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Original Article

ORIGINAL ARTICLE

What Role Does "Elongation" Play in "Tool-Specific" Activation and Connectivity in the Dorsal and Ventral Visual Streams?

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Abstract

Images of tools induce stronger activation than images of nontools in a left-lateralized network that includes ventral-stream areas implicated in tool identification and dorsal-stream areas implicated in tool manipulation. Importantly, however, graspable tools tend to be elongated rather than stubby, and so the tool-selective responses in some of these areas may, to some extent, reflect sensitivity to elongation rather than "toolness" *per se*. Using functional magnetic resonance imaging, we investigated the role of elongation in driving tool-specific activation in the 2 streams and their interconnections. We showed that in some "tool-selective" areas, the coding of toolness and elongation coexisted, but in others, elongation and toolness were coded independently. Psychophysiological interaction analysis revealed that toolness, but not elongation, had a strong modulation of the connectivity between the ventral and dorsal streams. Dynamic causal modeling revealed that viewing tools (either elongated or stubby) increased the connectivity from the ventral- to the dorsal-stream tool-selective areas, but only viewing elongated tools increased the reciprocal connectivity between these areas. Overall, these data disentangle how toolness and elongation affect the activation and connectivity of the tool network and help to resolve recent controversies regarding the relative contribution of "toolness" versus elongation in driving dorsal-stream "tool-selective" areas.

Key words: tool, elongation, connectivity, dynamic causal modeling (DCM), psychophysiological interactions (PPIs)

Introduction

Tools are objects that people use to perform actions. More specifically, tools have been defined as manipulable objects that can transform people's "motor output into predictable mechanical actions" (Frey 2007). Therefore, unlike many other objects in the world, such as furniture, animals, body parts, and buildings, tools are tightly linked to specific actions (Mruczek et al. 2013). For this reason, images of tools activate not only ventral-stream areas implicated in tool identification, but also dorsal-stream areas implicated in the visual control of actions (for review, see Lewis 2006). Tool-selective areas in the ventral stream that are typically activated by images of tools include the medial fusiform gyrus (mFG) (Chao et al. 1999; Whatmough et al. 2002; Mahon et al. 2007; Garcea and Mahon 2014) and the lateral occipito-temporal cortex (LOTC) (Bracci et al. 2012; Perini et al. 2014), which encompasses the middle temporal gyrus (MTG) (Chao et al. 1999; Kellenbach et al. 2003; Emmorey et al. 2004; Boronat et al. 2005; Valyear and Culham 2009; Macdonald and Culham 2015). Tool-selective areas activated in the dorsal stream include the intraparietal sulcus (IPS), the inferior parietal lobule (IPL [it should be noted that it is not clear whether or not IPL should be regarded as strictly a dorsal area, given that it receives inputs from both the dorsal and the ventral streams {Milner and Goodale 2006; Milner and Goodale 2008}]), and superior parietal lobule (SPL) (Chao and Martin 2000; Buxbaum and Saffran 2002; Boronat et al. 2005; Hermsdörfer et al. 2007; Peeters et al. 2009;

Mruczek et al. 2013; Macdonald and Culham 2015). Finally, tool-selective activation has also been reported in regions within the ventral and dorsal premotor (PM) cortex (Chao and Martin 2000; Kellenbach et al. 2003; Creem-Regehr and Lee 2005; Johnson-Frey et al. 2005).

The ventral- and dorsal-stream tool-selective areas have been shown to play different roles in processing information about tools (Carey et al. 1996; Buxbaum et al. 1997; Buxbaum et al. 2000; Buxbaum and Saffran 2002; Boronat et al. 2005; Negri et al. 2007; Canessa et al. 2008; Goldenberg and Spatt 2009; Almeida et al. 2010; Almeida et al. 2013; Mahon et al. 2013; Kristensen et al. 2016; Chen et al. 2016a). For example, damage to MTG and lateral occipital complex disrupts knowledge about the identity and function of tools (Buxbaum and Saffran 2002; Negri et al. 2007), whereas and damage to IPL, especially the supramarginal gyrus (SMG), interferes with the ability to manipulate a tool (Randerath et al. 2010). In contrast, damage to SPL and the posterior IPS affects reaching toward tools and/or selecting the correct posture of the grasping hand (Buxbaum and Saffran 2002; Binkofski and Buxbaum 2013; Wood et al. 2016). The idea that these different areas in the parietal cortex play different roles in tool processing is also supported by connectivity studies showing that, compared with the tool-selective region in SPL, the tool-selective regions within IPL and the anterior part of the IPS have stronger connectivity with the tool-selective areas in the ventral stream (left mFG or left MTG) (Almeida et al. 2013; Mahon et al. 2013; Garcea and Mahon 2014; Kristensen et al. 2016).

Fang and He (2005) showed that images of tools made invisible with continuous flash suppression (CFS) continued to activate the dorsal but not the ventral pathway (but see Hesselmann and Malach 2011). They suggested that ventral-stream areas might not be necessary for processing tool stimuli and that the dorsal stream by itself can process actions related to tools. This conclusion would appear to be supported by behavioral CFS studies showing that participants were faster at categorizing a visible picture of a tool when it was preceded by an invisible tool, but this priming effect was not observed with pictures of animals primed with invisible animals (Almeida et al. 2008; Almeida et al. 2010). It could indeed be the case that the activity in the dorsal stream observed by Fang and He (2005) reflects the involvement of this stream in tool-related action—and that this activity can somehow prime the categorization of tools. But there is another possibility. Most tools are elongated, whereas animals, faces, and other stimuli used in these studies are not (Almeida et al. 2008; Almeida et al. 2014; Fang and He 2015). Thus, the activity in the dorsal stream and the priming of tool categorization might not be due to the toolness of the stimuli as much as to their characteristic shape (i.e., elongation). In other words, any elongated objects, not just tools, may escape the effects of CFS. Indeed, 2 recent studies using a CFS paradigm showed that even elongated vegetables or elongated stick figures or animals, but not stubby or round tools, induced a significant priming effect with tool targets but not with animal targets (Sakuraba et al. 2012; Almeida et al. 2014). The possibility that some part of the dorsal stream is sensitive to elongation is supported by the observation that there are neurons in caudal IPS that prefer elongated stimuli (Sakata et al. 1998). Additional evidence comes from the observation that patient DF, who has visual form agnosia from a bilateral ventral-stream lesion, is able to grasp objects proficiently when they have a clear principal axis (i.e., when they are elongated) but not when they have more than 1 axis (Goodale et al. 1994; Carey et al. 1996). Together, these findings suggest that elongation may drive some of the "tool-related" activity in the dorsal stream and it is far from clear how the elongated shape of tools and their "toolness" interact in driving tool-specific activation and connection (Macdonald and Culham 2015; Bracci and Op de Beeck 2016).

Here, we address this issue by examining the extent to which activity in different "tool-selective" areas in the dorsal and ventral streams, and their interconnectivity, are modulated by toolness versus elongation. Psychophysiological interaction (PPI) (Friston et al. 1997) and dynamic causal modeling (DCM) (Friston et al. 2003) were applied in the connectivity analyses.

Materials and Methods

Participants

Twenty-one participants (10 males and 11 females) took part in the main functional magnetic resonance imaging (fMRI) experiment. The data from 2 participants were discarded because of excessive head movements (>3 mm in translation or >1° in rotation within a run). Data from one other participant were also discarded because she fell asleep during the scanning. Therefore, 18 participants' data were included in the analysis of the main experiment. Seven of the 18 included participants also completed 2 separate runs for a functional localizer (see Stimuli and Procedures for details). Eleven of the 18 participants and a new participant completed 3 questionnaires as to the familiarity, toolness, and graspability/manipulability of all stimuli after the fMRI experiment. The participants were students of the University of Western Ontario. All were right-handed and had normal or corrected-to-normal vision. Their ages ranged between 18 and 30 years (mean age = 21.3). All participants gave informed consent and the protocol was approved by the University of Western Ontario Ethics Review Board.

Stimuli

The stimuli used in the main experiment consisted of grayscale images of everyday elongated tools, stubby tools, elongated nontools, and stubby nontools (Fig. 1, see Supplementary Fig. 1 for all exemplars). There were 20 exemplars for each category. Following Frey (2007), we define tools as graspable and manipulable objects that can transform "motor output into predictable mechanical actions for the purposes of attaining specific goals." We think that there are 3 features that are typically associated with the concept of "tool." First, tools usually increase the mechanical advantage and/or the reach of our limbs. For example, a rake extends the reach of our arms and allows us to

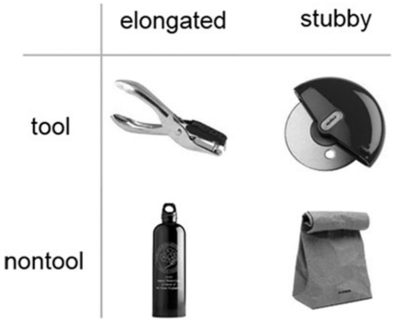

Figure 1. Stimuli. The 4 kinds of grayscale photographs that were used in the main experiment including elongated tools, stubby tools, elongated nontools, and stubby nontools.

gather up leaves efficiently. Second, there is a systematic relationship between the physical form of a tool and the manner in which the tool is typically manipulated (Mahon et al. 2007; Skiba and Snow 2016). Third, there is consensus about how particular tools should be employed, which is why we give tools particular names, such as "hammer" or "screwdriver." All the tool stimuli were selected based on these 3 features of the concept of "tool." Elongated objects were objects whose visual length/width ratios were at least 2.5. Stubby objects were objects whose length/width ratios were smaller than 2.5. The average length/width ratios of the 4 categories, elongated tools, stubby tools, elongated nontools, and stubby nontools, were 4.54, 1.52, 4.89, and 1.26, respectively. Note that although the stimuli were selected according to the length/width ratio, we did not match perfectly the overall ratios for the 2 stubby conditions. Specifically, the stubby tools had a slightly higher length/width ratio than the stubby nontools (independent sampled t-test, $P = 0.021$). We discuss the potential influence of this difference in the Results section. The images subtended a visual angle of 10° ×10°. All of nontools were graspable objects (Rice et al. 2007; Valyear et al. 2007; Mruczek et al. 2013). To avoid a confound due to the animate versus inanimate difference (Bracci et al. 2016; Lu et al. 2016; Proklova et al. 2016), all the nontools were inanimate objects.

Numerous studies have used a completely different category of objects, such as animals or faces as a contrasting category to define tool-selective areas (Perani et al. 1995; Chao and Martin 2000; Lewis et al. 2005; Garcea and Mahon 2014). Tools tend to be elongated, and are inanimate and graspable, whereas animals are typically not. Also, many animals are much larger in real world than typical tools that are graspable. As a result, some of the differences between tools and animals in activation in these studies may be attributed to differences in animacy (Lu et al. 2016; Proklova et al. 2016), overall shape (Sakuraba et al. 2012; Bracci and Op de Beeck 2016; Proklova et al. 2016), real-world size (Konkle and Oliva 2012), graspability (Rice et al. 2007; Valyear et al. 2007; Macdonald and Culham 2015), or their interactions. In the current study, we controlled for these potential confounds even though we expected that fewer areas would be activated, because we were focusing on the particular attributes of tools that are central to their "toolness." Nevertheless, given that a (tools > animals) contrast has been used frequently to identify tool areas in other studies, we also examined how tool areas identified by this contrast responded to toolness and elongation. Specifically, we also tested 7 of our participants with images of tools and animals in 2 separate runs to localize tool-selective areas using this contrast (tools > animals). These areas were used in the region of interest (ROI) analysis and one of these areas (i.e., left mFG) was used in the connectivity analysis. The stimuli used in the 2 separate localizer runs were grayscale images of animals and tools, which have been used in previous studies (Mahon et al. 2013; Chen et al. 2016b). There were 12 items per category and 8 exemplars per item. The localizer images were the same size as the images used in the main experiment.

Procedure and Design

A block design was adopted in both the main experiment and the 2 localizer runs. In the main experiment, MATLAB software (MathWorks) and PsychToolbox (Brainard 1997; Pelli 1997) were used for stimulus presentation. In each run, 8 stimulus blocks were interleaved with 8 blocks of rest (fixation). In a stimulus block, 18 images were presented in the center of the screen, each for 0.5 s, followed by a 0.5-s fixation. These 18 images were randomly selected from the 20 exemplars of a particular category. The fixation point was always located in the center of the screen during the stimulus block. During the 18-s rest block, only the central fixation point was present. There were 8 stimulus blocks in each run, that is, 2 blocks for each of the 4 different stimulus categories presented in random order. All participants completed 9 runs. Participants were instructed to maintain fixation at the center of the screen throughout the run and the stimuli were viewed passively as in previous imaging studies that have demonstrated stronger activation for tools than nontools (Chao and Martin 2000; Creem-Regehr and Lee 2005; Macdonald and Culham 2015).

Seven participants completed 2 additional runs designed to localize tool-selective areas by the (tools > animals) contrast. "A Simple Framework" (Schwarzbach 2011) was used for stimulus presentation. Two types of stimulus blocks were presented, one with tools, and the other with animals. Each stimulus block was 12 s in duration, interleaved with a 12-s rest block. In a stimulus block, 24 images were presented, each image lasting 0.5 s. There were 8 blocks in each run for each type of stimulus (tools and animals) and 16-s blank at the beginning and the end of each run.

To examine the nature of the influence of elongation on tool processing, participants also completed 3 questionnaires after the fMRI experiment to rate how familiar they were with the images, the extent to which they regarded each of the object as a tool, and how graspable/manipulable the objects were on a scale from 1 to 5. Three statements were presented: "I am familiar with this object", "I think this is a tool," and "This object is easy to grasp or manipulate". In all cases, "1" indicated "strongly disagree" and "5" indicated "strongly agree."

MRI Data Acquisition

fMRI data were collected using a 3-T Siemens Tim Trio system at the Robarts Research Institute with the posterior 20 channels of a 32-channel head coil placed beneath the head, and a 4-channel flex coil suspended over the forehead (to increase signal in frontal areas). In the scanner, the stimuli were back-projected via a video projector (refresh rate, 60 Hz; spatial resolution, 1024 × 768) onto a translucent screen placed inside the scanner bore. Participants viewed the stimuli via a mirror, mounted to the head coil. Functional images were collected with an echo planar imaging sequence (echo time, 30 ms; repetition time, 2000 ms; field of view, 196 × 196 mm^2; matrix, 64 × 64; flip angle, 90°; slice thickness, 3 mm; gap, 0 mm; number of slices, 36; slice orientation, axial). The lowest slice was aligned with the bottom of the temporal lobules. A high-resolution 3D structural dataset (3D magnetization-prepared rapid acquisition gradient echo; 1 × 1 × 1 mm^3 resolution) was collected in the same session as the functional data, midway through the functional runs.

Data Analysis

SPM8 (Statistical Parametric Mapping software, University College of London, London, UK; available at: http://www.fil.ion.ucl.ac.uk/spm) was used to preprocess the data, and to perform general linear model (GLM) analysis, PPI analysis, and DCM analysis.

fMRI Data Preprocessing

First, a slice-time correction algorithm was used to correct for differences in acquisition times between slices by resampling all slices to match the 18th slice of the 36 slices for each functional image. Images from the 9 runs were coregistered by aligning the first image from each run to that of the first run, and then the remaining images from each run were aligned to the first image within the run. The functional images were then coregistered with the anatomical images using the mean functional image of the first run as reference. Anatomical images were segmented so that a spatial normalization file was generated, which was then used to normalize the functional images into the standardized Montreal Neurological Institute (MNI) space. Lastly, all functional images were smoothed with a 6-mm full-width half-maximum Gaussian filter.

Voxel-Wise GLM Group Analysis

To investigate how "toolness" and "elongation" modulate the activation in the cortex, we performed voxel-wise GLM group analysis using a random-effects model. The 4 stimulus types, elongated tools, stubby tools, elongated nontools, and stubby nontools, were included as regressors in the analysis. Regressors were based on square-wave functions for each type of block (i.e., 18 s or 9 volumes), convolved with the default hemodynamic response function (HRF). Head movements during each run were also included as regressors of no interest. The *P* values were corrected with a false discovery rate (FDR) correction at cluster-level with a starting voxel-level *P* value of 0.001. We identified areas that were activated by the (tools > nontools) contrast and the (elongated > stubby) contrast. No areas were identified by the interaction between toolness and shape, therefore, we did not identify areas that were activated by the (tools > nontools) contrast for elongated and stubby shape separately (i.e., [elongated tools > elongated nontools] and [stubby tools > stubby nontools]) and the (elongated > stubby) contrast for tools and nontools separately. The same method was used to identify areas that were activated by the (tools > animals) contrast but with a liberal *P* value ($P < 0.05$, uncorrected).

ROI Analysis

We also investigated activity related to toolness and elongation in tool-selective areas using a ROI analysis in which the ROIs were defined by a (tools > animals) contrast, a contrast that has been often used before (Perani et al. 1995; Chao et al. 1999; Lewis et al. 2005; Garcea and Mahon 2014). We used a liberal *P* value ($P < 0.05$, uncorrected). Note that this liberal *P* value was used only to identify ROIs. All statistical inferences (i.e., repeated-measures ANOVAs and paired-samples *t*-tests) were performed on the beta values extracted from each ROI.

ROI Definitions for Connectivity Analyses

To investigate how toolness and elongation modulate the connectivity between the tool-selective areas in the ventral and dorsal streams, we performed PPI and DCM analyses. The ROIs for these analyses were defined based on the GLM results or Atlas template. Because the voxel-wise GLM results revealed a left-lateralized tool network, which is consistent with previous studies (Gallivan et al. 2013b; Mruczek et al. 2013; Brandi et al. 2014; Macdonald and Culham 2015; Bracci et al. 2016), we conducted the connectivity analyses "only" in the left hemisphere. The left anterior IPS (ant IPS), left SPL, and left MTG were defined based on the (tools > nontools) contrast at group level ($P < 0.05$, FDR corrected). The left mFG was defined based on the (tools > animals) contrast from the localizer data at group level but with a relatively liberal *P* value ($P < 0.05$, uncorrected). Note again that this liberal *P* value was used only to identify ROIs for the connectivity analysis. All statistical inferences were based on corrected group data (corrected group voxel-wise data and conventional approaches to connectivity analyses). Left V1 was defined by the (all conditions > rest) contrast ($P < 0.05$, FDR corrected) masked by the Atlas template of left V1 (Wake Forest University Pick Atlas; Maldjian et al. 2003). Left ant IPS, SPL, MTG, and mFG were used as seed areas for PPI analysis. These 4 areas together with left V1 were used for DCM analysis.

Connectivity Analysis: Method 1—PPI

We first performed PPI analysis to investigate how toolness and elongation modulate the interaction between areas in the tool network. PPI analysis looks for a significant difference in the regression slopes of the activity in 2 areas in different contexts or tasks. It searches for significant context-specific or task-specific changes in connectivity, not just a correlation between the signals of 2 areas in general. One advantage of PPI is that it is data—rather than hypothesis-driven, thereby ensuring that the results are not constrained by a particular hypothesis (Friston et al. 1997; O'Reilly et al. 2012).

The PPI analysis was performed following the standard procedures described in the SPM8.0 manual (http://www.fil.ion.ucl.ac.uk/spm/doc/spm8_manual.pdf). For each participant, we first extracted the time course of each ROI. Then, the time course of each experimental contrast was created using a value of −1, 0, or 1 for each time point, depending on the contrast weight of the corresponding condition at that time point: the contrast weights of conditions of interest were 1 or −1; whereas the contrast weights of conditions of no interest were 0. For example, to explore the effect of toolness, the contrast weights were 1 for all the time points when elongated tools or stubby tools were presented, −1 for all the time points when elongated nontools or stubby nontools were presented, and 0 for all time points of the rest blocks. Similarly, to explore the effect of elongation, the contrast weights were 1 for all the time points when elongated tools or elongated nontools were presented, −1 for all the time points when stubby tools or stubby nontools were presented, and 0 for all time points of the rest blocks. The time course of the experimental contrast was then convolved with the HRF to generate an HRF-convolved task time course. After that, the PPI variables were created as the element-by-element product of the HRF-convolved task time course and the seed ROI time course. A new GLM was designed with the first regressor as the PPI variable created above (i.e., the psychophysiological interaction term). The significance of this regressor indicates which area is more correlated with the seed area under a specific experimental contrast (e.g., [tools > nontools] or [elongated > stubby], or the contrast between any pairs of conditions). Using this method, the interaction term is generated as the product of the seed ROI time course and the HRF-convolved experimental contrast time course; however, regions that show an effect of the contrast or are correlated with the seed ROI regardless of task may also show a significant interaction. To deal with this, 2 additional regressors were included as covariates of no interest: one regressor was the seed ROI time course and the other was the HRF-convolved experimental contrast time course. The psychophysiological interaction was estimated for each voxel in the whole brain for each participant, and was then subjected to a second-level random-effects analysis in order to evaluate group differences. In summary, an area composed of voxels with significant psychophysiological interactions suggests that the coupling between this area and the seed area is stronger in one condition than it is in the other, depending on the contrast weights of the conditions of interest.

Connectivity Analysis: Method 2—DCM

PPI tested for context-dependent connectivity across the entire brain. With a combination of voxel-wise GLM and PPI, we have a better idea of which areas are involved in tool network. Unfortunately, PPI is based on regression analysis, and therefore cannot indicate the direction of the modulation between 2 connected areas. It is possible to get different results if the seed and target areas are switched, just like in any regression, but the asymmetry does not indicate the direction of modulation because the quality of fit depends only on residuals in the dependent variable. In the next step, we used DCM to test how each condition modulated the connection between ventral tool areas and dorsal tool areas. This allowed us to determine what the direction of the modulation was (i.e., from ventral to dorsal or from dorsal to ventral) and how strong the modulation was in each direction. Statistical analyses were performed on the strengths of the modulation in each direction.

The DCM analysis followed the standard procedures described in the SPM8.0 manual (http://www.fil.ion.ucl.ac.uk/spm/doc/spm8_manual.pdf). Broadly speaking, DCM is a method for making inferences about the neural processes that underlie measured fMRI data. Unlike PPI, which rests directly upon fMRI signals, DCM employs an explicit forward model of how the fMRI signals were caused based on the hidden neuronal and biophysical state and the hemodynamic model. Both the neuronal states and hemodynamic model are specified by nonlinear differential equations in continuous time with parameters that encode the strength and direction of connections and the modulation of experimental factors. These parameters were estimated with Bayesian theory so that the predicted fMRI signal of the model fits the observed fMRI signal. Causality in DCM means that the dynamics in one area cause dynamics in another area in a control theory sense (Friston 2009). Different models incorporating different hypotheses of neural connectivity must be constructed at the beginning of the analysis. Statistical analyses can be performed on the estimated parameters that reflect the strength of the modulations.

Here, we defined our model space according to the results of the voxel-wise GLM and PPI analyses, previous findings on the tool network, and prior knowledge about the inputs from early visual areas. Similar to the PPI analysis, the DCM analysis was also performed only on the left hemisphere. First, given that our research question centers on how toolness and elongation modulated the effective connectivity between the ventral and dorsal "tool-specific" areas, we included only those areas that responded to tools more strongly than nontools (i.e., left ant IPS, SPL, and MTG) in the current DCM analysis. The left PM cortex, which was activated only by the (elongated > stubby) contrast, was not included. The left mFG, which was defined by the (tools > animals) contrast, was also included because previous studies show that it has connections with the left IPL and left MTG (e.g., Mahon et al. 2007; Garcea and Mahon 2014). Second, for simplicity, we include only one area in the ventral stream (either left MTG or left mFG), one area in the dorsal stream (either left ant IPS or left SPL) in each model. Third, we hypothesized that the input to the tool network comes from the primary visual cortex (V1). Therefore, there are 4 groups of ROIs (i.e., V1-MTG-ant IPS, V1-MTG-SPL, V1-mFG-ant IPS, and V1-mFG-SPL). Fourth, we assumed that the connections between 2 areas were always bidirectional. This is a conservative assumption, given that the interconnectivity between areas could be direct or indirect. Finally, in separate models, we hypothesized that the experimental factor modulates only the projection from the ventral (V) stream to the dorsal (D) stream, or only the projection from D to V, or both (Fig. 2). The PPI results suggest that toolness or elongation does not modulate the connectivity between V1 and the ventral tool areas (left MTG or left mFG) or the connectivity between V1 and the dorsal tool areas (left ant IPS or left SPL). Therefore, we did not test the direction of modulation between V1 and D or between V1 and V. In summary, there are 3 kinds of modulations resulting in a model space with 3 models for each pair of the ventral and dorsal areas (Fig. 2). The model parameters were estimated for each direction of modulation and for each of the 3 conditions: elongated tools, stubby tools, and elongated nontools, with the stubby nontool condition as baseline. The parameters of each model were estimated with Bayesian theory so that the predicted fMRI signal of the model fits the observed fMRI signal. The model parameters that indicated the strength of modulation were then averaged across the 3 models in model space with weights that were given by the evidence of each model (i.e., Bayesian model averaging; Penny et al. 2010). This was done for each subject. The parameters that reflect the strength of each direction of modulation of all subjects were then put into group analyses (one sample *t*-test, paired *t*-test, or ANOVA).

It should be emphasized that PPI analysis was important in the current study. The PPI and DCM results are complementary to each other. Although PPI cannot indicate the "direction" of connection between brain areas (as does DCM), PPI is data-driven and therefore is not constrained by any particular hypothesis. Thus, PPI analysis can reveal task-modulated connectivity between areas within the whole brain volume. It is possible that PPI can reveal areas that are not shown by simple (tools > nontools) contrast but have task-modulated connection with tool areas. For this reason, we used PPI as a first step to reveal areas whose connection with tool-selective areas activated by the (tools > nontools) contrast are modulated by toolness or elongation. We then selected ROIs for the DCM analysis on the basis of the PPI analysis as well as the GLM analysis. If an area was revealed in both GLM and PPI analyses, then this area was considered as a candidate for the subsequent hypothesis-driven DCM analysis. Moreover, if PPI revealed that the connectivity between 2 areas was modulated by "toolness" or elongation, then we tested the direction of this modulation

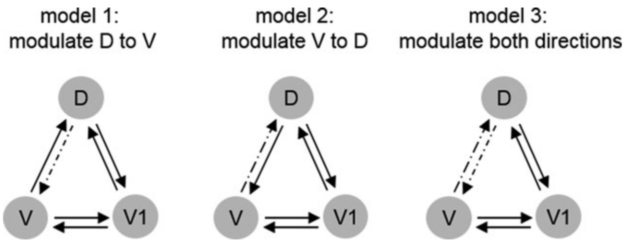

Figure 2. The model space for the DCM analysis. The lines with arrows, either dashed or solid, indicate that there are intrinsic connections between the different ROIs. Dashed lines indicate that a connection is modulated by a specific condition; arrows indicate the direction of that modulation. "V" indicates a ventral tool area, which was either left MTG or left mFG, depending on the analysis that was conducted. "D" indicates a dorsal tool area, which was either left ant IPS or left SPL, again depending on the analysis that was conducted.

in the DCM analysis. In other words, we used the results of PPI analysis to create and constrain the model space of the DCM analysis.

Results

Voxel-Wise GLM Group Analysis

The overall (tools > nontools) contrast, with both elongated and stubby shapes included, activated bilateral anterior IPS (ant IPS), SPL, and MTG (Table 1 and Fig. 3A). The activations were stronger and larger in the left hemisphere than in the right. This left lateralization is consistent with previous networks identified for tool-related (Johnson-Frey 2004; Lewis 2006) and action-related (Culham and Valyear 2006; Gallivan and Culham 2015) stimuli. No activation was observed in left mFG. The overall (elongated > stubby) contrast, with both tools and nontools included, revealed significant activity in bilateral MTG and SPL, left middle and posterior IPS (mid and post IPS), and left PM cortex (Table 1 and Fig. 3B). Compared with the (tools > nontools) contrast, the (elongated > stubby) contrast appeared to activate larger areas in bilateral MTG and left posterior parietal cortex and was less left-lateralized. Left mid and post IPS and left PM are activated only by the (elongated > stubby) contrast but not by the (tools > nontools) contrast.

The interaction between "toolness" and shape (elongation vs. stubby) was not significant in any area, suggesting that modulation of toolness by shape was not significantly different for tools and nontools, and the modulation of shape by toolness was not significantly different for elongated and stubby shapes (see Supplementary Fig. 2 for the univariate contrast results for each pair of conditions). Overall, we found a preference for elongated objects over stubby ones in the left mid/post IPS and left PM, but no preference for tools over nontools. In MTG and SPL in both hemispheres, however, a preference for elongation coexisted with a preference for tools. In left ant IPS, there was a preference for tools but not for elongation. The activation associated with tools in MTG, SPL, and ant IPS of both hemispheres was present even when both the tools and nontools were either elongated or stubby, suggesting that the stronger activation induced by images of tools in these areas cannot be attributed simply to the elongated shape of those tools. Nevertheless, the main effect for shape in these areas suggests that elongation also plays a role in the processing of objects, whether they are tools or nontools.

Table 1 MNI coordinates of activations ($P < 0.05$, FDR corrected)

Area	Coordinates			No. of voxels
	x	y	z	
Tools > nontools				
Left MTG	−51	−70	4	217
Left ant IPS	−36	−43	52	111
Left SPL	−21	−67	55	92
Right MTG	54	−64	−2	47
Right ant IPS	27	−43	46	23
Right SPL	15	−58	67	32
Elongated > stubby				
Left MTG	−48	−73	1	313
Left post IPS, mid IPS and SPL	−21	−58	55	221
Left PM	−48	8	40	238
Right MTG	51	−67	1	217
Right SPL	24	−64	61	105

ROI Analysis

Previous studies have used a (tools > animals) contrast to identify tool-selective areas (Martin et al. 1996; Chao et al. 1999; Chao and Martin 2000; Grossman et al. 2002; Mahon et al. 2007; Mahon et al. 2013; Garcea and Mahon 2014; Kristensen et al. 2016; Chen et al. 2016b). To take a close look at how elongation and toolness modulate the activity in tool-selective areas that were defined by this (tools > animals) contrast, we performed an ROI analysis, with the ROIs defined by a (tools > animal) contrast in 7 of our participants (Table 2 and Fig. 4).

The (tools > animals) contrast revealed activation in bilateral mFG, bilateral IPL, left dorsal occipital cortex (dOC), left ant IPS and anterior SMG (ant IPS/aSMG), and left PM (Fig. 4), largely consistent with an earlier study using the same stimuli and design (Garcea and Mahon 2014) in which 25 participants were tested. A repeated-measures ANOVA revealed that there were

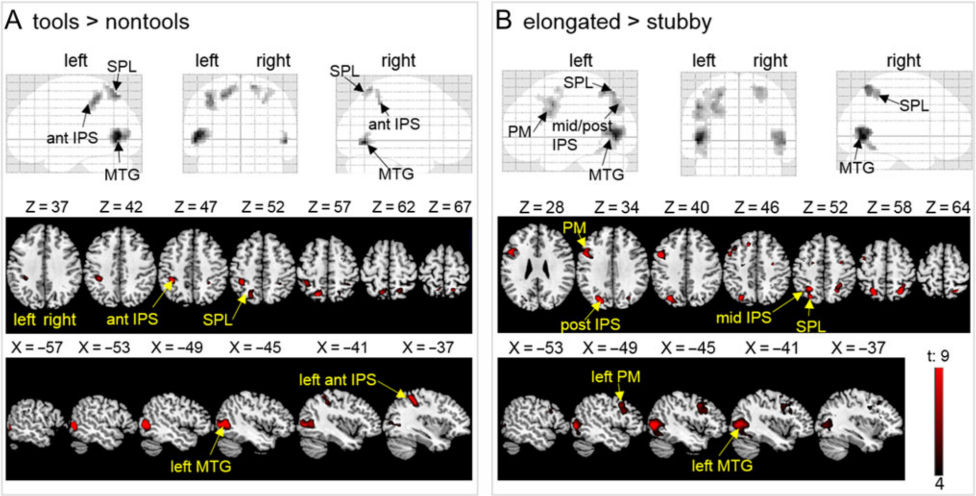

Figure 3. Results of the (tools > nontools) contrast and the (elongated > stubby) contrast. (A) Activation revealed by the (tools > nontools) contrast, which includes both the elongated and the stubby shapes. (B) Activations revealed by the (elongated > stubby) contrast, which includes both tools and nontools. Only activations that are significant after correcting for multiple comparisons are shown ($P < 0.05$, FDR corrected).

significant main effects of toolness (tool vs. nontools) and shape (elongation vs. stubby) in left MTG ($F(1,17) > 24.57$; $P < 0.001$). This is consistent with the voxel-wise GLM results, which revealed this area with both the (tools > nontools) and the (elongated > stubby) contrast. In left ant IPS/aSMG, only the main effect of toolness was significant (toolness: $F(1,17) = 10.32$; $P = 0.005$), which is also consistent with the GLM result that left ant IPS was activated by the (tools > nontools) contrast but not the (elongated > stubby) contrast. In left dOC and left PM, only the main effect of shape was significant (dOC: $F(1,17) = 15.28$; $P = 0.001$; PM: $F(1,17) = 17.32$; $P = 0.001$), a finding that is also consistent with our voxel-wise GLM analysis, which showed that the PM and the post IPS, an area close to dOC, were revealed only by the (elongated > stubby) contrast but not by the (tools > nontools) contrast. The interaction between shape and toolness was not significant in any of these areas. Taken together, this suggests that the activation in the so-called "tool-selective area" left PM and left dOC may in fact reflect the elongated shape of tool, rather than its toolness *per se*.

Table 2 MNI coordinates of ROIs defined by the (tools > animals) contrast ($P < 0.05$, uncorrected)

Area	Coordinate			No. of voxels
	x	y	z	
Left mFG	−26	−57	−20	117
Left MTG	−44	−66	−3	137
Left IPL	−38	−63	38	26
Left ant IPS and aSMG	−48	−32	41	490
Left PM	−34	13	17	152
Left dOC	−25	−65	28	46

Connectivity Analysis: PPI Results

To examine how toolness or elongation modulate the connectivity between the ventral- and dorsal-stream tool-specific areas, we first performed PPI analyses. As explained earlier, PPI identifies areas in the whole brain whose connectivity with the seed area is modulated by context (i.e., stimulus condition). We used the ant IPS, SPL, MTG, and mFG in the left hemisphere as seed areas. The results with left MTG and left mFG as seed areas did not reveal any areas in the dorsal stream. We thereby present these results only in the Supplementary material (see Supplementary Fig. 3) because the focus of this study is on the

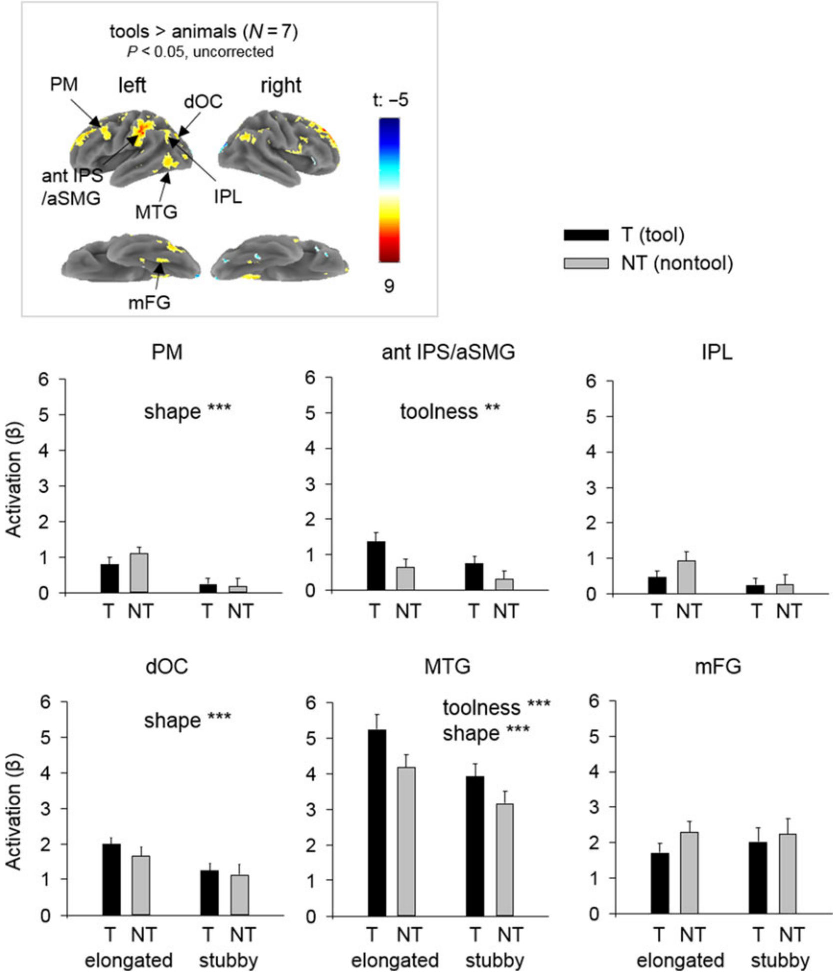

Figure 4. A summary of the ROI analysis. The top panel shows the location of the ROIs defined by the (tools > animals) contrast with a liberal P value ($P < 0.05$, uncorrected). The contrast map is displayed on a brain surface using the bspmview toolbox (http://www.bobspunt.com/bspmview/). The bar graphs show the results of the ROI analysis using these areas (only the areas in the left hemisphere were analyzed). The stars in each graph indicate whether the main effect of toolness or shape was significant. $^{*}P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$. Error bars show ±1 SEM.

interaction between the ventral and the dorsal visual streams. Here, we focus on the PPI results with left ant IPS and left SPL as seed areas, in which areas in the ventral stream were revealed in some conditions.

The PPI analysis revealed that a large area in the LOTC in the left and the right hemisphere was more strongly connected with the left ant IPS when participants viewed tools as opposed to nontools (contrast weights [1,1,−1,−1]; $P < 0.05$, FDR corrected; Fig. 5A, left panel, top row). The center of the LOTC in the left hemisphere is inferior to the left MTG activated by the (tools > nontools) contrast but incorporates it when a liberal contrast is used. The left LOTC also has a stronger connectivity with the left ant IPS when participants viewed elongated tools than when they viewed elongated nontools, and when they viewed stubby tools than when they viewed stubby nontools (Fig. 5A, left panel, second and third row). No area showed stronger connectivity with left ant IPS when participants viewed elongated shapes than when they viewed stubby shapes (Fig. 5A, right panel, top row), although a small area in the right LOTC showed stronger connectivity with left ant IPS when participants viewed elongated tools than when they viewed stubby tools (Fig. 5A, right panel, second row). These results suggest in general that toolness, but not elongation, modulates the connectivity between the ventral and dorsal tool-selective areas in the left hemisphere. As such, it is unlikely that the stronger connectivity between left ant IPS and left LOTC when participants viewed stubby tools than when they viewed stubby nontools could be attributed to the fact that stubby tools had an overall greater length/width ratio than do stubby nontools.

When left SPL was the seed area, only left LOTC, including most of left MTG, showed a stronger connectivity with left SPL when participants viewed tools than when they viewed nontools (Fig. 5B, left panel, top row). It should be noted, however, that this modulation was not evident when the analysis was restricted to elongated tools versus elongated nontools or stubby tools versus stubby nontools (Fig. 5B, left panel), suggesting that the modulation of the connectivity between left SPL and left LOTC by toolness is not as strong as the modulation of the connectivity between left ant IPS and left LOTC described earlier. Finally, modulation of connectivity between left SPL and any other brain area was not revealed by the overall (elongated > stubby) contrast or by the (elongated > stubby) contrast separately for tools and nontools (Fig. 5B, right panel).

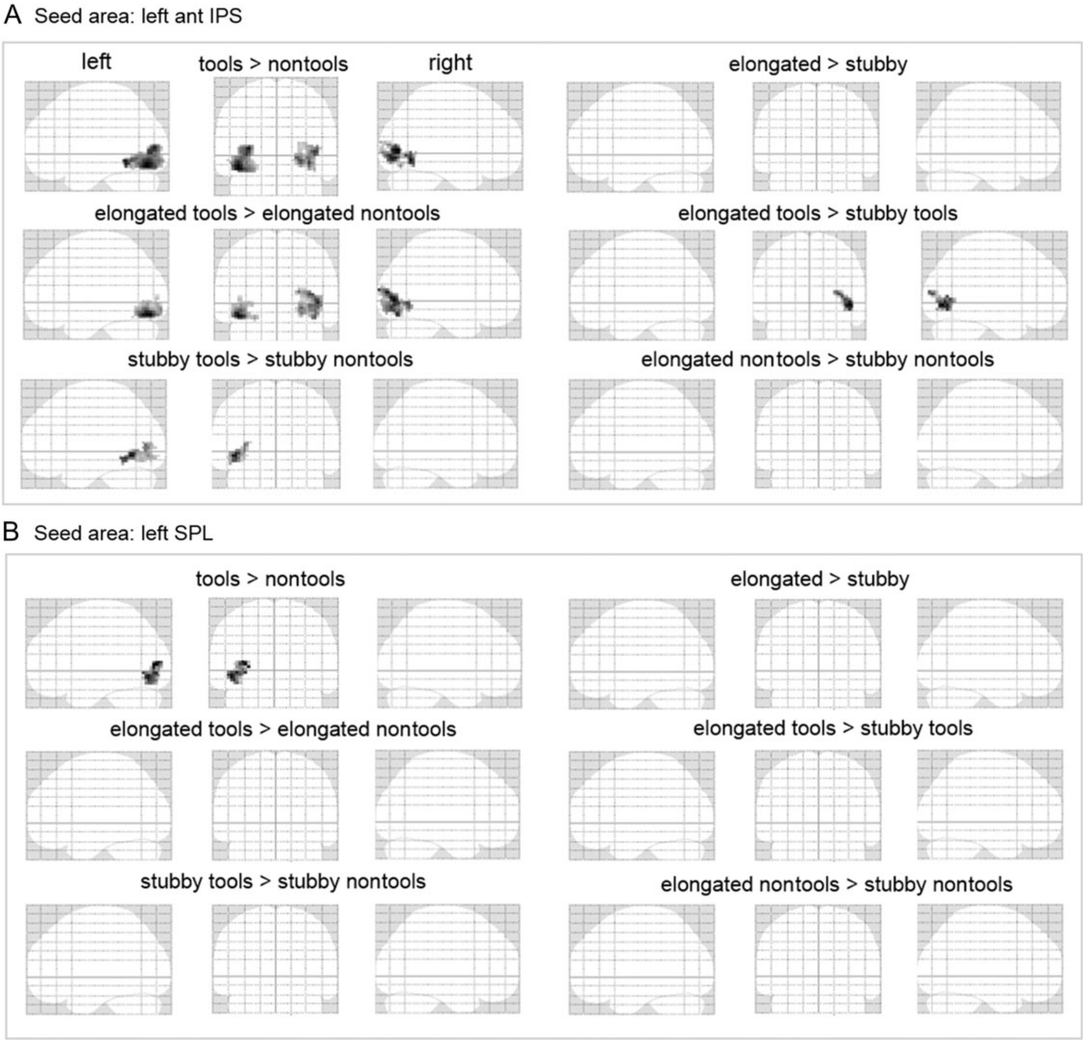

Figure 5. Results of the PPI analysis. (*A*) The results of the PPI analysis with the left ant IPS as a seed area. (*B*) The results of the PPI analyses with the left SPL as a seed area. Only activations that are significant after correction are shown ($P < 0.05$, FDR corrected).

Overall, these results suggest that toolness, but not elongation, exhibited a strong modulation of the connectivity between left ant IPS and the left LOTC (extended into the MTG) in the ventral stream. In comparison, the connectivity between left SPL and areas in the ventral stream would appear to be much less strongly modulated by toolness.

Connectivity Analysis: DCM Results

Overall, our PPI analysis showed that the connectivity between left ant IPS and left LOTC in the left hemisphere was modulated predominantly by toolness, but not elongation. Because PPI does not indicate in what direction the connectivity between areas is modulated, we could not determine whether toolness strengthens the connectivity from LOTC to ant IPS or from ant IPS to LOTC, or both. For this reason, we used DCM to examine the direction of the modulatory effect.

As described in the Methods section, left MTG and left mFG in the ventral stream, and left ant IPS and left SPL in the dorsal stream were included in DCM analysis. We investigated how each of the 3 conditions (elongated tools, stubby tools, and elongated nontools) modulated the connectivity between left MTG and left ant IPS, between left mFG and left ant IPS, between left MTG and left SPL, and between left mFG and left SPL, relative to the baseline condition (stubby nontools). We will focus on the modulation strength of the connectivity in each direction (from ventral to dorsal or from dorsal to ventral or both) for each of the 3 conditions for each pair of ventral- and dorsal-stream areas.

One-sample *t*-tests were performed to assess the significance of the modulation of each connection in each direction. All P values were FDR corrected. Both the elongated-tool and stubby-tool conditions increased the connectivity from left MTG to left ant IPS, from left mFG to left ant IPS, and from left mFG to left SPL (i.e., from the ventral- to the dorsal-stream tool-selective areas; all $P < 0.038$; Fig. 6). There was no difference in the modulation of the connectivity by the elongated-tool and stubby-tool conditions in any of these 3 pairs of ROIs (all $P > 0.22$), suggesting that toolness by itself is the critical factor driving the modulation of the connections from the ventral- to the dorsal-stream tool-selective areas. None of the 3 stimulus conditions (i.e., elongated tools, stubby tools, and elongated nontools) significantly modulated connectivity between left MTG and left SPL in either direction (Fig. 6, up right panel, all $P > 0.15$). This pattern of modulation is consistent with the PPI results, which showed that toolness strongly modulated the connectivity between left ant IPS and left LOTC (which extended into MTG), but only weakly modulated the connectivity between left SPL and left LOTC (Fig. 5).

It is interesting to note that among the 3 stimulus conditions, only elongated tools increased the connectivity from left ant IPS to left MTG (Fig. 6, $P = 0.021$). A paired *t*-test revealed that the modulation of the connectivity from the left ant IPS to left MTG by elongated tools was marginally greater than the modulation by stubby tools ($P = 0.051$). This result provides support for the idea that elongation plays some role in facilitating the communication from ant IPS to MTG in the left hemisphere, possibly to refine the processing of the identity or function

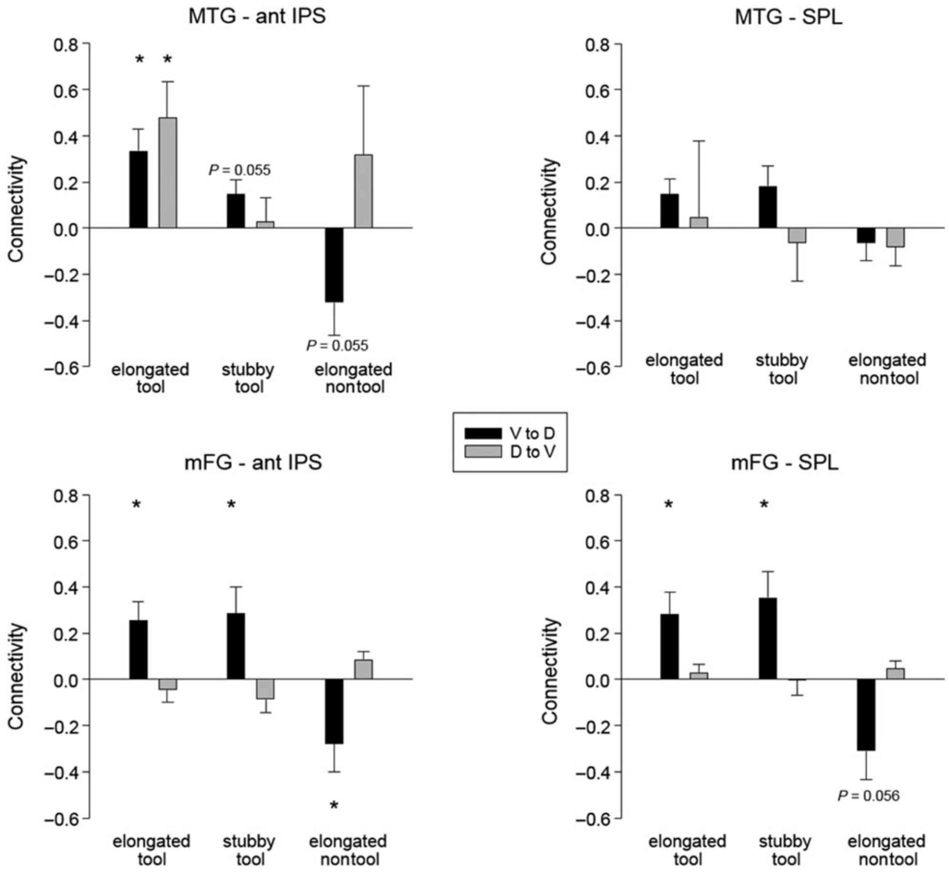

Figure 6. The strength and direction of modulation for each condition on each pair of ventral and dorsal tool areas. The inset of each of the 4 graphs shows the optimal intrinsic model for the specific pair of areas. *Modulations that are significantly different from zero ($P < 0.05$, FDR corrected). Error bars show ±1 SEM.

information of tools based on the action-related (i.e., tool use) circuits in the dorsal stream.

Interestingly, elongated nontools decreased the connectivity from ventral-stream areas to dorsal-stream areas (i.e., from left MTG to left ant IPS, $P = 0.055$; from left mFG to ant-left IPS, $P = 0.048$; and from left mFG to left SPL, $P = 0.056$; Fig. 6, upper left, bottom left and right). It could be the case that an inhibitory mechanism is engaged to prevent the ventral stream from activating dorsal-stream tool-selective areas when the elongated objects are recognized as nontools.

Overall, DCM results support the PPI data showing that, compared with the left mFG, the left MTG is more closely connected with dorsal-stream areas, especially the left ant IPS. In addition, compared with the left SPL, the left ant IPS has more communication with the ventral stream areas. In other words, the left MTG and left ant IPS, not the left mFG and the left SPL, are the main players in the interactions between ventral- and dorsal-stream tool-selective areas. Moreover, only in the elongated-tool condition was there evidence of bidirectional interactions between left MTG and left ant IPS, suggesting that elongation plays a role in driving the reciprocal connections between the left MTG and the left ant IPS during the processing of tools. The pattern of interactions revealed by the DCM analysis are summarized schematically in Fig. 7.

Familiarity, Toolness, and Manipulability

The voxel-wise GLM, ROI, and DCM analyses all revealed a strong effect of elongation on the patterns of tool-related activation observed in different brain areas and the connectivity between them. It is unclear, however, what the nature of the main effect of elongation is. Clearly, elongated tools are much more common than stubby tools, and therefore, one might expect people to be more familiar with elongated tools than stubby tools and more accustomed to manipulating them. It is also possible that people regard stubby tools as nontools rather than tools. To examine these possibilities, participants were asked to complete 3 questionnaires to indicate their familiarity with the stimuli we used, the extent to which they recognized the objects as tools, and the ease of graspability/manipulability of the objects. They were asked to rate these features on a scale ranging from 1 to 5 (see Methods).

The familiarity scores averaged across participants for the elongated tools, stubby tools, elongated nontools, and stubby nontools were 4.32, 3.66, 4.38, and 4.56, respectively. Stubby tools had significantly lower familiarity scores than the other 3 conditions (all $P < 0.001$). The mean familiarity score for elongated tools was not significantly different from mean score for elongated nontools (t (1,11) = 0.72; $P = 0.49$), but was significantly lower than that for the stubby nontools (t (1,11) = 4.87, $P < 0.001$). Overall, participants were more familiar with nontools than tools (main effect of toolness: $F(1, 11) = 26.83$, $P < 0.001$) and more familiar with elongated than stubby objects (main effect of shape: $F(1,11) = 12.66$, $P = 0.004$). If familiarity was driving the observed activation in bilateral MTG, SPL, and ant IPS then we would predict stronger activation for nontools than tools, which clearly was not the case. Similarly, if the activation was driven more by novelty than by familiarity then there should have been more activation for stubby than for elongated objects, which again was not the case. The same arguments apply when considering the possible role of familiarity in explaining the connectivity results. In short, our results cannot be explained by the differences in familiarity across the 4 stimulus conditions we used.

The toolness score averaged across participants for the 4 conditions (elongated tools, stubby tools, elongated nontools, and stubby nontools) were 4.66, 4.00, 2.18, and 2.15, respectively. The mean toolness score for stubby tools was significantly lower than the mean score for elongated tools ($t(11) = -4.49$, $P = 0.001$) but was larger than the mean score for elongated nontools and stubby nontools (stubby tools vs. elongated nontools and stubby tools vs. stubby nontools: both $t(11) > 7.11$, $P < 0.001$). This pattern of ratings is consistent with the finding that elongated tools induced stronger activation in various tool-selective areas than stubby tools, and the finding that stubby tools modulated the connectivity between left ant IPS and left MTG significantly more strongly than stubby nontools (PPI result, Fig 5A, left panel, third row). The mean toolness scores for the elongated nontool and stubby nontool conditions did not differ from one another ($t(11) = 0.116$, $P = 0.909$). This means that the effects of elongation on activation and connectivity that we observed could not have been due to differences in toolness.

Another possibility for why elongation facilitated the processing of tools (i.e., enhanced activation and connectivity) is that elongated tools are easy to grasp and manipulate compared with stubby tools. To test this possibility, we asked participants to rate the graspability/manipulability of each object on a scale from 1 to 5. The average score for the elongated tools, stubby tools, elongated nontools, and stubby nontools were 4.59, 4.55, 4.59, and 4.29, respectively. Repeated ANOVA with toolness and

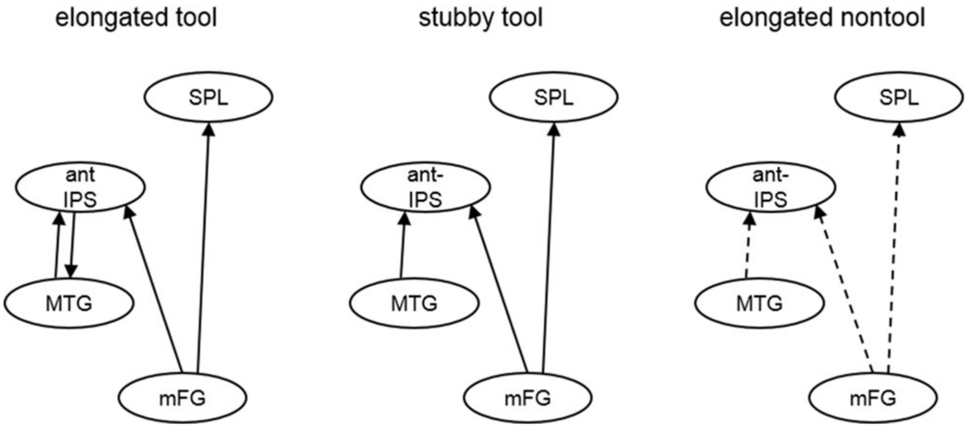

Figure 7. Schematic diagrams showing how each condition modulated the connectivity between areas relative to the stubby nontool condition. The arrows indicate the direction of modulation. Solid lines indicate increased connectivity. Dashed lines indicate decreased connectivity. All areas are in the left hemisphere.

shape as main factors revealed a significant main effect of shape ($F(1,11) = 14.01$, $P = 0.003$) but not toolness ($F(1,11) = 1.13$, $P = 0.31$). *Post hoc* paired *t*-test revealed that both elongated tools and elongated nontools were rated as easier to grasp/manipulate than stubby nontools (elongated tools vs. stubby nontools, $t(11) = 2.20$, $P = 0.05$; elongated nontools vs. stubby nontools, $t(11) = 2.51$, $P = 0.029$). No other pair-wise comparisons were significant. These results suggest that the elongated shape of an object modulates its graspability/manipulability. Therefore, it is likely that the shape of elongated tools increased their graspability/manipulability.

Discussion

In this study, we examined how viewing images of tools (vs. nontools) modulates the activity of areas in the ventral and dorsal streams and the connectivity between these areas. We were particularly interested in disentangling how much of the modulation can be attributed to the “toolness” of the image (tool vs. nontool) and how much to its shape (elongated vs. stubby). This is a critical issue because most tools are elongated and thus the effects of toolness and shape on brain activity can be confounded. To tackle this issue, we asked participants to view grayscale images of elongated tools, stubby tools, elongated nontools, and stubby nontools so that we could separate the effects of toolness from the effects of shape.

The Effects of Toolness versus Elongation on Activation

The overall (tools > nontools) and the overall (elongated > stubby) contrasts activated the MTG in the ventral stream and the SPL in the dorsal stream in both hemispheres. The overall (tools > nontools) but not the overall (elongated > stubby) contrast activated the anterior IPS (ant IPS). The overall (elongated > stubby) but not the overall (tools > nontools) contrast activated the left middle and posterior IPS (mid and post IPS) and the left PM cortex. There were no significant interactions between toolness and shape in any of these brain areas. This pattern of activation was largely confirmed by the ROI analysis, using ROIs defined by the conventional (tools > animals) contrast. These findings are also consistent with the results of a recent study in which a representational similarity analysis showed that both object shape and object category are represented in SPL and the lateral occipito-temporal cortex (including MTG), but only category information is represented in IPS (Bracci and Op de Beeck 2016). Taken together, these results suggest that there is a clear distinction in the coding of toolness and the coding of shape in brain areas that have been typically associated with tools—and that this distinction should be taken into account when investigating tool-related brain activity.

For example, the middle and posterior IPS areas, which were sensitive to elongation but not toolness in our study, appear to correspond to the dorsal-stream areas identified by Fang and He (2005) that were activated by images of tools even when the images were made invisible by CFS. It is possible, therefore, that it was the elongation of the invisible tool images, rather than their toolness, that drove the observed dorsal-stream activation in their experiment, just as it did in ours. In other words, the dorsal pathway may be able to process the elongation of an object entirely on the basis of input from early visual areas or subcortical structures, but not its toolness. Others have also argued that previously reported tool-specific activations in the dorsal stream under CFS (Fang and He 2005) may have reflected the elongated shape of the tool stimuli that were presented (Sakuraba et al. 2012; Almeida et al. 2014). As we argue later, information about whether or not an object is a tool depends on processing in the ventral stream. Because we did not use a CFS paradigm, however, we could not determine whether elongation or toolness could be processed under CFS. To answer that question, additional studies employing a CFS paradigm are required.

There are other cases where the observed activation associated with the presentation of tool stimuli in previous studies may have been due to the elongation of the stimuli rather than their toolness. For example, several studies have reported stronger tool-selective activation in the left PM and left dOC (Perani et al. 1995; Chao and Martin 2000; Garcea and Mahon 2014). In these studies, however, the contrast used to define these tool-selective areas was tools versus animals, buildings, or faces—and therefore some of the activation that was observed could have been driven by the elongated shapes of the tools rather than by the tool category itself. This possibility is supported by our finding that the left PM and left dOC were activated by elongated objects more than stubby ones, but were not activated by tools any more than they were by nontools.

Why do areas in the dorsal stream including left mid and post IPS, left PM and left dOC show stronger responses to elongated objects than to stubby objects? One possibility is that these areas are related to the selection of grasping posture (Wood et al. 2016). Elongated objects afford a consistent grasping posture (Skiba and Snow 2016) whereas stubby objects (including stubby tools) do not have well-defined (geometric) principal axes, and therefore could be grasped in more varied ways. The difference in grasp consistency between elongated and stubby objects may have driven the difference in activation in these areas.

Using the contrast of tools versus other object categories, such as animals, buildings, or faces, often activates areas that we did not observe using our tool versus nontool contrast that controlled for overall shape. Thus, left mFG, an area that has been frequently reported with the (tools > animals) contrast (Chao et al. 1999; Almeida et al. 2013; Garcea and Mahon 2014; Chen et al. 2016b), was not shown in our (tools > nontools) contrast even with a liberal P value ($P < 0.05$, uncorrected) and a group of 18 participants. Mahon et al. (2007) did not observe stronger activation for tools versus other nonliving objects either, and Macdonald and Culham (2015) did not observe differential activation in left mFG with real objects that were either elongated tools or elongated nontools. We were able to observe the activation in this area with the (tools > animals) contrast, suggesting that the absence of activation in the left mFG by the (tools > nontools) contrast cannot be because there were not enough participants. The ROI analysis with the mFG defined by the (tools > animals) contrast, did not show a significant main effect of shape or toolness. It is possible that the absence of left mFG activation in our study may simply be due to the number of nontool-coding neurons and tool-coding neurons being equivalent and greater than the number of animal-coding neurons, as Mahon et al. (2007) suggested. Yet, another possibility is that the activity in mFG in some of the previous studies was driven by differences in the real-world size or animacy between tools and animals (Konkle and Oliva 2012; Bracci and Op de Beeck 2016). Finally, it is worth noting that, although left mFG was not activated by the (tools < nontools) contrast in our study, viewing tools versus nontools did modulate the connectivity from left mFG to left ant IPS and left SPL (see below), suggesting that the left mFG may play a role in the processing of tools. This consistent with the results of Mahon et al. (2007)

and the recent finding that tool preferences in mFG are related to connectivity with the left IPL (Chen et al. 2016b). In any case, further studies are needed to address the exact role of left mFG in tool processing.

Surprisingly, we did not see activation in the IPL or the SMG, neither with our (tools > nontools) contrast, nor with our (elongated > stubby) contrast. This finding contrasts with some of the earlier neuroimaging and neuropsychological studies, which suggested that these 2 areas are critical for tool use (Barbieri and De Renzi 1988; Buxbaum and Saffran 2002; Randerath et al. 2010). Our (tools > animals) contrast did reveal activation in the inferior parietal cortex, but in a location more posterior to the tool-related IPL area that has been typically reported (see Lewis 2006 for review). Moreover, our ROI analysis showed that the main effects of shape and toolness were not significant in this area. With respect to SMG, Macdonald and Culham (2015) did find activation in this region using an (elongated tools > elongated nontools) contrast, but with real objects. One possibility is that IPL and SMG become engaged in tool processing only when real tools or tool-related actions are involved; images of tools may not be potent enough to engage this circuitry. Indeed, compared with viewing tools, pantomiming tool use often activates large areas in the IPL and SPL (Lewis 2006).

Our results are consistent with other recent findings (Fabbri et al. 2016) suggesting that elongation is a particularly relevant (though understudied) property of shape in both streams of the human brain, including the post and mid IPS. Elongation has also been found to be an important property in the caudal IPS (cIPS) in nonhuman primates, which contains subpopulations of neurons responsive to elongated versus planar objects, to be tuned to the 3D orientation of long objects and planes, and to provide output to the anterior intraparietal area (Taira et al. 2000; Sakata et al. 2005). Although a number of past studies have suggested a human homolog of cIPS (James et al. 2002; Shikata et al. 2003; Rice et al. 2007; Valyear et al. 2007; Shikata et al. 2008), there has been little consensus on its exact location. Our results here suggest the post and mid IPS foci as possible candidates.

Toolness versus Elongation in Connectivity

The PPI analysis revealed that in general toolness, but not elongation, strongly modulated the connectivity between left ant IPS and a large swath of cortex in the left LOTC that extended into left MTG. The DCM analysis confirmed this finding and further revealed the direction of modulation that occurred when participants viewed tools. Specifically, tools (either elongated tools or stubby ones) increased the connectivity from the ventral to the dorsal stream (i.e., from the left MTG to left ant IPS, from left mFG to left ant IPS, and from left mFG to left SPL). Taken together, these results suggest that the information about the identity and function of a tool is conveyed from the ventral to the dorsal stream, for facilitating the programming of appropriate actions. In contrast, elongated nontools did not increase the connectivity from the ventral to the dorsal stream, a finding that is consistent with the results of the PPI analysis, which showed that in general elongation did not modulate the connectivity between ventral and dorsal stream areas. These observations, together with the results of the CFS study (Fang and He 2005) discussed earlier, suggest that information about the elongation of an object, tool, or nontool can be processed by the dorsal stream entirely on the basis of input from early visual areas and/or subcortical structures and without the participation of the ventral pathway. This distinction in the processing of toolness and elongation resonates with earlier observations in patient DF, who has visual form agnosia from large bilateral lesions in the ventral stream (Goodale et al. 1991). Even though DF cannot distinguish between an elongated object and a stubby one, she is nevertheless sensitive to the elongation of an object as well as the orientation of its principal axis when she picks it up (Carey et al. 1996), which is consistent with our suggestion that information about the elongation of objects can reach the dorsal stream without the participation of ventral-stream processing. But DF makes telling mistakes when confronted with a tool; for example, when presented with a screwdriver with the handle pointing away from her, she will pick it up by the shaft rather than the handle. Presumably, because of her ventral-stream lesions, she cannot recognize the screwdriver and as a consequence the hand posture she uses is functionally inappropriate, which is consistent with our suggestion that the recognition of tools depends on processing in the ventral stream.

The DCM analysis revealed some other possible complexities in the way in which toolness and elongation might affect the communication between the dorsal and ventral streams. First, viewing elongated tools appeared to modulate the connectivity from the left ant IPS to the left MTG, as well as in the other direction. This reciprocal modulation between these areas was not true for the stubby tools; instead, only the connectivity from the left MTG to the left ant IPS was increased. In addition, there was no evidence for reciprocal modulation of connectivity between any other dorsal- and ventral-stream areas by any of the 3 conditions in the DCM analysis. The reciprocal upregulation of connectivity between the left MTG and the left ant IPS in the case of elongated tools may reflect a dynamic interaction between ventral- and dorsal-stream mechanisms that ultimately facilitate the visual extraction of object affordances and the selection of an appropriate posture for grasping and manipulating that tool. To be clear: we know already that the dorsal stream can process information about the orientation of an elongated object from work with DF (Goodale et al. 1991; Goodale et al. 1994), for example. We also know that areas in the ventral stream are critical for identifying objects and their function. Thus, information about the object from both the dorsal and ventral streams could be effectively combined in determining how one might interact with it. This dynamic reciprocal interaction may help to explain why motor aspects of the grasping task and upcoming actions associated with tools have been decoded in ventral-stream areas (Gallivan et al. 2013a; Tucciarelli et al. 2015; Fabbri et al. 2016). In contrast, because stubby objects (including stubby tools) do not have well-defined (geometric) principal axes, the dorsal stream would not have any useful information to provide and the selection of hand posture would depend more on the analysis of the object's function provided by areas in the ventral stream, such as MTG. This could explain why stubby tools show an increase in the modulation of the connectivity from the ventral (left MTG) to the dorsal stream (left ant IPS) but not vice versa.

Second, elongated nontools actually decreased the connectivity (relative to the stubby nontools) from the ventral- to the dorsal-stream tool-selective areas (i.e., from left MTG to left ant IPS, and from left mFG to left ant IPS and left SPL). It could be the case that when the ventral stream codes an object both as a nontool and as elongated, an inhibitory mechanism is engaged to prevent the ventral stream from activating dorsal-stream areas involved in grasping and manipulating objects. In this way, the dorsal stream, which is able to process elongation entirely on the basis of input from V1 and/or subcortical structures, can quickly program an optimal grasp without any interference from ventral stream inputs. This, of course, is completely speculative, and awaits empirical investigation. It is interesting to note, however, that this suppression is present for 3 of the 4 possible connections between the ventral and dorsal stream that we tested.

Finally, both the PPI and DCM results showed that compared with left SPL, left ant IPS has more connections with ventral-stream areas (i.e., left MTG and left mFG), which is consistent with previous findings showing that the connectivity between IPS and post/middle MTG is stronger than the connectivity between SPL and post/middle MTG (Almeida et al. 2013; Garcea and Mahon 2014; Kristensen et al. 2016). In addition, both PPI and DCM results showed that compared with left mFG, left MTG has more connectivity with left ant IPS. All of this suggests that the connections between the left MTG and the left ant IPS may play the key role in identifying the function and affordances of tools—and the selection of tool-appropriate actions—a conclusion that is consistent with much of the neuropsychological literature (Goodale 2011).

Categories and Shape

Tools form a special category—and, as we have already discussed, most tools have a characteristic shape, that is, elongation. How shape modulates the coding of different categories is an intriguing research question that has generated a good great deal of investigation (Op de Beeck et al. 2008; Li et al. 2011; Bracci and Op de Beeck 2016; Kaiser et al. 2016; Proklova et al. 2016). In the current study, we showed that the coding of toolness and the coding of shape are relatively independent. Our PPI results, for example, showed that toolness but not elongation modulated the connectivity between the left ant IPS and the LOTC. At the same time, elongation and toolness have an intimate relationship: the DCM analysis showed that elongated tools, but not stubby tools, increased the reciprocal modulation of the connections between the left MTG and the left ant IPS. This complex representation of toolness and shape is in line with previous work showing that shape and category across a broad range are represented relatively independently but at the time can be closely related with one another (Bracci and Op de Beeck 2016; Kaiser et al. 2016; Proklova et al. 2016).

Conclusion

Overall, our study shows that it is possible to disentangle how toolness and the characteristic shape of tools (i.e., elongation) affect the activation and connectivity of the tool network. Although both toolness and elongation are coded in many nodes of this network, in other nodes only toolness or elongation, but not both, modulated the response. In addition, our data make it clear that viewing tools that have a characteristic elongated shape enhances the reciprocal connectivity between the ventral and dorsal streams. Moreover, our results, together with previous imaging and behavioral studies, suggest that the processing of elongation and “toolness” involve different neural circuits: information about the elongation of objects can reach the dorsal stream without the participation of ventral-stream processing, but the recognition of tools depends on processing in the ventral stream. Taken together, our results help to resolve some of the recent controversies regarding the relative contribution of toolness and elongation in driving dorsal-stream “tool-selective” areas, and provide an account of tool processing that is consistent with neuropsychological observations.

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Supplementary Material

Supplementary material is available at *Cerebral Cortex* online.

Notes

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