Functional connectivity associated with hand shape generation: Imitating novel hand postures and pantomiming tool grips challenge different nodes of a shared neural network

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Running head: Functional connectivity of hand shape generation

Abstract

Clinical research suggests that imitating meaningless hand postures and pantomiming tool-related hand shapes rely on different neuroanatomical substrates. We investigated the BOLD responses to different tasks of hand posture generation in 14 right handed volunteers. Conjunction and contrast analyses were applied to select regions that were either common or sensitive to imitation and/or pantomime tasks. The selection included bilateral areas of medial and lateral extrastriate cortex, superior and inferior regions of the lateral and medial parietal lobe, primary motor and somatosensory cortex, and left dorsolateral prefrontal, and ventral and dorsal premotor cortices. Functional connectivity analysis revealed that during hand shape generation the BOLD-response of every region correlated significantly with every other area regardless of the hand posture task performed, although some regions were more involved in some hand postures tasks than others. Based on between-task differences in functional connectivity we predict that imitation of novel hand postures would suffer most from left superior parietal disruption and that pantomiming hand postures for tools would be impaired following left frontal damage, whereas both tasks would be sensitive to inferior parietal dysfunction. We also unveiled that posterior temporal cortex is committed to pantomiming tool grips, but that the involvement of this region to the execution of hand postures in general appears limited. We conclude that the generation of hand postures is subserved by a highly interconnected task-general neural network. Depending on task requirements some nodes/connections will be more engaged than others and these task-sensitive findings are in general agreement with recent lesion studies.

Keywords: hand posture, imitation, pantomime, tool use, fMRI, functional connectivity

Introduction

Clinical data suggest that distinct functional and neuroanatomical systems subserve different tasks of hand gesture generation. Neuropsychological research in patients with apraxia revealed (double) dissociations between impaired gesture imitation and defective (pantomime of) tool use, between poor imitation of meaningful and meaningless gestures, and even between impaired copying of meaningless hand versus finger postures (Bartolo et al., 2001; Goldenberg and Hagmann, 1997; Goldenberg and Karnath, 2006). Two major elements considered in most theoretical models of praxis include a representational or semantic component and a kinematic or action production component (Buxbaum, 2001; Buxbaum et al., 2014; Cubelli et al., 2000; Rothi et al., 1991; Roy and Hall, 1992). The semantic component refers to stored action knowledge about familiar objects gained over repetitive encounters, i.e. a representation of how we generally hold and use a hammer. The integrity of this ‘action semantics’ component is commonly assessed by asking the patient to pantomime the appropriate grip and movement associated with a shown tool object (Goldenberg, 2013). The kinematic-postural component is best understood as the actual on-line realization of the action given the constraints of the current task, i.e. using this type of hammer for this particular job under these specific circumstances. This component is believed to rely predominantly on the integration and transposition of visuospatial and proprioceptive information in concert with the motor output (for a discussion on imitation see (Goldenberg, 2013). The imitation of meaningless hand configurations[1] is taken as a sensitive test for this component as this task is not influenced by learned representations and is completely dependent on the ad hoc production of a bodily template.

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[1] Although most researchers use this terminology, only few hand configurations are truly meaningless and a better description would probably be non goal-directed hand configurations. For the sake of uniformity we will use the term meaningless postures when referring to other research, but we prefer to describe the hand configurations used in this study as non goal-directed or novel.

The neural circuitry underlying these hypothetical components remains to be explored in detail, but tool use research proposed to separate the classic dorsal visual stream into a dorso-dorsal part important for the on-line control of the action and a ventro-dorsal route involved with action organization and semantics (Buxbaum et al., 2006; Buxbaum et al., 2007; Daprati and Sirigu, 2006; Johnson and Grafton, 2003; Johnson-Frey, 2004; Rizzolatti and Matelli, 2003; Tanne-Gariepy et al., 2002; Vingerhoets et al., 2009). The dorso-dorsal stream runs from visual areas over the superior parietal cortex to the dorsal premotor cortex and is believed to be specialized in the visual analysis of spatial stimulus features toward sensorimotor control. The ventro-dorsal stream connects temporal regions with the inferior parietal cortex and ventral premotor cortex, and supports conceptual representations of skilled actions involving familiar objects (Binkofski and Buxbaum, 2013; Buxbaum and Kalenine, 2010; Vingerhoets, 2014). Recent voxel-based lesion-symptom mapping (vlsm) studies have employed the imitation of meaningless gestures and the pantomiming of tool use to test the integrity of the dorso-dorsal and ventro-dorsal streams respectively (Buxbaum et al., 2014; Hoeren et al., 2014). Buxbaum et al. reported that imitation of meaningless gestures relied predominantly on the inferior parietal lobule and that gesture to the sight of tools depended on posterior temporal activation (Buxbaum et al., 2014). Hoeren et al. found that imitation of meaningless gestures was impaired following damage to the posterior intraparietal sulcus and the superior parietal lobule, whereas tool pantomiming suffered with lesions of the supramarginal gyrus and areas of the ventral stream (Hoeren et al., 2014). Lesion studies focus on brain regions critical to the performance of a given task but they are less concerned with the neural network that supports more general task requirements. Functional neuroimaging in healthy participants on the other hand is able to reveal the wider pattern of task-associated neural activation but lacks precision with regard to how critical the contribution of each region is, and research on gesture imitation *and* gesture pantomime tasks uncovered widespread and bilateral activation in similar parietal, frontal, and temporo-occipital regions (Caspers et al., 2010; Hermsdorfer et al., 2007).

We aim to test the neural response of imitating non goal-directed and pantomiming goal-directed gestures in healthy volunteers. Depending on commonalities and differences in the neural patterns elicited by different hand shape generation tasks we will explore the functional connectivity of several of these regions and investigate whether some nodes might be more crucial for a given task than others and whether this confirms the differential involvement of the dorso-dorsal and ventro-dorsal pathways predicted by lesion research. We will focus on the imitation of hand postures rather than hand gestures thus emphasizing the configurational instead of the movement component of the imitation task. Visual analysis of a moving hand is more complex than that of a static hand posture, since the spatial relations among body parts keep changing and the observer has to update the state of the hand posture continuously (Makuuchi, 2005). We employed three tasks, each with their own control condition, within the same paradigm. The imitation of non goal-directed hand configurations challenges a kinematic approach as the volunteer has to rely on a visual analysis of the unfamiliar hand posture for a kinematic build-up of her/his own hand shape. The generation of a functional hand posture triggered by the image of a tool challenges action semantics because the absence of a hand model necessitates the semantic retrieval of the appropriate hand posture. Finally, the imitation of common functional hand shapes benefits from the direct presentation of the visual model (kinematic component) and from the familiarity of the hand shape (semantic component) and may serve to delineate differences and similarities of imitation and pantomime of goal-directed hand shapes. Following the identification of regions common and specific to these tasks, we will explore the functional connectivity of a selection of areas that contribute to the hand shape network and use this model to generate predictions regarding different symptoms of apraxia.

Methods

Stimuli and Paradigm

We constructed three sets of still images: non goal-directed hand configurations (set 1, n=18), common grip postures (set 2, n=18), and familiar tools (set 3, n=18). The 'meaningless' configurations were based on the Finger Posture task developed by Goldenberg (Goldenberg, 1996). The grip posture and tool stimuli were taken from Vingerhoets et al. (Vingerhoets et al., 2013). It is important to note that the grip postures of set 2 match the depicted tools of set 3.

The paradigm consists of three experimental conditions each of which is paired with its proper control condition. In the 'Imitate Novel Hand Postures' condition (ImiNov), participants view slides depicting three photographs of non goal-directed hand configurations (set 1) and are asked to imitate these configurations consecutively (from left to right) with their right (dominant) hand. In the 'Imitate Grip Postures' condition (ImiGrip), slides of three photographs of common functional grip configurations are shown (set 2) and again the task is to imitate the hand shapes with the right hand. In the 'Pantomime Tool Posture' condition (PanTool), slides of three common tools (set 3) are shown and the participants are required to pantomime the hand shapes befitted to functionally grasp the objects. The control conditions use exactly the same stimulus sets as the experimental conditions, but this time a green mark is placed over one of the fingers (sets 1 and 2) or somewhere on the tool (set 3). In these control tasks volunteers are asked to indicate whether or not the mark is placed on the middle finger (in the case of hand stimuli) or at the center (in the case of tools) of the stimulus. A positive answer would be signaled with a palm down tap of the hand, a negative response with a palm up tap of the hand. These tasks aimed to control for the visual input and motor output of the experimental conditions. Participants were further instructed that each slide would show three pictures and remain visible for 5s and that they had to perform the task for each picture working from the left to the right until the slide disappeared, repeating (part of) the sequence if necessary. Between trials and blocks they were asked to reassume the baseline position (arms resting on the table alongside the body) and await the beginning of the next trial. The paradigm was arranged as a randomized block design with six conditions. Each condition consisted of 6 blocks. Each block started with an instruction word that was displayed for 2s ('Imitate' and 'Pantomime' for the experimental hands and tool conditions respectively, 'Middle finger?' and 'Middle?' for the control hands and tool conditions respectively). The instruction screen was then followed by 6 slides of images of the same condition and each slide was shown for 5 seconds. Between trials inter stimulus intervals randomly varied between 250 and 1000 ms. Average duration of a block was 36.3s, resulting in a total paradigm length of 24.3 minutes.

Participants

Seventeen healthy volunteers participated in the study, but due to head movements that exceeded the size of a functional voxel (>3mm) three volunteers were excluded for further analysis. The fourteen included participants were 8 women and 6 men with a mean age of 21.8 (age range: 19-27 years). All were right-handed as determined by the Edinburgh Handedness Inventory: *M* = 90.9%, *SD* = 13.2% (Oldfield, 1971) and none had a history of neurological or psychiatric disease. Scanning protocols were approved by the local ethics committee and all subjects gave written informed consent after the experimental procedure had been explained to them.

Procedure

Prior to scanning the volunteers completed a pre-scan MRI-safety questionnaire and the Edinburgh Handedness Inventory. After the tasks were explained carefully, the participants familiarized themselves with the speed and different conditions of the paradigm in some exercise trials on a laptop computer. Next, the volunteers were positioned head first and supine in the magnet with their left and right arms placed alongside the body on the scanner table. Their heads were gently fixed in place with foam cushions. Participants were reminded of the fact that MR-imaging is very sensitive to movement and were required to restrict head movements and to lie as still as possible. To minimize movement artefacts, the participants were instructed to perform the hand posture sequences gently. Stimulus presentation was controlled by a commercially available experiment generator (E-Prime 2.0, Psychology Software Tools Inc., Pittsburgh, USA) digitally synchronized with the MRI-scanner. The stimuli were back projected on a screen at the back of the magnet bore and viewed via a mirror attached to the head coil. The performance of the participants was monitored by observing the gestures of the volunteers inside the magnet, but no recordings for off-line analysis of performance quality were made. All participants were able to comply with the task instructions and performed the hand/tool gestures as accurately as possible. In the post-scan session, participants completed a post-scan MRI safety questionnaire and were debriefed.

Scanning procedure

Scanning was performed at 3.0 T on a Siemens Trio MRI scanner (Siemens Medical Systems, Erlangen, Germany) that was equipped with echo planar imaging (EPI) capabilities and used an 32-channel head coil for radio frequency transmission and signal reception. After automatic shimming of the magnetic field on each participant, a 3-D high-resolution T 1 anatomical image of the whole brain in the sagittal plane was acquired for coregistration with the functional images

(3D MPRAGE, 176 slices, slice thickness = 1.0, in-plane resolution = 1.0 x 1.0 mm, TR = 2250 ms, TE = 4.18). Next, 590 functional EPI images in the axial plane were acquired. They had the following parameters: TR = 2.5 s, TE = 27 ms; flip angle = 62°, 33 slices, slice thickness = 2.5 mm, slice gap = 1.25 mm, FOV = 192 mm and matrix = 64 x 64, resulting in a resolution of 3 x 3 x 2.5 mm.

Image analysis

Data analysis was performed using Brain Voyager QX for preprocessing and statistical inference (Goebel et al., 2006). Functional data were subjected to a standard sequence of preprocessing steps comprising slice scan time correction, 3-D motion correction by spatial alignment to the first volume, and temporal filtering using linear trend removal and high pass filtering for low-frequency drifts of 3 or fewer cycles. Spatial smoothing with a Gaussian filter (FWHM = 6 mm) was applied for the volume-based analysis. The anatomical data for each subject were transformed into Talairach standard space using sinc interpolation. The functional data for each subject were coregistered with the subject's 3-D anatomical dataset and transformed into Talairach space.

For each subject's paradigm, a protocol file was derived representing the epochs from the onset of the hands/tools slide until its offset for each trial of the different conditions. Factorial design matrices were automatically defined from the created protocols. The BOLD response in each condition was modeled by convolving these neural functions with a canonical hemodynamic response function (gamma) to form covariates in a General Linear Model (GLM). After the GLM had been fitted and the effects of temporal serial correlation allowed for (using AR(1) modeling), group (random effects procedure) *t*-maps were generated to evaluate the effects of hand posture generation under different conditions.

We started our analysis with a general evaluation of the ImiNov, ImiGrip, and PanTool conditions compared to their respective control conditions (ContrImiNov, ContrImiGrip, and ContrPanTool). Next, we performed a conjunction analysis to investigate activation common to the three tasks. First, we performed a ‘strict’ conjunction of the conditions compared to their control tasks ((ImiNov > ContrImiNov) ∩ (ImiGrip > ContrImiGrip) ∩ (PanTool > ContrPanTool). Second, we conducted a more general conjunction by evaluating regions common to the experimental tasks themselves (ImiNov ∩ ImiGrip ∩ PanTool). Finally, we directly compared the ImiNov condition with the PanTool condition to evaluate the major differences between postural and semantic challenges in hand posture generation. Although a lot of other contrasts can be performed, the ImiNov>PanTool and PanTool>ImiNov comparisons are the most promising to explore possible differences as they investigate the more extreme task versions with ImiNov requiring the correct imitation of non goal-directed hand postures and PanTool probing the ability to generate tool-appropriate hand postures from semantic memory. For all analyses minimum cluster threshold was set to 300 (anatomical) voxels and an uncorrected statistical threshold of $p<.001$ was applied. Based on the conjunction and contrast analyses, we selected the most relevant clusters for the ImiNov and PanTool tasks depending on the strength of their t-value, significant ImiNov/PanTool difference, and previous research. We do not claim that the selection of clusters constitutes an exhaustive list of regions participating in hand posture generation, but rather that the selected regions are likely to contribute to this task and that their functional connectivity could reveal valuable information regarding its organization. A region of interest (ROI) of between 180 – 250 voxels was defined around the peak voxel of each of the clusters. We then extracted the response time course for each ROI of each participant and, after normalization, selected the response time course blocks belonging to the conditions ImiNov and PanTool. A correlation analysis using Pearson’s bivariate coefficients was performed on the selected time points for the ImiNov and PanTool datasets to reveal the functional connectivity between all ROI's for each condition.

Results

Main contrasts: Experimental versus control tasks

Figure 2A depicts the neural activation of each condition compared to its proper control task to correct for visual input and motor output. Details of activated regions can be found in supplementary Table S1. All contrasts reveal robust activation over the bilateral pre- and postcentral gyri (PPCG), and the bilateral inferior parietal lobuli (IPL). Both imitation tasks recruit additional occipital regions, whereas the pantomime task reveals more substantial frontal activity. When comparing both imitation tasks the novel postures elicit a more bilateral and superior pattern of parietal activation than the grip posture task.

Regions commonly involved in hand shape generation: Conjunction analysis of all tasks

We first performed a conjunction analysis to investigate which regions were commonly involved in all three hand posture tasks. We limited commonalities based on visual input and motor output by performing the conjunction on the primary contrasts described above, that is, following subtraction of the respective control conditions: (ImiNov > ContrImiNov) ∩ (ImiGrip > ContrImiGrip) ∩ (PanTool > ContrPanTool). Results are described in Figure 2B and Table 1. Regions commonly involved in (right) hand shape generation include mainly the PPCG (on a superior z=60, intermediate z=50, and inferior z=30 level) and the IPL. Although activation is bilateral there is a clear lateralization bias in favor of the left hemisphere. We wondered why the superior PPCG cluster showed a strong right sided bias and investigated whether subtraction of the control conditions could have filtered out some of the lateralized activation in this region. The conjunction analysis without subtracting the control tasks (ImiNov ∩ ImiGrip ∩ PanTool) clearly revealed strong left>right pre- and postcentral activation around z=65-50 compatible with right hand action execution (see Figure 2C). Apparently, our control tasks were more demanding than anticipated and may have challenged areas subserving hand and tool-related visuospatial and somatosensory processing. For this reason we decided not to use the control conditions in secondary contrasts, but to compare the experimental conditions directly.

Differences between visuo-imitative and semantic-pantomime tasks of hand shaping

The most robust contrast to differentiate the neural correlates of both challenges would be to compare the imitation of non goal-directed hand postures and the pantomimed hand shape in response to a tool object. The results of the ImiNov > PanTool and PanTool > ImiNov contrasts are described in Table 2 and Figure 3. The novel posture task reveals stronger neural responses over the superior parietal lobule (SPL; R>L), right superior precuneus (sPCu), visual cortex (R>L), PPCG (L>R), and right IPL. Tool-triggered hand shaping on the other hand reveals more activation in left dorsolateral prefrontal cortex (DLPFC; BA 46), posterior temporal cortex (L>R), visual cortex, bilateral inferior precuneus (iPCu), left ventral and dorsal premotor cortex (vPMC, dPMC) , and IPL. The main differences between both tasks are an increased involvement of right superior parietal and bilateral lateral occipital regions during imitation of non goal-directed hand postures, and an increased left frontal, left temporal, and medial occipital engagement during the pantomiming of tool grips.

Functional connectivity analysis

We investigated the relation between a selection of the regions unveiled by the previous analyses to determine their functional connectivity during each task. The selection of the ROIs included the left and right IPL and PPCG as they seem common to hand shape generation in general. We also included the left and right SPL, sPCu, and middle occipital gyri (MOG) as they seem more involved during imitation of novel postures, and the medial lingual gyrus (LG), left DLPFC, vPMC and dPMC, and bilateral iPCu because they contribute to the pantomiming of tool grips. ROIs were drawn around the peak voxel of each region and their normalized response time courses during the ImiNov and PanTool conditions were correlated separately. The correlation matrix revealed that each ROI (whether common to ImiNov and PanTool, more active during ImiNov, or more active during PanTool) was positively and significantly associated with every other ROI regardless of condition. R-values ranged between .607 and .955 (always $p<.001$) for the ImiNov condition and between .549 and .961 (always $p<.001$) for the PanTool condition. In Figure 4 we only depict the highest correlations ($r > .9$) for each condition. During imitation of novel hand postures all its major activation foci (blue and yellow dots in Figure 4A) showed such high intercorrelation with at least one other ROI, the only exception being the right PPCG region ($r=.842$ with the left pre/postcentral ROI, dotted line in Figure 4A). In this condition high homotopic interhemispheric connectivity seemed abundant (MOG, IPL, sPCu, SPL, and PPCG), as well as symmetrical within (SPL-iPCu, IPL-MOG, MOG-iCPu) and between hemispheric (SPL-iPCu, MOG-IPL) connectivity. Asymmetries in functional connectivity were noted for the left PPCG region (strongly associated with left and right IPL), for the left SPL (strongly associated with left and right sPCu), and for the sPCu (strongly associated with the right IPL). In this condition, no correlations higher than .90 were found between ROIs that showed more activation during the PanTool task (red dots in Figure 4A).

During pantomiming of tool grips all of its major foci (red and yellow dots in Figure 4B) showed high correlations with at least one other ROI, except for vPMC ($r=.889$ with left IPL and LG, dotted lines in Figure 4B). Strong homotopic associations were again present (MOG, iPCu, sPCu, SPL, PPCG), just like symmetrical within (LG – iPCu, sPCU – SPL, IPL – PPCG, and LG – PPCG) and between hemisphere (IPL – PPCG, sPCU – SPL) correlations. Asymmetries were found for the frontal clusters (vPMC with left IPL and LG, dPMC with DLPFC) and left and right IPL (with LG and with bilateral iPCu respectively). In this condition strong correlations were also found for ROIs that were more active in the ImiNov condition, notably homotopic connections between the MOGs and SPLs and the symmetric associations between bilateral sPCu and SPL, akin to the ImiNov organization.

Familiarity of hand postures and the role of pMTG

Compared to novel hand posture imitation, pantomiming tool grips revealed left lateralized activation in some frontal regions (DLPFC, vPMC and dPMC) and in the posterior middle temporal gyrus (pMTG). As explained earlier, this contrast differentiates between a visuo-imitative and semantic-pantomime challenge of hand shape generation. We wondered which of these differences would remain when we contrast the PanTool condition with an imitation task that does not require the formation of a novel hand posture (a ‘puzzle’), but the formation of a meaningful, familiar and thus ‘preset’ hand configuration (a ‘template’). We can investigate this question by contrasting the PanTool condition with the ImiGrip condition instead of the ImiNov condition. In the PanTool condition the memory component is imperative to the performance, whereas the ImiGrip condition can be solved by imitation and the performance is likely to be facilitated by the familiarity of the grip postures. The PanTool > ImiGrip contrast revealed a significantly higher hemodynamic response over the left supramarginal gyrus (SMG; x = -52, y = -38, z = 36), left vPMC (x=-42, y=35, z=9), left dPMC (x = -44, y = 12, z = 36), left DLPFC (x = -33, y = 38, z = 18), and cuneus/lingual gyrus (x = 2, y = -78, z = 9). Subtraction of the ImiGrip condition thus primarily removed the left pMTG activation form the contrast map, suggesting that the increased familiarity of the hand postures in this imitation condition somehow engaged the ventral pMTG region. The ImiGrip > PanTool contrast showed predominantly bilateral activation over the lateral occipital areas (x = 29, y = -86, z = 9; x = -45, y = -80, z = -6).

We also extracted the normalized hemodynamic time course for the pMTG ROI during the PanTool and ImiNov conditions in order to evaluate its connectivity with the other ROIs. During the ImiNov task, pMTG did not correlate with any of the ImiNov ROIs and there were only small (but significant, $p<.05$) correlations with PanTool ROIs (the largest $r=.19$ with LG and the inferior precunei). In the PanTool task however, pMTG correlated modestly with all ROIs (ImiNov and PanTool), though correlations were clearly higher for the PanTool sensitive regions (the largest $r=.34$ again with LG and the inferior precunei).

Discussion

Hand posture generation tasks appear to elicit widespread neural responses in parietal, frontal, temporal and occipital regions with imitation tasks revealing more occipital and bilateral parietal activity (especially when meaningless) and pantomime tasks showing additional frontal and temporal responses. What all tasks seem to have in common is bilateral activation over the primary motor and sensorimotor cortices and inferior parietal lobules. Contrasting the ImiNov and PanTool tasks amplifies the differences observed in the main contrasts. The imitation of novel postures results in increased recruitment of superior regions including primary motor and sensorimotor cortices, regions of the superior parietal lobuli and precunei, and lateral occipital areas. Pantomiming of tool grips shows significantly stronger activity in medial occipital and inferior precunei, over left ventral and dorsal premotor regions and dorsolateral prefrontal cortex, and over the left posterior temporal cortex. As the latter contrasts were not corrected for stimuli-differences (tools versus hands) by the control tasks, it cannot be excluded that activation differences in particular in the occipital regions, may have been influenced by differences in stimuli (for a discussion of these effects, see the next paragraph). Before discussing the implications of the functional connectivity analysis, we will briefly address the relevant cortical foci in relation to task demands. For more detailed discussions regarding the functional role of these regions see (Binkofski and Buxbaum, 2013; Buxbaum and Kalenine, 2010; Johnson-Frey, 2004; Kroliczak and Frey, 2009; Lewis, 2006; Vingerhoets, 2014).

Occipital regions

Imitation of non goal-directed hand postures elicits bilateral activation of the lateral occipital surface. Although this region has generally been associated with object recognition and tool perception (Grill-Spector and Malach, 2004; Valyear et al., 2007; Vingerhoets et al., 2011; Weisberg et al., 2007), recent fMRI evidence reveals the existence of adjacent and partly overlapping hand-selective regions (Bracci et al., 2012; Perini et al., 2014). It seems plausible that the imitation of an unfamiliar hand posture requires a close visual inspection of the hand stimulus, thus challenging the hand-selective neural population in this region. Since copying novel hand postures is a visually more demanding task than the recognition of familiar tools, the recruitment of the MOG is significantly higher in the ImiNov condition, and even in the ImiGrip condition where performance might also have been facilitated by the familiarity of the postures. The lingual gyrus occupies the medial occipitotemporal cortex and is considered part of the visual cortex. Its activation extended into the cuneus and this ROI appeared particularly responsive to the PanTool task. This region is implicated in target and novelty detection and has been reported in the perception of tools before (Gur et al., 2007; Vingerhoets, 2008). The LG has also been significantly responsive in a learning paradigm in which finger movements were associated with visual patterns, underlining the visual memory component of this region (Toni and Passingham, 1999). Visuo-motor associations may have challenged this region more in the PanTool task than in the ImiNov task, and may also explain its preferred functional connection with left vPMC, a region involved in the matching of hand posture configurations in accordance with visual and functional demands (Vingerhoets et al., 2013).

Temporal regions

Significant responses of left fusiform and inferior temporal gyrus, and bilateral middle temporal gyri were recorded during the PanTool compared to the ImiNov condition. Posterior temporal lobe activation is typically found in studies assessing semantic action knowledge and recent publications emphasized the visual format of these action representations in pMTG (Binkofski and Buxbaum, 2013; Buxbaum et al., 2014; Kable et al., 2005; Kalenine et al., 2010). The proposed functional link between pMTG and extrastriate regions is in agreement with the finding that the highest (of albeit weak) pMTG resonance was observed with the lingual gyrus and the inferior precunei, whereas correlations of pMTG with the frontal and parietal ROIs were very modest. The strong relation of the posterior temporal region with human tool use is demonstrated by the finding that lesions to the left posterior temporal gyrus were associated with poor tool-related gesture performance (Buxbaum et al., 2014; Hoeren et al., 2014). In a recent study combining fMRI and DTI, Vry and colleagues stressed the relevance of the infra-Sylvian ventral pathway supporting the semantic operations of pantomimed gestures. Their analysis was based on a preparatory interval before the execution of the pantomime was allowed for (Vry et al., 2015). In addition, Gallivan et al. showed the specificity of the pMTG region for tools that could be separated from hand-specific regions and from effector-independent higher-level brain regions coding the action itself (Gallivan et al., 2013). Interestingly, our results indicated that the imitation of familiar grip postures appeared to engage the pMTG area as it removed this region from the PanTool>ImiGrip contrast while it was present in the PanTool>ImiNov contrast.

Although no tools were shown in the ImiGrip condition it may be that tool-specific pMTG nevertheless was stimulated because the familiar grip positions reminded of tools shown in the other condition.

On the other hand, no temporal regions were observed in our conjunction analysis and our data showed that posterior temporal involvement was predominantly activated with the tool pantomime task, not with imitating novel gestures. The functional connectivity analysis also revealed virtually absent correlations between the pMTG time course and those of the selected ROIs during the ImiNov task, that were slightly higher during the PanTool task but still quite smaller than between the selected ROIs themselves. These findings suggest that when it comes to the imitation of hand postures without the involvement of a tool, pMTG does not seem to play a major role. The modest resonance of pMTG with the selected ROI's during the PanTool task (compared to previous claims regarding its importance for pantomiming) may be influenced by our focus on the execution phase of the action and on the imitation of hand configurations rather than hand gestures. We conclude here that although the pMTG may provide crucial information about the type of gesture to be performed (retrieval of tool-associated knowledge), our connectivity data based on the execution phase of the action suggest that the contribution of this ventral region to the actual formation of a hand posture is limited, in particular when no tool stimuli are involved.

Primary motor and somatosensory regions

The conjunction analyses unveiled extensive recruitment of the precentral and postcentral gyri during hand shape generation. Activation was bilateral but more robust on the side contralateral to the performing hand. Increasing the threshold demonstrated several foci the most consistent of which was situated bilaterally around x = ± 35-40, y = -17-23, z = 55-60. The latter region is situated in the vicinity of the hand motor region, x = ± 34, y = -29, z = 50 according to anatomical and functional localizations (Caulo et al., 2007).

Inferior parietal regions

Bilateral inferior parietal activation appeared common to both tasks, again with a more robust response in the left hemisphere. These data are consistent with a number of functional imaging studies (Molenberghs et al., 2012; Muhlau et al., 2005; Peeters et al., 2013; Vingerhoets et al., 2009). Activation was most prominent over the SMG, a region typically associated with object use (Hermsdorfer et al., 2013; Johnson-Frey, 2004; Lewis, 2006; Vingerhoets, 2014). Within the SMG region shared activation was more focused over the inferior anterior supramarginal area (iaSMG; around x= -52, y = -27, z = 37) whereas task specific activation centered more over the superior posterior supramarginal region (spSMG; around x = -37, y = -43, z = 48). A distinction between both SMG foci was proposed in a recent review with iaSMG being more involved in goal-specific movement planning toward tool-like objects, and spSMG believed to subserve functional motor schemata for familiar objects (Vingerhoets, 2014). Clearly this interpretation does not fit the current data as these object-driven regions also appear active when participants imitate meaningless hand postures. Unraveling the functional mosaic of intraparietal and lateral inferior parietal foci that participate in transitive actions remains an important challenge in cognitive neuroscience.

Pantomiming tool grips also activated an inferior medial parietal area, that is the lower (BA 31) part of the precuneus in each hemisphere. The precuneus has been associated with highly integrative, yet diverse functions (Cavanna and Trimble, 2006). Important here is its role in the visual guidance of hand movements and reaching associated with projections to the lateral parietal and premotor regions described in the monkey (Caminiti et al., 1999; Ferraina et al., 1997). Our functional connectivity model in particular highlights iPCu's relation with the right IPL.

Superior parietal regions

The left superior parietal cortex appears activated in all conditions (Figure 2C). The greater involvement of bilateral superior parietal cortex during novel hand posture imitation compared to tool pantomiming is in agreement with the presumed function of the dorso-dorsal stream and the role of SPL in proprioception and body schema (Binkofski and Buxbaum, 2013; Creem-Regehr et al., 2007; Lewis, 2006; Vingerhoets, 2014). Again, involvement of superior medial regions is observed in bilateral superior precuneus. Superior precuneus involvement around z = 50 is reported during several motor imagery tasks in particular when elaborating egocentric and allocentric spatial relations for body movement control (Cavanna and Trimble, 2006).

Frontal regions

Tool grip pantomimes elicited a hemodynamic response in DLPFC, vPMC and dPMC that was strongly lateralized to the left hemisphere. Their function has been interpreted in terms of goal-directed planning, planning of hand movements, and adequate sequencing of motor commands respectively (Buxbaum et al., 2006; Davare et al., 2010; Grafton et al., 1998; Lewis, 2006; Makuuchi et al., 2012; Meister et al., 2009; Vingerhoets et al., 2013). The focus of vPMC of matching hand posture configurations in accordance to visual demands is nicely demonstrated by its close correspondence with inferior parietal and extrastriate regions, whereas the focus of DLPFC and dPMC on the planning of motor control is underlined by its strong reciprocal connections (see Figure 4B). DLPFC and dPMC, and possibly also the frontal midline region seem more sensitive to the PanTool condition and may reflect the involvement of domain-general cognitive control processes necessary to perform such an abstract task (Goldenberg et al., 2007).

Functional connectivity

Regions of interest were drawn over the peak voxels of the foci mentioned above to determine the functional connectivity of each ROIs normalized time course with the other ROIs during ImiNov and PanTool conditions. Although we do not claim that these regions provide an exhaustive list of hand shape generation areas, the selection is data-driven and represents the major foci mentioned in similar research. One of the most important findings of the functional connectivity analysis was that all included regions were significantly correlated with every other region, regardless of the condition that was evaluated. Although correlation coefficients were generally higher between regions that showed preferential activation within conditions, all between condition correlations also appeared highly significant (always $p<.001$), that is even between regions that responded preferentially to different conditions. We take this as evidence for the existence of a general functional network involved in the production of hand postures that, depending on the task at hand, challenges certain nodes more than others, while maintaining the neural time course echoed in the entire system. These results help to explain why prefrontal and premotor regions are also reported in imitation tasks (Caspers et al., 2010), and why superior parietal activation is sometimes described in tool pantomime tasks (Vingerhoets et al., 2011). The finding further suggests that areas that are significantly more active in one condition compared to another should be considered as condition or task-sensitive rather than task-specific, as they also resonate within the network when challenged less. At the same time it seems reasonable to assume that the more task-sensitive a region appears to be, the more likely it will be critical to a normal performance of that task and we will compare our findings with lesion research below. Although it is unlikely that every node of the network will prove critical for a given task, a possible advantage of a multifocal reverberatory affinity is fine-tuning and, if necessary, compensation if nodes get damaged or disrupted. Indeed, a lot of the strongest correlations (r>

.90, displayed in Figure 4) are between homotopic regions that, in turn, share highly associated response curves with symmetrical intra- and interhemisferic heterotopic connections.

Apart from the symmetrical patterns of functional connectivity it is also relevant to focus on nodes showing high asymmetrical correlations. Based on Figure 4A it could be predicted that damage to bilateral MOG is likely to hamper the imitation of novel hand postures, although clinically such a case would be rare. A more likely scenario to disturb this task would be a left superior parietal lesion involving PPCG, SPL or sPCu. Such a relation was not reported by Buxbaum et al. but the authors explained this absence by their limited number of patients with superior parietal injuries (Buxbaum et al., 2014). Hoeren et al. included a larger group of patients and confirm that SPL disruptions are more strongly associated with deficits of imitation (Hoeren et al., 2014), a finding that is backed-up by previous reports (Koski et al., 2003; Menz et al., 2009; Rumiatil et al., 2005). Finally, Figure 4A also suggests that damage to either IPL could have a detrimental impact given its strong and asymmetric connection with left PPCG. Both vlsm studies (that included only left brain damaged patients) mentioned the adverse effect of left IPL damage on the imitation of novel gestures (Buxbaum et al., 2014; Hoeren et al., 2014). Previous research also reported that patients with right brain damage perform more poorly in finger configuration tasks compared to hand configuration tasks (Goldenberg, 1996).

Figure 4B, on the other hand, suggests that disruption of the medial occipital cortices would impair the tool pantomime task, as would damage to the right or left IPL. Only the latter observation is confirmed by the vlsm study of Hoeren et al. (Hoeren et al., 2014). In addition, the connectivity schema would predict that left frontal damage is also likely to impair tool pantomiming, a repeated observation that has been hotly debated in the past (Goldenberg et al., 2007; Haaland et al., 2000). The finding that given their strategic relations, inferior parietal and frontal areas may disrupt tool pantomiming is in agreement with the conclusions of a recent meta-analysis of structural and functional neuroimaging studies on pantomime (Niessen et al., 2014). The results of our contrasts and connectivity analyses support the idea that tasks of imitation, in particular of novel hand postures, place more weight on the superior parietal cortex as part of a dorso-dorsal pathway. We found less evidence for a predominant inferior parietal involvement (ventro-dorsal pathway) in pantomiming tool grips as the IPL was also strongly recruited during imitation. Instead, pantomiming elicited activation of ventral regions (consistent with lesion research (Buxbaum et al., 2014)) although their importance for the general posture production network appeared limited. Connections between the ventral and the ventral part of the dorsal stream have been described repeatedly and it was suggested that the ventro-dorsal substream may act as an interface between the ventral and dorsal streams of visual information processing (Binkofski and Buxbaum, 2013).

Limitations of the study

Most important, the regions included in the functional connectivity analysis represent a selection that is partly based on data-driven information (the results of the conditions’ conjunction and contrast analyses) and partly based on the authors understanding of the relevance of these regions. We by no means claim this selection to represent a ‘complete’ network of hand shape generation. In addition to the fact that certain areas may be lacking in the selection, some of the selected areas should have to be subdivided. Strong BOLD-activation over the PPCG and IPL regions for example, is likely due to responses of more than one subregional focus. We always selected the most robust focus to represent that region, but this strategy probably also results in a simplification of the functional connectivity model. It seems important to keep this limitation in mind as not all subregional foci may share exactly the same connections and functions that are generally attributed to the overarching region.

Our functional connectivity analysis provided interesting data with regard to the strength of the crosstalk between regions of the hand posture network, but it did not reveal anything about the direction of these relationships. Our paradigm was designed to compare (subtle) differences between tasks of hand posture generation, but not to apply methods of effective connectivity. Future research could focus on more extended ImiNov and PanTool conditions at shorter sample rates (TR) to optimize the design for causal connectivity inferences.

Another shortcoming would be the choice of our control conditions. Designed to control for motor output and differences in visual input, they also were quite demanding in a visuospatial and perhaps even somatosensory way. As such they may have filtered out more hand and tool-relevant activity than was intended and rendered them unsuitable for use in secondary contrasts, thereby limiting the interpretation of the ImiNov versus PanTool contrasts concerning stimuli differences.

Conclusion

The voluntary generation of hand postures involves a bilateral neural network comprising medial and lateral extrastriate cortex, superior and inferior regions of the lateral and medial parietal lobe, primary motor and somatosensory cortex, and a predominantly left frontal contribution of dorsolateral prefrontal, and ventral and dorsal premotor cortices. The BOLD-response in each of these ROIs is significantly correlated with that of every other ROI of the network regardless of which hand posture task is performed. While these regions appear to resonate the activation within a network of homotopic and heterotopic areas, their vast interconnectivity suggests that not all regions are critical for hand shaping as they can be compensated via redundant pathways.

At the same time some nodes of the network are more challenged by certain tasks than by others and damage to such task-sensitive regions may give rise to selective problems in hand posture generation in brain injured patients. Task-dependent differences in functional connectivity predict that damage of left superior parietal cortex and bilateral inferior parietal lobule may impair the imitation of non goal-directed hand postures, whereas pantomiming tool postures seems especially vulnerable following lesions to left frontal and again bilateral inferior parietal lobules. In addition, disruption to pMTG is likely to hamper tool associated gestures, although this area does not seem critical for hand posture generation per se. Many of these findings are supported by recent functional neuroimaging fostering the distinction between dorso-dorsal and ventro-dorsal pathways and by vlsm-studies in patients with apraxia.

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Figure captions

Figure 1. Overview of the paradigm with task instructions and examples of stimuli. ISI = interstimulus interval.

Figure 2. A. Primary contrasts of the experimental versus their respective control conditions. B. Conjunction analysis of primary contrasts. C. Conjunction analysis of experimental conditions.

Figure 3. Regions significantly more involved during the imitation of non goal-directed hand postures versus pantomiming of familiar tool grips (in blue) and vice versa (in orange). DLPFC: dorsolateral prefrontal cortex; dPMC: dorsal premotor cortex; iPCu: inferior precuneus; IPL: inferior parietal lobule; LG: lingual gyrus; MOG: middle occipital gyrus; PPCG: precentral and postcentral gyri; sPCu: superior precuneus; SPL: superior parietal lobule; vPMC: ventral premotor cortex.

Figure 4. Functional connectivity during imitation of non goal-directed hand postures (A) and pantomiming of familiar tool grips (B). Each circle represents an area whose BOLD-signal is significantly correlated with every other area of the network in that condition. Lines depict only the highest correlations within that condition (r>.90). When a condition-sensitive region has no connection that reaches this criterium, its highest correlation is indicated with a dotted line. DLPFC: dorsolateral prefrontal cortex; dPMC: dorsal premotor cortex; iPCu: inferior precuneus; IPL: inferior parietal lobule; ITG; inferior temporal gyrus; LG: lingual gyrus; MOG: middle occipital gyrus; pMTG: posterior middle temporal gyrus; sPCu: superior precuneus; SPL: superior parietal lobule; vPMC: ventral premotor cortex.

Table 1. Peak voxel coordinates of significant activation clusters of the conjunction analysis over all three hand shape generation tasks: (ImiNov > ContrImiNov) ∩ (ImiGrip > ContrImiGrip) ∩ (PanTool > ContrPanTool)

		Peak voxel coordinates / t- values			
Anatomical region	BA	x	y	z	t*
Right Precentral Gyrus	4	35	-17	60	7,77
Left Postcentral Gyrus	2	-49	-29	36	7,62
Left Inferior Parietal Lobule	40	-44	-32	39	6,71
Left Postcentral Gyrus	3	-40	-23	57	6,26
Left Inferior Parietal Lobule	40	-37	-41	48	6,00
Left Precentral Gyrus	6	-55	1	36	5,91
Right Postcentral Gyrus	3	59	-17	24	5,69
Left Postcentral Gyrus	2	-60	-23	33	5,5
Right Postcentral Gyrus	2	37	-26	36	4,79
Right Inferior Parietal Lobule	40	35	-41	54	4,74
Left Medial Frontal Gyrus	6	-4	-8	51	4,73
Right Precentral Gyrus	6	56	1	30	4,59

*p<.001 uncorrected, extent threshold k=300

Table 2. Peak voxel coordinates of significant activation clusters of the contrasts ImiNov > PanTool and PanTool > ImiNov

		Peak voxel coordinates / t-values			
Anatomical region	BA	x	y	z	t*
ImiNov > PanTool					
Right Middle Occipital Gyrus	18	32	-93	9	9,69
Right Precuneus	7	17	-77	49	8,12
Left Postcentral Gyrus	3	-46	-20	54	7,82
Right Superior Parietal Lobule	7	23	-58	60	7,67
Right Superior Parietal Lobule	7	14	-65	56	7,55
Left Postcentral Gyrus	2	-43	-29	54	7,50
Left Postcentral Gyrus	1	-50	-20	51	7,37
Right Inferior Parietal Lobule	40	35	-44	51	7,31
Right Insula	13	52	-20	24	7,16
Right Precuneus	7	23	-74	37	7,11
Left Inferior Occipital Gyrus	17	-28	-95	-6	6,61
Right Inferior Parietal Lobule	40	35	-41	48	6,53
Left Precentral Gyrus	4	-37	-24	54	6,42
Right Superior Occipital Gyrus	19	32	-80	24	6,37
Right Middle Occipital Gyrus	19	40	-80	3	6,20
Right Inferior Parietal Lobule	40	47	-32	54	6,18
Right Inferior Parietal Lobule	40	41	-29	42	6,05
Left Precentral Gyrus	4	-34	-26	48	5,58
Left Middle Occipital Gyrus	19	-49	-74	-3	5,56
Left Precentral Gyrus	4	-32	-23	61	5,56
Left Postcentral Gyrus	2	-49	-26	36	5,51
Left Postcentral Gyrus	3	-58	-20	36	5,47
Left Cerebellum		-31	-89	-21	5,39
Right Precentral Gyrus	4	38	-17	61	5,25
Right Precentral Gyrus	6	23	-14	66	4,79
Left Superior Parietal Lobule	7	-25	-53	48	4,73
Right middle frontal gyrus	9	53	4	24	4,40
PanTool > ImiNov					
Left Middle Frontal Gyrus	46	-43	37	18	6,99
Left Inferior Frontal Gyrus	46	-43	31	9	6,75
Left Inferior Temporal Gyrus	20	-62	-56	-12	6,75
Right Precuneus	31	8	-68	24	6,66
Right Lingual Gyrus	18	2	-83	-1	6,53
Left Middle Frontal Gyrus	6	-43	4	45	6,51
Left Middle Frontal Gyrus	46	-46	25	25	6,47
Left Middle Temporal Gyrus	39	-43	-62	27	6,41

Right Inferior Parietal Lobule	40	47	-56	39	6,00
Left Cuneus	18	-3	-95	21	5,88
Left Precuneus	31	-7	-71	27	5,74
Right Middle Temporal Gyrus	20	59	-41	-12	5,60
Right Middle Frontal Gyrus	9	54	19	30	5,50
Left Inferior Frontal Gyrus	44	-52	10	15	5,48
Left Middle Frontal Gyrus	9	-46	13	34	5,46
Left Inferior Parietal Lobule	40	-52	-50	39	5,39
Left Fusiform Gyrus	37	-47	-41	-12	5,30
Right Cuneus	17	2	-86	9	5,26
Left Cerebellum		-25	-38	-15	4,84
Left Inferior Frontal Gyrus	47	-49	19	0	4,78
Left Inferior Frontal Gyrus	10	-40	52	0	4,76
Left Cingulate Gyrus	31	-4	-35	30	4,74
Right Cerebellum		5	-83	-18	4,67
Left Cuneus	18	-1	-83	24	4,53
Left Inferior Frontal Gyrus	10	-49	43	0	4,48

*p<.001 uncorrected, extent threshold k=300

Table S1. Peak voxel coordinates of significant activation clusters of the contrasts ImiNov > ContrImiNov, ImiGrip > ContrImiGrip, and PanTool > ContrPanTool.

		Peak voxel coordinate / t-value			
Anatomical region	BA	x	y	z	t*
Imitate Novel Posture > Control Novel Posture					
Left Postcentral Gyrus	3	-46	-20	54	10,0
Left Inferior Parietal Lobule	40	-43	-32	39	9,44
Left Cerebellum		-25	-53	-19	8,9
Left Postcentral Gyrus	2	-55	-29	39	8,65
Right Precentral Gyrus	4	38	-17	61	8,53
Right Inferior Parietal Lobule	40	35	-41	48	8,08
Left Postcentral Gyrus	40	-40	-29	45	7,99
Right Precentral Gyrus	4	53	-17	24	7,8
Left Postcentral Gyrus	3	-58	-20	42	7,71
Right Inferior Parietal Lobule	40	41	-32	38	7,54
Right Middle Frontal Gyrus	6	53	1	39	7,36
Right Postcentral Gyrus	3	47	-20	39	7,04
Right Postcentral Gyrus	40	41	-35	51	7,04
Right Postcentral Gyrus	3	44	-20	54	6,76
Left Inferior Occipital Gyrus	19	-37	-71	-3	6,68
Left Fusiform Gyrus	19	-52	-65	-12	6,49
Right Precentral Gyrus	6	60	1	6	6,47
Right Precentral Gyrus	6	26	-16	67	6,4
Left Precentral Gyrus	6	-55	-2	39	6,06
Imitate Grip Posture > Control Grip Posture					
Left Middle Occipital Gyrus	19	-52	-62	-3	8,9
Right Precentral Gyrus	4	35	-17	60	8,45
Right Inferior Temporal Gyrus	19	50	-58	0	7,43
Right Inferior Frontal Gyrus	47	38	22	-12	7,34
Left Inferior Frontal Gyrus	9	-52	4	24	7,0
Left Precentral Gyrus	6	-56	4	36	6,98
Left Cerebellum		-25	-50	-15	6,56
Right Inferior Parietal Lobule	40	38	-30	36	6,32
Left Fusiform Gyrus	37	-43	-47	-12	6,29
Right Postcentral Gyrus	3	29	-41	42	5,86
Right Postcentral Gyrus	3	59	-17	24	5,69
Left Medial Frontal Gyrus	6	-1	-8	51	5,65
Left Precuneus	7	-25	-71	48	5,5
Right Precentral Gyrus	6	56	1	30	4,91
PantomimeTool Posture > Control Tool Posture					
Right Precentral Gyrus	6	35	-14	60	9,22

Left Medial Frontal Gyrus	6	-4	-2	60	9,22
Left Inferior Frontal Gyrus	44	-46	-3	18	8,83
Right Medial Frontal Gyrus	6	2	-2	60	8,48
Left Middle Frontal Gyrus	46	-46	22	27	7,65
Left Postcentral Gyrus	2	-49	-29	36	7,62
Left Postcentral Gyrus	2	-55	-27	39	7,28
Left Inferior Parietal Lobule	40	-46	-35	39	7,23
Right Postcentral Gyrus	3	56	-17	24	7,02
Left Inferior Frontal Gyrus	46	-43	34	9	6,84
Left Medial Frontal Gyrus	6	-4	-8	51	6,76
Left Precentral Gyrus	44	-55	10	12	6,74
Left Precentral Gyrus	6	-61	-17	39	6,71
Left Inferior Parietal Lobule	40	-31	-50	57	6,52
Left Postcentral Gyrus	3	-40	-23	57	6,49
Right Postcentral Gyrus	40	32	-35	51	6,42
Left Insula	13	-39	7	0	6,4
Left Postcentral Gyrus	2	-61	-23	33	6,36
Left Precentral Gyrus	6	-52	1	33	6,34
Left Medial Frontal Gyrus	32	-4	7	46	6,31
Left Inferior Parietal Lobule	40	-37	-41	48	6,19
Right Precentral Gyrus	44	57	10	6	6,08
Left Inferior Parietal Lobule	40	-52	-27	32	5,69
Left Middle Frontal Gyrus	46	-43	40	18	5,69

*p<.001 uncorrected, extent threshold k=300

Figure 1


Imi Nov
Imitate
Imi Grip
Imitate
Pan Tool
Pantomime
Contr Imi Nov
Middle Finger?
Contr Imi Grip
Middle Finger?
Contr Pan Tool
Middle?
Instruction (2s)
Stimulus and performance (5s)
ISI (250ms - 1s)
Six slides within one conditions' block

Figure 2

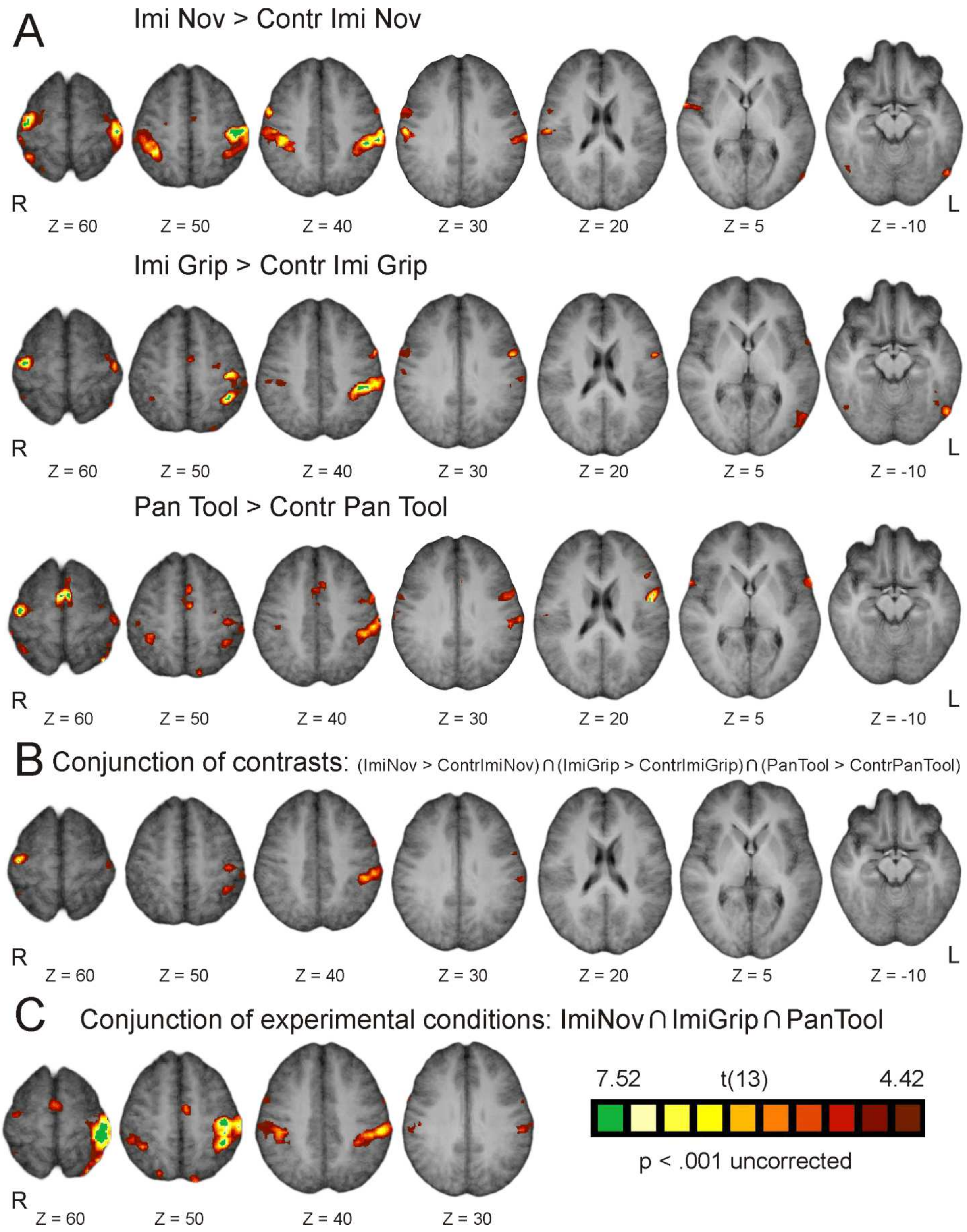

A
Imi Nov > Contr Imi Nov
R
L
Z = 60
Z = 50
Z = 40
Z = 30
Z = 20
Z = 5
Z = -10
Imi Grip > Contr Imi Grip
R
L
Z = 60
Z = 50
Z = 40
Z = 30
Z = 20
Z = 5
Z = -10
Pan Tool > Contr Pan Tool
R
L
Z = 60
Z = 50
Z = 40
Z = 30
Z = 20
Z = 5
Z = -10
B Conjunction of contrasts: (ImiNov > ContrImiNov) ∩ (ImiGrip > ContrImiGrip) ∩ (PanTool > ContrPanTool)
R
L
Z = 60
Z = 50
Z = 40
Z = 30
Z = 20
Z = 5
Z = -10
C Conjunction of experimental conditions: ImiNov ∩ ImiGrip ∩ PanTool
R
Z = 60
Z = 50
Z = 40
Z = 30
7.52
t(13)
4.42
p < .001 uncorrected

Figure 3

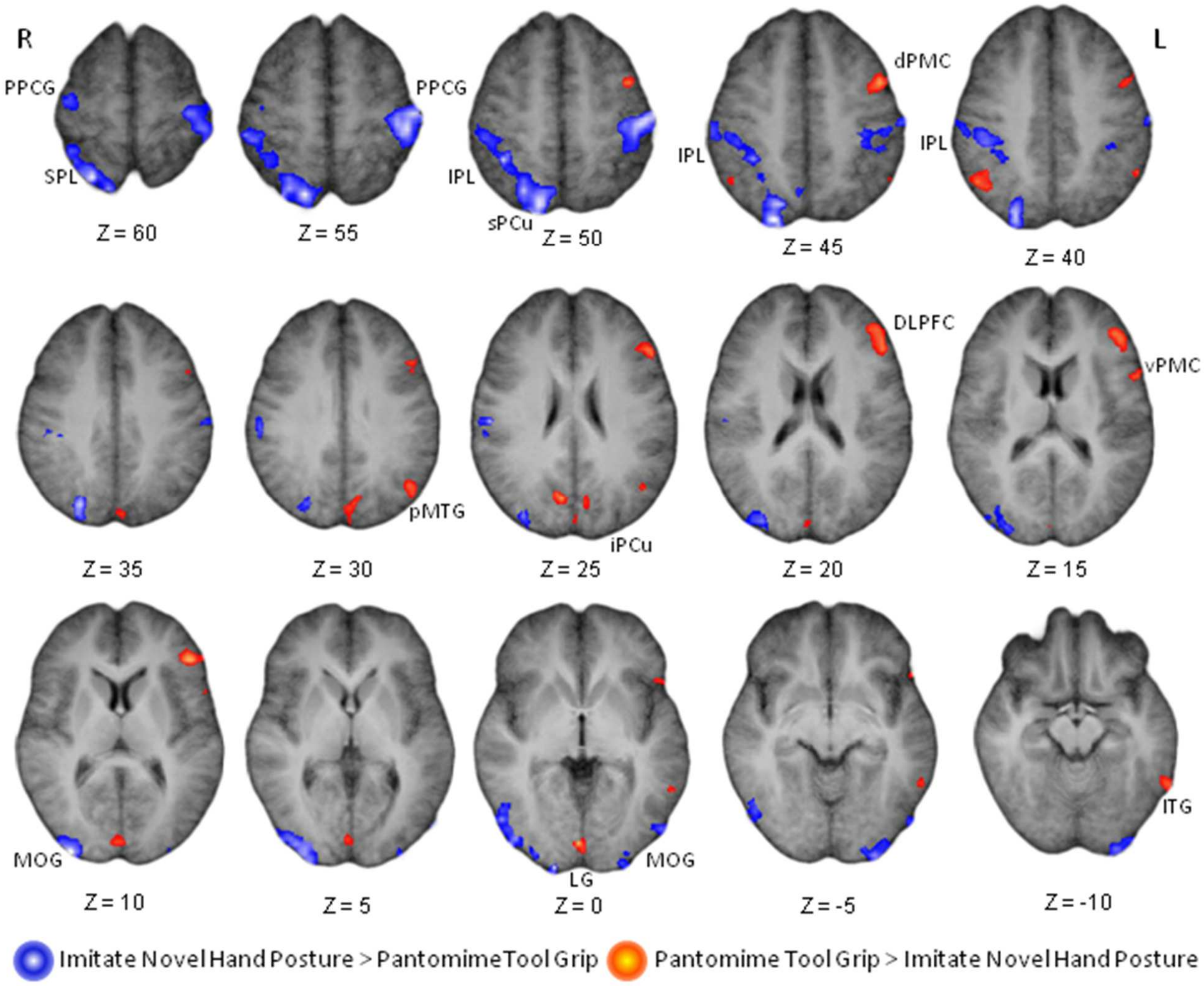
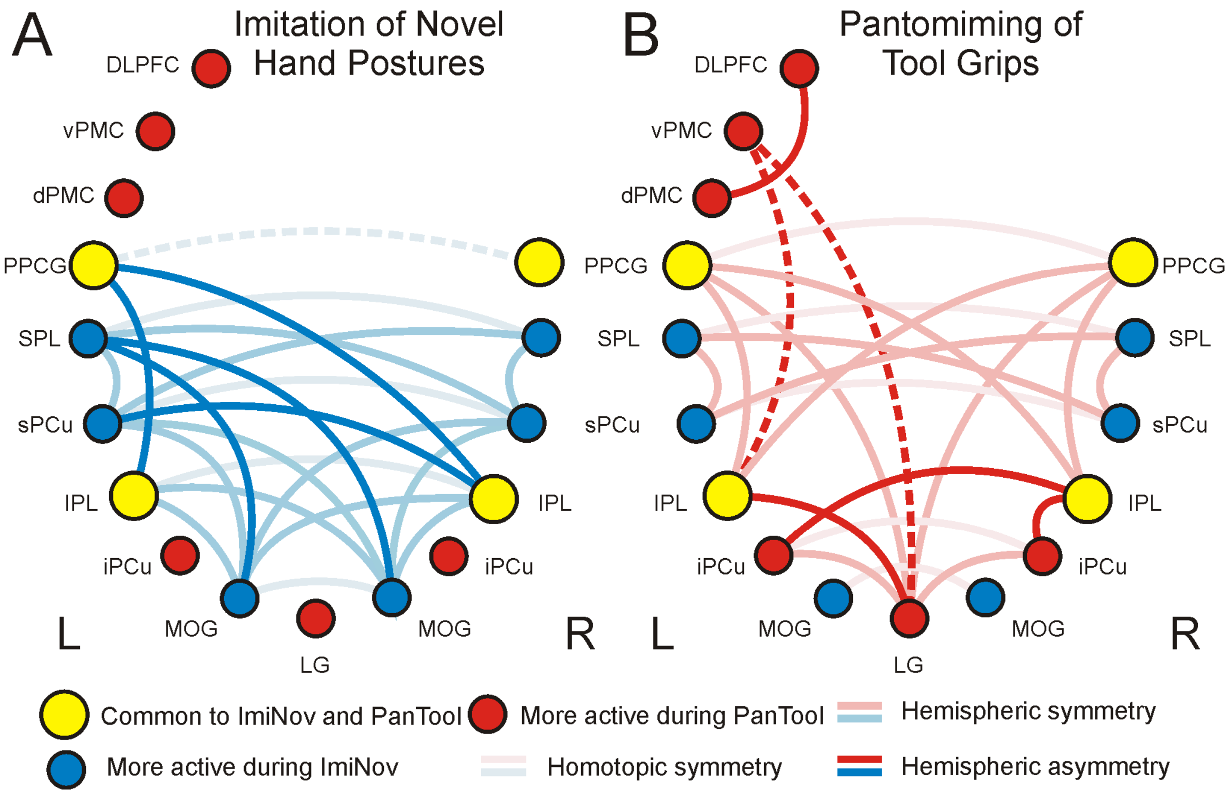

R
L
PPCG
SPL
PPCG
IPL
sPCu
dPMC
IPL
IPL
Z = 60
Z = 55
Z = 50
Z = 45
Z = 40
DLPFC
vPMC
pMTG
iPCu
Z = 35
Z = 30
Z = 25
Z = 20
Z = 15
MOG
LG
MOG
ITG
Z = 10
Z = 5
Z = 0
Z = -5
Z = -10
Imitate Novel Hand Posture > Pantomime Tool Grip
Pantomime Tool Grip > Imitate Novel Hand Posture

Figure 4


A
Imitation of Novel
Hand Postures
DLPFC
vPMC
dPMC
PPCG
SPL
sPCu
IPL
iPCu
MOG
LG
L
R
B
Pantomiming of
Tool Grips
Common to ImiNov and PanTool
More active during PanTool
Hemispheric symmetry
More active during ImiNov
Homotopic symmetry
Hemispheric asymmetry