animals] & [left tools] > [left animals]—any voxel that survives this conjunction would exhibit tool preferences regardless of whether the stimuli are presented in the left or right visual field (see Nichols, Brett, Andersson, Wager, & Poline, 2004). The resulting whole-brain contrast map is plotted in Fig. 2. The results from that conjunction analysis identify the left posterior/inferior middle temporal gyrus, bilateral medial fusiform gyri, and critically the left inferior parietal lobule. It is important to note the lack of significant BOLD contrast in the left superior parietal lobule and in any of the right hemisphere regions that expressed significant BOLD

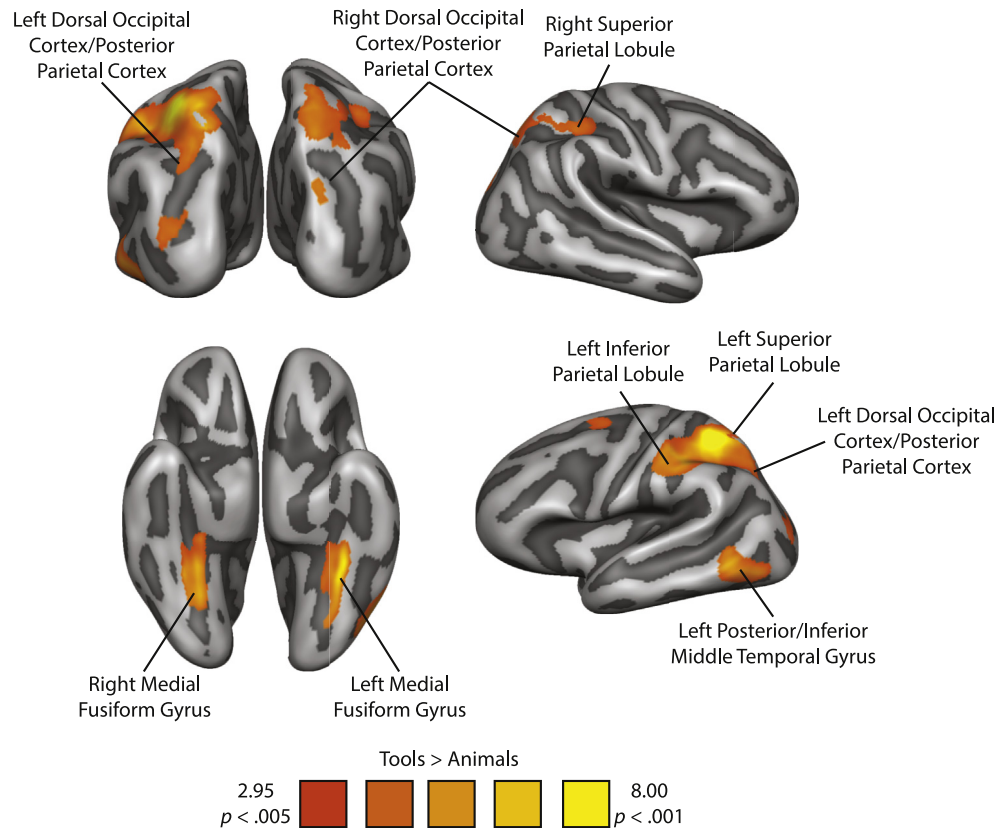


Fig. 1 – Tool Preferences in the Right and Left Dorsal and Ventral Visual Pathways. Tool preferences were identified with the contrast of ‘Tools > Animals’ ($p < .005$). The whole-brain contrast map was corrected using a Monte-Carlo style permutation test that thresholds voxel cluster size to maintain a Type I error rate of 5% (AlphaSim, 1000 iterations). This contrast identifies bilateral superior parietal lobules, bilateral medial fusiform gyri, bilateral posterior parietal/dorsal occipital cortices (identified at a more lenient threshold of $p < .01$), the left inferior parietal lobule, and the left posterior/inferior middle temporal gyrus.

Table 1 – Talairach coordinates for peak voxels from regions showing differential BOLD contrast for Tool stimuli in the TAFP Localizer.

Region	Peak voxel coordinates (XYZ)			Statistical value for peak voxel	Volume (mm ³)
Left parietal cortex	-34	-50	51	$t(15) = 8.94, p < .001$	15,328
Left medial fusiform gyrus	-25	-35	-24	$t(15) = 7.43, p < .001$	4803
Left posterior/inferior middle temporal gyrus	-49	-56	-6	$t(15) = 5.49, p < .001$	4196
Left posterior parietal/dorsal occipital cortex	-25	-71	36	$t(15) = 4.82, p < .001$	918
Right superior parietal lobule	17	-62	48	$t(15) = 4.42, p < .001$	3499
Right medial fusiform gyrus	29	-56	-6	$t(15) = 8.39, p < .001$	2884
Right posterior parietal/dorsal occipital cortex	35	-83	19	$t(15) = 4.45, p < .001$	4978

contrast for tool stimuli in the independent category localizer. This can be seen in Fig. 2, as the borders of the independently defined tool preferring regions from the functional localizer experiment are outlined in yellow.

3.3. Tool preferences modulated by visual field of presentation

We next sought positive evidence that more posterior parietal or dorsal occipital regions would exhibit tool preferences that are driven by contralateral stimulus presentation. To that end, we carried out a whole-brain repeated measures ANOVA over the data from Experiment 2, the experiment in

which participants maintained central fixation while images of tools and animals were presented in the left and right visual fields. The ANOVA modeled the main effects of category (two levels; tool, animal), visual field location (two levels; left visual field, right visual field), stimulus identity (two levels; intact, scrambled), and the interaction among the three factors. A second goal was to confirm that any regions that exhibit a significant 3-way interaction were showing modulation of category by location only for intact stimuli: to that end, a separate whole-brain 2-way ANOVA between category (tools, animals) and location (left, right) was run over only the intact stimuli (i.e., excluding the scrambled images).

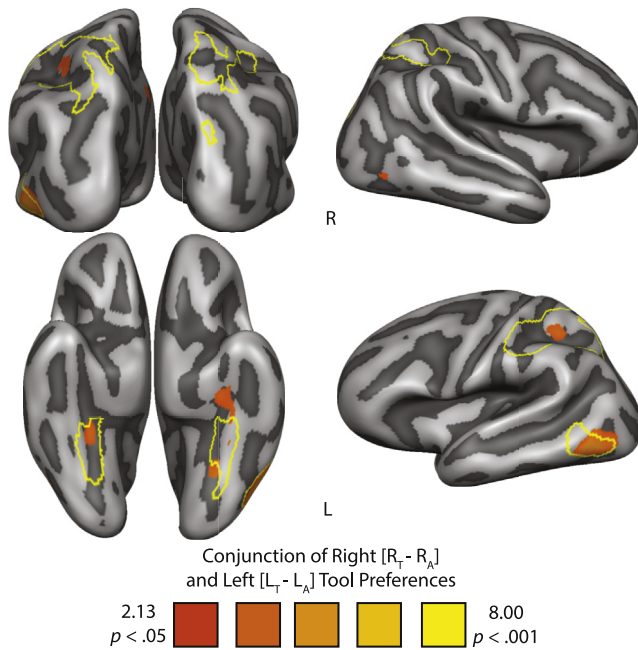


Fig. 2 – Whole-brain increase in BOLD contrast for the conjunction of right [Right_{Tool} – Right_{Animal}] and left [Left_{Tool} – Left_{Animal}] tool preferences in the lateralized picture viewing experiment. The ROIs from the independent functional category localizer (Fig. 1) are outlined in yellow. All whole-brain maps were cluster-corrected.

The most conservative test to identify regions in which tool preferences are modulated by side of presentation is to take the intersection of two maps: the 3-way interaction between category*visual field location*stimulus identity and the 2-way category*visual field location (only for intact stimuli). Any voxel identified as overlapping those two interaction tests would exhibit modulation of category-preferences by side of presentation only for intact stimuli. The resulting intersection map is plotted in Fig. 3A. The only region of the brain identified in this interaction map, that was also independently identified as exhibiting tool preferences in the category localizer session, was the right posterior parietal/dorsal occipital region (see Fig. 3B). A visualization of BOLD contrast by condition for those intersecting voxels confirmed that responses were driven by contralaterally presented tool stimuli (see Fig. 3C).

3.4. ROI analysis

As a final test, we carried out an ROI analysis in which we tested for interaction effects between ‘Category’ and ‘Visual Field Location’ using data from the lateralized viewing experiment (Experiment 2, only for intact stimuli). This was carried out in ROIs that were independently defined with the category-localizer experiment (Experiment 1). BOLD contrast values were extracted from the lateralized viewing experiment for all of the independently defined ROIs (see Fig. 4). As expected, there was a significant interaction between Visual Field Location and Category in only one ROI: the right posterior parietal/dorsal occipital cortex [$F(1, 15) = 5.60, p < .05$; see Fig. 4G]. BOLD contrast in that region during the lateralized

viewing experiment was maximal for tools presented in the left (i.e., contralateral) visual field. The planned contrast of $(\text{Left}_{\text{Tool}} - \text{Left}_{\text{Animal}}) > (\text{Right}_{\text{Tool}} - \text{Right}_{\text{Animal}})$ was significant [$t(15) = 2.37, p < .05$]. There was no interaction between Visual Field Location and Category in any of the other regions identified by the independent functional localizer (all $p > .17$).

4. Discussion

The goal of the current investigation was to advance our understanding of how three fundamental properties of high level vision interact: category preferences, contralateral visual processing, and the distinction between the dorsal and ventral visual pathways. We reasoned that tool-preferring regions of parietal cortex whose inputs have been filtered through object recognition processes in ventral temporal-occipital cortex would exhibit a higher degree of tolerance to the visual field location of the stimuli. In contrast, tool-preferring regions of parietal cortex whose inputs come by way of the dorsal visual pathway (i.e., independent of processing in ventral temporal-occipital cortex) should exhibit a strong interaction between the side of presentation of the visual stimulus and any category-preferences. A conjunction analysis that identified regions exhibiting tool preferences regardless of whether the stimuli were presented in the left or right visual fields identified the left inferior parietal lobule, the left medial fusiform gyrus, and the left posterior/inferior middle temporal gyrus (Fig. 2). By comparison, a whole-brain repeated measures ANOVA that identified regions in which category preferences were modulated by the side of presentation only for intact stimuli identified the right dorsal occipital cortex bordering on posterior parietal cortex. In a final test, we found that of all of the regions identified as exhibiting tool preferences using an independent functional localizer, the only region that showed a significant interaction between category and side-of-presentation was the right posterior parietal/dorsal occipital cortex.

There is a long history of lesion work which shows that limb apraxia, a neuropsychological deficit in using objects correctly according to their function, is associated with lesions to the left inferior parietal lobule (see e.g., Buxbaum, Veramonti, & Schwartz, 2000; Garcea, Dombrov, & Mahon, 2013; Garcea & Mahon, 2014; Ochipa, Rothi, & Heilman, 1989; Mahon et al., 2007; Negri et al., 2007; for reviews, see Binkofski & Buxbaum, 2013; Cubelli, Marchetti, Boscolo, & Della Salla, 2000; Goldenberg, 2009; Johnson-Frey, 2004; Mahon & Caramazza, 2005; Osieurak, 2014; Rothi, Ochipa, & Heilman, 1991). On the basis of those patient data, and additional neuroimaging findings (Boronat et al., 2005; Canessa et al., 2008; Chen, Garcea, & Mahon, 2016; Garcea & Mahon, 2014; Kellenbach, Brett, & Patterson, 2003; Mahon et al., 2007; Rumiati et al., 2004), it has been suggested that complex object associated manipulation knowledge is represented in the left inferior parietal lobule. Our findings and interpretation are entirely in line with that proposal, as complex object manipulation knowledge could only be accessed subsequent to accessing the identity of the object. In other words, the knowledge that a hammer is manipulated with a pounding motion presupposes that the object has been identified as a hammer, and possibly as well that the function of

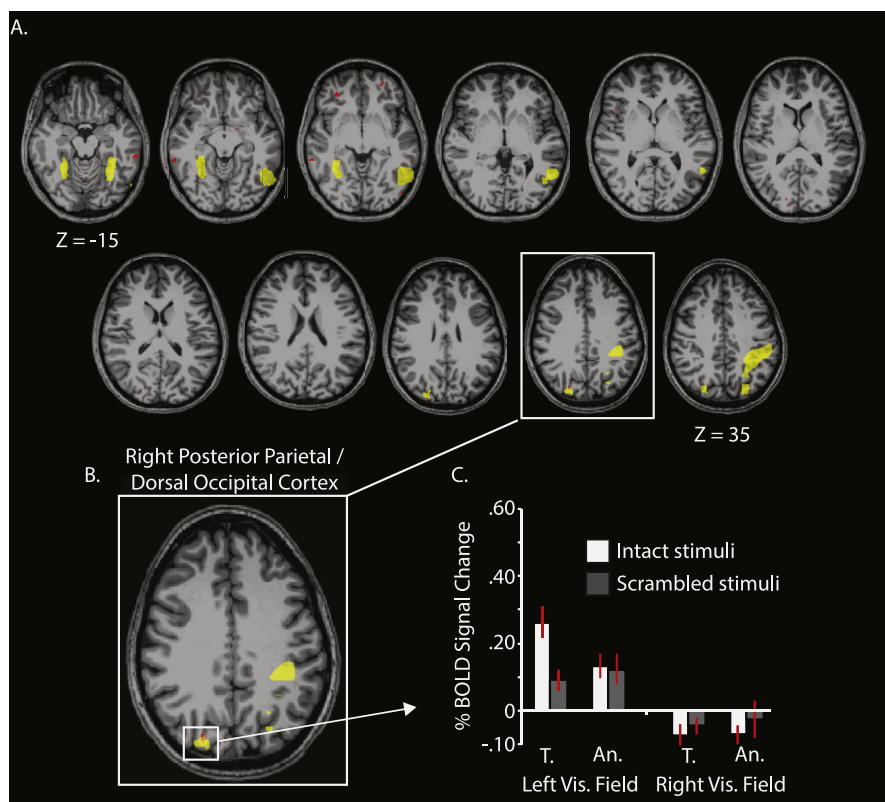


Fig. 3 – Whole-brain overlap between the Category*Visual Field Location*Stimulus Identity interaction and the Category*Visual Field Location interaction for intact stimuli identifies the right posterior parietal/dorsal occipital cortex. The whole-brain results are plotted as axial slices (panel A). A gray-matter mask was used to indicate which cortical voxels showed robust category preferences that were modulated by the side of presentation for intact stimuli only. The ROIs from the independent category localizer (Fig. 1) are outlined in yellow; the overlap between the 3-way interaction map and the 2-way interaction map is marked in red. The only region that emerges in common to the two whole-brain ANOVAs and which was also identified by the category-localizer experiment as exhibiting tool preferences was the right posterior parietal/dorsal occipital cortex (panel B). Responses in the right posterior parietal/dorsal occipital region were driven by contralaterally presented tool stimuli (panel C). T., tools; An., animals.

the object has been accessed (for discussion, see Almeida, Fintzi, & Mahon, 2013; Binkofski & Buxbaum, 2013; Bruffaerts et al., 2014; Gallivan et al., 2014; Gallivan, Johnsrude, & Flanagan, 2016; Garcea & Mahon, 2014; Mahon et al., 2013). It is difficult to envision how those types of information could be extracted bottom up from the volumetric properties of the object, which is the information that the dorsal visual pathway has available.

The conclusion that tool preferences in the left inferior parietal lobule are contingent on analysis of the visual input by the ventral visual pathway is not incompatible with the view that inferior parietal BOLD responses are likely an aggregation of processing that occurs at varying time scales and across multiple brain regions. For instance, Bar et al. (2006) found that object recognition-associated responses in orbito-frontal cortex preceded activity in ventral temporal cortex (see also Fintzi & Mahon, 2014). On the basis of those and other findings, Bar and colleagues argued that prefrontal processing of object information provides an initial first pass analysis of the visual input, that can then be used to bias slower, and more detailed visual processing in the ventral stream. However, this does not change the conclusion that the retrieval of

object-associated manipulation knowledge is contingent upon the retrieval of object identity via the ventral visual pathway. That proposal could explain why responses in the left inferior parietal lobule are robust to changes in the visual field location of the stimuli. It is also consistent with observations that psychophysical treatments of stimuli that bias processing away from the dorsal visual pathway result in tool preferences that are restricted to the left inferior parietal lobule (Almeida et al., 2013; Mahon et al., 2013).

It is also important to note that our findings are not incompatible with the fact that higher order object responsive areas in the ventral stream exhibit robust modulation by the visual field location of stimuli (Kravitz, Kriegeskorte, & Baker, 2010; Levy, Hasson, Avidan, Hendler, & Malach, 2001; Orban, Zhu, & Vanduffel, 2014). For instance, we observed a clear and strong contralateral bias in the strength of neural activity induced by lateralized stimuli throughout the ventral visual pathway (see Fig. 4). However, there was no statistical interaction between visual field and category in the medial fusiform gyri (Fig. 3), indicating that tool preferences in the fusiform gyri are not modulated by visual hemifield location (see also Fig. 2). The proposal that representations of objects that result from

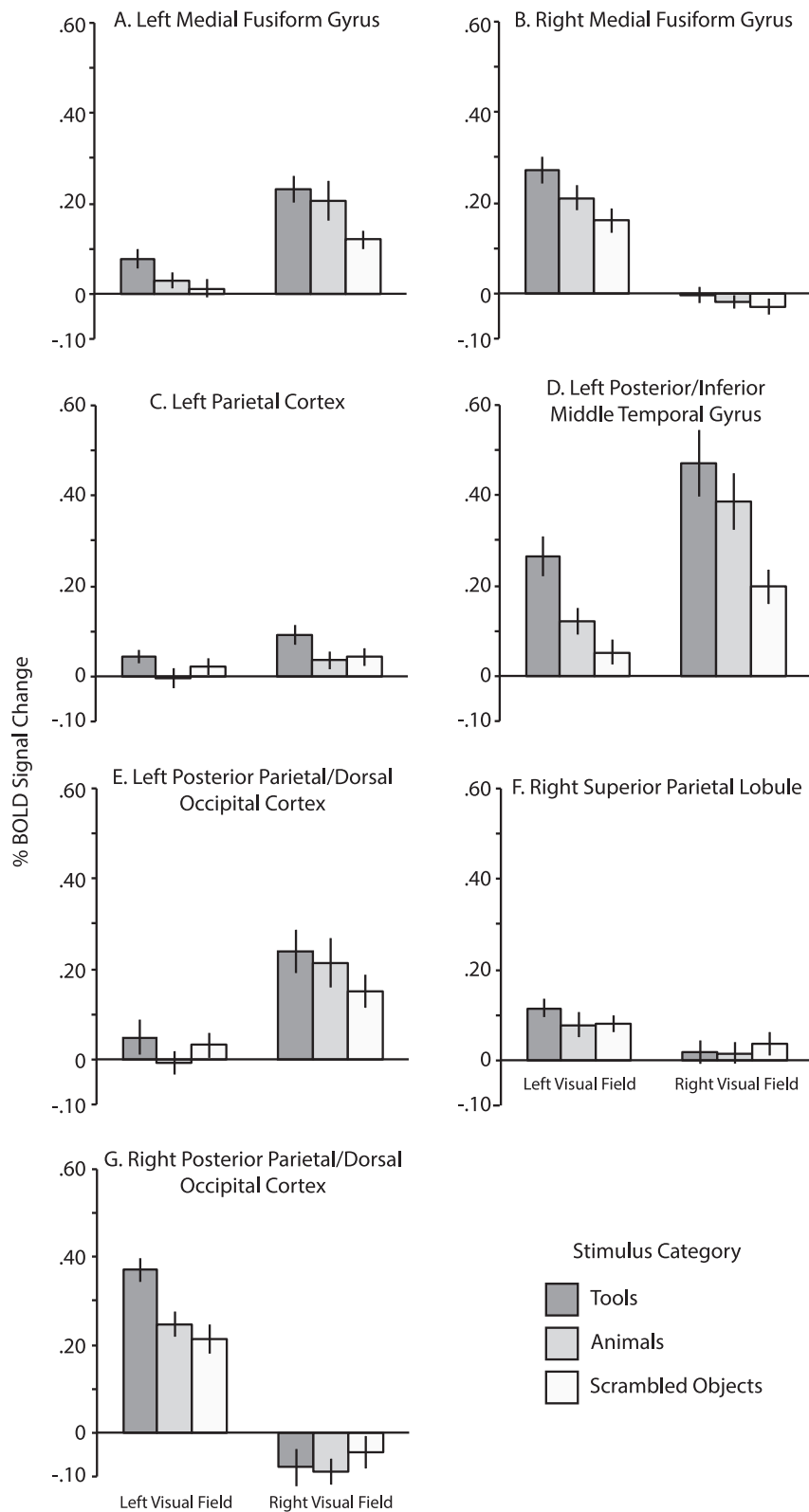


Fig. 4 – Percent Signal Change (BOLD) for the functionally-defined ROIs as a function of stimulus category and visual field location. BOLD contrast from the scrambled tool and animal miniblocks were averaged into one scrambled condition and are included for reference.

processing in ventral visual pathway would be tolerant to changes in visual field location of the stimulus is not incompatible with the view that some representations in the ventral stream may be category- and visual-field specific (e.g., see Kravitz, Peng, and Baker, 2011; Kravitz, Vinson, & Baker, 2008).

A second aspect of our findings that is important to note is that tool preferences in dorsal occipital/posterior parietal regions were significantly modulated by visual field location only in the right hemisphere. The lack of an interaction in the left hemisphere is interesting considering there were robust responses for tools in dorsal occipital regions of that hemisphere when contrasting the BOLD signal for contralaterally-presented tools with all other conditions (see [Supplemental Figure 1](#)). It remains an open issue for future research how tool representations in posterior dorsal structures may be influenced by handedness, language dominance, and the interaction of those factors during visual object recognition of tools (see e.g., Vingerhoets, 2014).

More generally, our results are consistent with the broader theoretical framework that the left inferior parietal lobule (left supramarginal gyrus, anterior intraparietal sulcus) integrates volumetric information relevant for shaping the hand when grasping objects, with complex object-associated manipulation knowledge. While the retrieval of complex object-associated manipulation knowledge is contingent on the computation of object identity by the ventral visual pathway (e.g., see Cant & Goodale, 2007; Gallivan et al., 2014), hand shaping for grasping can plausibly be driven bottom-up by volumetric information communicated by the dorsal stream. For instance, Culham et al. (2003) found that reaching actions maximally activate posterior/superior parietal regions, in the vicinity of the dorsal occipital region we identified herein (i.e., in the vicinity of V6/V6a; see also Cavina-Pratesi, Goodale, & Culham, 2007; Fang & He, 2005; Gallivan, Cavina-Pratesi, & Culham, 2009; Konen, Mruczek, Montoya, & Kastner, 2013; Pitzalis et al., 2006; Rossit, McAdam, Mclean, Goodale, & Culham, 2013); in contrast, reach-to-grasp actions maximally activate the anterior intraparietal sulcus (for patient evidence, see Binkofski et al., 1998). It is important to underline, however, that object grasping in the service of object manipulation presupposes a functionally appropriate grasp—thus, while basic grasp points may be derivable bottom up on the basis of information propagated through the dorsal stream (e.g., Goodale et al., 1991), functionally appropriate grasps likely require inputs from computations that are supported by the ventral visual pathway (Carey, Harvey, & Milner, 1996; Valyear & Culham, 2010). Our findings suggest that the left inferior parietal lobule may be at least one of the brain regions that supports the integration of information communicated by the ventral visual pathway with information communicated via the dorsal visual pathway.

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Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.cortex.2016.04.006>.

REFERENCES

- Allison, T., McCarthy, G., Nobre, A., Puce, A., & Belger, A. (1994). Human extrastriate visual cortex and the perception of faces, words, numbers, and colors. *Cerebral Cortex*, 4(5), 544–554.
- 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, 2334–2344.
- Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., et al. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 449–454.
- Binkofski, F., & Buxbaum, L. J. (2013). Two action systems in the human brain. *Brain and Language*, 127(2), 222–229.
- Binkofski, F., Dohle, C., Posse, S., Stephan, K. M., Hefter, H., Seitz, R. J., et al. (1998). Human anterior intraparietal area subserves prehension. A combined lesion and functional MRI activation study. *Neurology*, 50, 1253–1259.
- Boronat, C. B., Buxbaum, L. J., Coslett, H. B., Tang, K., Saffran, E. M., Kimberg, D. Y., et al. (2005). Distinctions between manipulation and function knowledge of objects: evidence from functional magnetic resonance imaging. *Cognitive Brain Research*, 23(2), 361–373.
- Bruffaerts, R., De Weer, A. S., De Grauwe, S., Thys, M., Dries, E., Thijs, V., et al. (2014). Noun and knowledge retrieval for biological and non-biological entities following right occipitotemporal lesions. *Neuropsychologia*, 62, 163–174.
- Buxbaum, L. J., Veramonti, T., & Schwartz, M. F. (2000). Function and manipulation tool knowledge in apraxia: knowing “what for” but not “how”. *Neurocase*, 6, 83–97.
- Canessa, N., Borgo, F., Cappa, S. F., Perani, D., Falini, A., Buccino, G., & Shallice, T. (2008). The different neural correlates of action and functional knowledge in semantic memory: an fMRI study. *Cerebral Cortex*, 18(4), 740–751.
- Cant, J. S., & Goodale, M. A. (2007). Attention to form or surface properties modulates different regions of human occipitotemporal cortex. *Cerebral Cortex*, 17, 713–731.
- Carey, D. P., Harvey, M., & Milner, A. D. (1996). Visuomotor sensitivity for shape and orientation in a patient with visual form agnosia. *Neuropsychologia*, 34(5), 329–337.
- 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, 1–14.
- Chao, L. L., Haxby, J. V., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about object. *Nature Neuroscience*, 2, 913–919.
- Chao, L. L., & Martin, A. (2000). Representation of manipulable man-made objects in the dorsal stream. *NeuroImage*, 12, 478–484.

- Chen, Q., Garcea, F. E., & Mahon, B. Z. (2016). The representation of object-directed action and function knowledge in the human brain. *Nature Neuroscience*, 26, 1609–1618.
- Cubelli, R., Marchetti, C., Boscolo, G., & Della Salla, S. (2000). Cognition in action: testing a model of limb apraxia. *Brain and Cognition*, 44, 144–165.
- Culham, J. C., Danckert, S. L., De Souza, J. F., Gati, J. S., Menon, R. S., & Goodale, M. A. (2003). Visually guided grasping produces fMRI activation in dorsal but not ventral stream brain areas. *Experimental Brain Research*, 153, 180–189.
- Downing, P. E., Jiang, Y., Shuman, M., & Kanwisher, N. (2001). A cortical area selective for visual processing of the human body. *Science*, 293(5539), 2470–2473.
- Epstein, R., Harris, A., Stanley, D., & Kanwisher, N. (1999). The parahippocampal place area: recognition, navigation, or encoding? *Neuron*, 23(1), 115–125.
- Fang, F., & He, S. (2005). Cortical responses to invisible objects in the human dorsal and ventral pathways. *Nature Neuroscience*, 8, 1380–1385.
- Fintzi, A. R., & Mahon, B. Z. (2014). A bimodal tuning curve for spatial frequency across left and right human orbital frontal cortex during object recognition. *Cerebral Cortex*, 24, 1311–1318.
- 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, 1–8.
- 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.
- Gallivan, J. P., Johnsrude, I. S., & Flanagan, J. R. (2016). Planning ahead: object-directed sequential actions decoded from human frontoparietal and occipitotemporal networks. *Cerebral Cortex*, 26, 708–730.
- Garcea, F. E., Almeida, J., & Mahon, B. Z. (2012). A right visual field advantage for visual recognition of manipulable objects. *Cognitive, Affective, and Behavioral Neuroscience*, 12, 813–825.
- Garcea, F. E., Dombovy, M., & Mahon, B. Z. (2013). Preserved tool knowledge in the context of impaired action knowledge: implications for models of semantic memory. *Frontiers in Human Neuroscience*, 7, 1–18.
- Garcea, F. E., & Mahon, B. Z. (2014). Parcellation of left parietal tool representations by functional connectivity. *Neuropsychologia*, 60, 131–143.
- Goldenberg, G. (2009). Apraxia and the parietal lobes. *Neuropsychology*, 47, 1449–1459.
- Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, 15(1), 20–25.
- Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature*, 349(6305), 154–156.
- Grill-Spector, K., & Malach, R. (2004). The human visual cortex. *Annual Review of Neuroscience*, 27, 649–677.
- Handy, T. C., Grafton, S. T., Shroff, N. M., Ketay, S., & Gazzaniga, M. S. (2003). Graspable objects grab attention when the potential for action is recognized. *Nature Neuroscience*, 6(4), 421–427.
- Hutchison, R. M., Culham, J. C., Everling, S., Flanagan, J. R., & Gallivan, J. P. (2014). Distinct and distributed functional connectivity patterns across cortex reflect the domain-specific constraints of object, face, scene, body, and tool category-selective modules in the ventral visual pathway. *NeuroImage*, 96, 216–236.
- Ishai, A., Ungerleider, L. G., Martin, A., Schouten, J. L., & Haxby, J. V. (1999). Distributed representation of objects in the human ventral visual pathway. *Proceedings of the National Academy of Sciences*, 96(16), 9379–9384.
- Johnson-Frey, S. (2004). The neural bases of complex tool use in humans. *Trends in Cognitive Sciences*, 8, 71–78.
- Kanwisher, N., McDermott, J., & Chun, M. M. (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. *The Journal of Neuroscience*, 17(11), 4302–4311.
- Kellenbach, M., Brett, M., & Patterson, K. (2003). Actions speak louder than functions: the importance of manipulability and action in tool representation. *Journal of Cognitive Neuroscience*, 15(1), 30–46.
- Konen, C. S., Mruczek, R. E. B., Montoya, J. L., & Kastner, S. (2013). Functional organization of human posterior parietal cortex: grasping- and reaching-related activations relative to topographically organized cortex. *Journal of Neurophysiology*, 109, 2897–1908.
- Kravitz, D. J., Kriegeskorte, N., & Baker, C. I. (2010). High-level visual object representations are constrained by position. *Cerebral Cortex*, 20(12), 2916–2925.
- Kravitz, D. J., Peng, C. S., & Baker, C. I. (2011b). Real-world scene representations in high-level visual cortex: it's the spaces more than the places. *The Journal of Neuroscience*, 31(20), 7322–7333.
- Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011a). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience*, 12(4), 217–230.
- Kravitz, D. J., Vinson, L. D., & Baker, C. I. (2008). How position dependent is visual object recognition? *Trends in Cognitive Sciences*, 12(3), 114–122.
- Levy, I., Hasson, U., Avidan, G., Hendler, T., & Malach, R. (2001). Center–periphery organization of human object areas. *Nature Neuroscience*, 4(5), 533–539.
- Lewis, J. (2006). Cortical networks related to human use of tools. *The Neuroscientist*, 12, 211–231.
- Liepmann, H. (1905). The left hemisphere and action. (Translation from Munch. Med. Wschr. 48–49). (Translations from Liepmann's essays on apraxia. In Research Bulletin (Vol. 506). London, Ont.: Department of Psychology, University of Western Ontario; 1980).
- Mahon, B. Z., & Caramazza, A. (2005). The orchestration of the sensory-motor systems: clues from neuropsychology. *Cognitive Neuropsychology*, 22, 480–494.
- Mahon, B. Z., & Caramazza, A. (2009). Concepts & categories: a cognitive neuropsychological perspective. *Annual Review of Psychology*, 60, 27–51.
- 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, 862–871.
- Mahon, B. Z., Milleville, S., Negri, G. A. L., Rumiati, R. I., Caramazza, A., & Martin, A. (2007). Action-related properties of objects shape object representations in the ventral stream. *Neuron*, 55, 507–520.
- Martin, A. (2007). The representation of object concepts in the brain. *Annual Review of Psychology*, 58, 25–45.
- Martin, A. (2009). Circuits in mind: the neural foundations for object concepts. In M. S. Gazzaniga (Ed.), *The Cognitive Neurosciences* (4th ed., pp. 1031–1046). Cambridge, MA: MIT Press.
- Milner, A. D., & Goodale, M. A. (2008). Two visual systems reviewed. *Neuropsychologia*, 46(3), 774–785.
- Mruczek, R. E., von Loga, I. S., & Kastner, S. (2013). The representation of tool and non-tool object information in the human intraparietal sulcus. *Journal of Neurophysiology*, 109, 2883–2896.
- Negri, G. A. L., Rumiati, R. I., Zadini, A., Ukmair, M., Mahon, B. Z., & Caramazza, A. (2007). What is the role of motor simulation in action and object recognition? Evidence from apraxia. *Cognitive Neuropsychology*, 24, 795–816.
- Nichols, T., Brett, M., Andersson, J., Wager, T., & Poline, J.-B. (2004). Valid conjunction inference with the minimum statistic. *NeuroImage*, 25, 653–660.
- Noppeney, U., Price, C. J., Penny, W. D., & Friston, K. J. (2006). Two distinct neural mechanisms for category-selective responses. *Cerebral Cortex*, 16, 437–445.

- Ochipa, C., Rothi, L. J. G., & Heilman, K. M. (1989). Ideational apraxia: a deficit in tool selection and use. *Annals of Neurology*, 25, 190–193.
- Op de Beeck, H. P., Haushofer, J., & Kanwisher, N. G. (2008). Interpreting fMRI data: maps, modules and dimensions. *Nature Reviews Neuroscience*, 9(2), 123–135.
- Orban, G. A., Zhu, Q., & Vanduffel, W. (2014). The transition in the ventral stream from feature to real-world entity representations. *Frontiers in Psychology*, 5.
- Osiurak, F. (2014). What neuropsychology tells us about human tool use? the four constraints theory (4CT): mechanics, space, time, and effort. *Neuropsychology Review*, 24(2), 88–115.
- Peelen, M. V., & Downing, P. E. (2007). The neural basis of visual body perception. *Nature Reviews Neuroscience*, 8(8), 636–648.
- Peeters, R. R., Rizzolatti, G., & Orban, G. A. (2013). Functional properties of the left parietal tool use region. *NeuroImage*, 78, 83–93.
- Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: transforming numbers into movies. *Spatial Vision*, 10, 377–401.
- Pitzalis, S., Galletti, C., Huang, R. S., Patria, F., Committeri, G., Galati, G., et al. (2006). Wide-field retinotopy defines human cortical visual area v6. *Journal of Neuroscience*, 26, 7962–7973.
- Rizzolatti, G., & Matelli, M. (2003). Two different streams form the dorsal visual system: anatomy and functions. *Experimental Brain Research*, 153, 146–157.
- 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, 2525–2541.
- Rothi, L. J. G., Ochipa, C., & Heilman, K. M. (1991). A cognitive neuropsychological model of limb praxis. *Cognitive Neuropsychology*, 8, 443–458.
- Rumiati, R. I., Weiss, P. H., Shallice, T., Ottoboni, G., Noth, J., Zilles, K., et al. (2004). Neural basis of pantomiming the use of visually presented objects. *NeuroImage*, 21(4), 1224–1231.
- Rushworth, M. F. S., Behrens, T. E. J., & Johansen-Berg, H. (2006). Connection patterns distinguish 3 regions of human parietal cortex. *Cerebral Cortex*, 16, 1418–1430.
- Schwarzbach, J. (2011). A simple framework (ASF) for behavioral and neuroimaging experiments based on psychophysics toolbox for MATLAB. *Behavioral Research*, 43, 1194–1201.
- Stevens, W. D., Tessler, M. H., Peng, C. S., & Martin, A. (2015). Functional connectivity constrains the category-related organization of human ventral occipitotemporal cortex. *Human Brain Mapping*, 36, 2187–2206.
- Talairach, J., & Tournoux, P. (1988). *Co-planar stereotaxic atlas of the human brain*. New York: Thieme.
- Ungerleider, L. G., & Mishkin, M. (1982). Two cortical visual systems. In D. J. Ingle, M. A. Goodale, & R. J. W. Mansfield (Eds.), *Analysis of visual behavior* (pp. 549–586). Cambridge: MIT Press.
- Valyear, K. F., & Culham, J. C. (2010). Observing learned object-specific functional grasps preferentially activates the ventral stream. *Journal of Cognitive Neuroscience*, 22(5), 970–984.
- Vingerhoets, G. (2014). Praxis, language, and handedness: a tricky triad. *Cortex*, 57, 294–296.