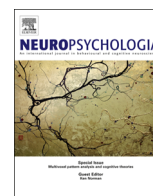




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Contents lists available at ScienceDirect

Neuropsychologia

journal homepage: www.elsevier.com/locate/neuropsychologia

Spatial imagery in haptic shape perception

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ARTICLE INFO

Article history:

Received 20 March 2014

Received in revised form

27 April 2014

Accepted 13 May 2014

Available online 2 June 2014

Keywords:

fMRI

Multisensory

Effective connectivity

Granger causality

Object familiarity

ABSTRACT

We have proposed that haptic activation of the shape-selective lateral occipital complex (LOC) reflects a model of multisensory object representation in which the role of visual imagery is modulated by object familiarity. Supporting this, a previous functional magnetic resonance imaging (fMRI) study from our laboratory used inter-task correlations of blood oxygenation level-dependent (BOLD) signal magnitude and effective connectivity (EC) patterns based on the BOLD signals to show that the neural processes underlying visual object imagery (objIMG) are more similar to those mediating haptic perception of familiar (fHS) than unfamiliar (uHS) shapes. Here we employed fMRI to test a further hypothesis derived from our model, that spatial imagery (spIMG) would evoke activation and effective connectivity patterns more related to uHS than fHS. We found that few of the regions conjointly activated by spIMG and either fHS or uHS showed inter-task correlations of BOLD signal magnitudes, with parietal foci featuring in both sets of correlations. This may indicate some involvement of spIMG in HS regardless of object familiarity, contrary to our hypothesis, although we cannot rule out alternative explanations for the commonalities between the networks, such as generic imagery or spatial processes. EC analyses, based on inferred neuronal time series obtained by deconvolution of the hemodynamic response function from the measured BOLD time series, showed that spIMG shared more common paths with uHS than fHS. Re-analysis of our previous data, using the same EC methods as those used here, showed that, by contrast, objIMG shared more common paths with fHS than uHS. Thus, although our model requires some refinement, its basic architecture is supported: a stronger relationship between spIMG and uHS compared to fHS, and a stronger relationship between objIMG and fHS compared to uHS.

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1. Introduction

Many studies have shown that various visual cortical regions are active during haptic perception (see Amedi, von Kriegstein, van Atteveldt, Beauchamp, & Naumer, 2005a; Sathian & Lacey, 2007; Lacey & Sathian, 2011, for reviews). Among such regions, the most extensively researched is the lateral occipital complex (LOC), a visually shape-selective region in the ventral visual pathway (Malach et al., 1995). The LOC is also haptically shape-selective for both 3D (Amedi, Malach, Hendler, Peled, & Zohary, 2001; Stilla & Sathian, 2008; Zhang, Weisser, Stilla, Prather, & Sathian, 2004) and 2D shapes (Prather, Votaw, & Sathian, 2004; Stoesz et al., 2003), but

is not activated during object recognition triggered by object-specific sounds (Amedi, Jacobson, Hendler, Malach, & Zohary, 2002), unless the task demands shape processing (James, Stevenson, Kim, VanDerKlok, & James, 2011) or when auditory object recognition is mediated by a visual–auditory sensory substitution device that converts shape information into an auditory ‘soundscape’ (Amedi et al., 2007); it is hence thought to be a processor of geometric shape.

An intuitive explanation for haptically-evoked activation of visual cortex is mediation by visual imagery (Sathian, Zangaladze, Hoffman, & Grafton, 1997). The LOC is active during mental imagery of familiar objects previously explored haptically by blind individuals or visually by sighted individuals (De Volder et al., 2001), and during recall of geometric and material object properties from memory (Newman, Klatzky, Lederman, & Just, 2005). In addition, individual differences in ratings of the vividness of visual imagery strongly predicted haptic shape-selective activation magnitudes in the right LOC

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(Zhang et al., 2004). One argument that has been advanced against the visual imagery hypothesis depends on the observation that the congenitally blind show shape-related activity in the same regions as the sighted: since the congenitally blind do not have visual imagery, such imagery, it is argued, cannot account for the activations seen in the sighted (Pietrini et al., 2004). However, the fact that the blind do not have visual imagery during haptic perception is certainly no reason to exclude this possibility in the sighted, particularly in view of the extensive evidence for cross-modal plasticity in studies of visual deprivation (Pascual-Leone, Amedi, Fregni, & Merabet, 2005; Sathian, 2005; Sathian & Stilla, 2010). Another argument against the role of visual imagery is that activation magnitude in the LOC during visual imagery was found to be only about 20% of that during haptic shape perception, implying that visual imagery is relatively unimportant to this process (Amedi et al., 2001). However, this study did not monitor performance on the visual imagery task and so the lower LOC activity during imagery could simply mean that participants were not performing the task consistently or were not maintaining their visual images throughout the imagery scan.

We recently tested the visual imagery hypothesis, predicting that, if visual imagery mediated LOC recruitment during haptic shape (HS) perception, these two conditions would activate common areas with activation magnitudes being correlated across conditions, and that the two conditions would also show similar patterns of effective connectivity (EC). In contrast to earlier studies, visual imagery was verified by monitoring participants' performance on a visual imagery task requiring a same-different judgment. Comparing this visual imagery task to HS perception of familiar objects yielded an extensive network of common regions, including bilateral LOC and a number of prefrontal areas, many of which showed significant, positive inter-task correlations (Lacey, Flueckiger, Stilla, Lava, & Sathian, 2010). When visual imagery was compared to HS perception of unfamiliar objects, however, there were very few common regions, with only one (in the intraparietal sulcus [IPS]) showing a significant, positive inter-task correlation (Lacey et al., 2010). Examination of EC within the cortical networks involved in visual imagery and HS perception revealed that the visual imagery network strongly resembled the familiar (fHS), but not the unfamiliar, haptic shape (uHS) network (Deshpande, Hu, Lacey, Stilla, & Sathian, 2010a). In sum, we demonstrated that visual imagery is strongly linked to haptic perception of familiar objects but only weakly associated with haptic perception of unfamiliar objects. We also noted that the visual imagery and fHS tasks probably engaged visual object imagery (objIMG) rather than spatial imagery (spIMG) (Blajenkova, Kozhevnikov, & Motes, 2006; Blazhenkova & Kozhevnikov, 2009; Kozhevnikov, Hegarty, & Mayer 2002; Kozhevnikov, Kosslyn, & Shephard, 2005), and that the latter might underpin the uHS task.

Based on these findings, we proposed a conceptual framework for visuo-haptic object representation that integrates the visual imagery and multisensory approaches (Lacey, Tal, Amedi, & Sathian, 2009). In this model, the LOC contains a representation that is independent of the input sensory modality and is flexibly accessible via either bottom-up or top-down pathways, depending on object familiarity (or other task attributes). For familiar objects, global shape can be inferred relatively easily, perhaps from distinctive features that suffice to retrieve a visual image, and so the model emphasizes top-down contributions from parietal and prefrontal regions that drive objIMG during fHS perception. By contrast, because there is no stored representation of an unfamiliar object, its global shape has to be computed by exploring it in its entirety; uHS may therefore rely more on bottom-up pathways from somatosensory cortex to the LOC. Since parietal cortex in and around the IPS is implicated in visuo-haptic perception of both shape and location (Sathian et al., 2011; Stilla & Sathian, 2008), the model also implicates these parietal regions in processing the

relative spatial locations of object parts to assemble a global object representation from its component parts, facilitated by spIMG.

Here, we tested the aspect of the model dealing with spIMG in relation to fHS and uHS. We compared a spIMG task, in which participants mentally construct a novel shape from its component parts, to fHS and uHS. We predicted that activation magnitude during the spIMG task, particularly in regions in and around the IPS, would correlate across participants with relevant behavioral variables: accuracy on the spIMG task and individual preference for spatial imagery as measured by the Object-Spatial Imagery and Verbal Questionnaire (OSIVQ) (Blazhenkova & Kozhevnikov, 2009). We expected, further, that there would be more common regions, and more inter-task correlations of activation magnitude, between spIMG and uHS, compared to spIMG and fHS. We also hypothesized that the EC network for spIMG would more closely resemble that of uHS than fHS. Our earlier study (Deshpande et al., 2010a) used EC analyses of the measured blood oxygenation level-dependent (BOLD) signal time series, whereas in the present study, the hemodynamic response function (HRF) was deconvolved from the measured BOLD signals to yield inferred neuronal time series (Havlicek, Friston, Jan, Brazdil, & Calhoun, 2011) on which the EC analyses were performed. The latter method removes the smoothing introduced by the HRF and has the advantage of being impervious to inter-regional as well as inter-individual variations of the HRF. Both simulations (Ryali, Supekar, Chen, & Menon, 2011) and experimental data (David et al., 2008) have demonstrated improvements in GC-based effective connectivity metrics obtained from deconvolved as compared to raw BOLD data. To allow proper evaluation of our model, we re-analyzed our earlier data (Deshpande et al., 2010a) using the same methods as here. We expected that, in contrast to spIMG, visual object imagery (objIMG) would have more paths in common with fHS than uHS.

2. Materials and Methods

2.1. Participants

Twelve neurologically normal participants (6 males, 6 females; mean age 22 years 7 months) took part after giving informed consent. All participants were right-handed, based on the validated subset of the Edinburgh handedness inventory (Raczkowski, Kalat, & Nebes, 1974). We excluded participants with calluses on their hands, and those for whom American English was a second/non-native language, because the control task for the spIMG task relied on verbal stimuli. The Institutional Review Board of Emory University approved all procedures.

2.2. Procedures

Participants performed three tasks, as detailed below: a spIMG task that was completed in one session and two haptic tasks (fHS, uHS), which were completed in either one or two sessions (6 participants each) in order to accommodate individuals' schedules. The order of the tasks was counterbalanced across participants; within each task, the order of runs was also counterbalanced.

2.2.1. Spatial imagery task

The spIMG task required imagining a previously memorized 4×4 matrix with one letter in each position (Fig. 1a). Participants imagined the shape that would result if four cells in the matrix, cued by an auditory four-letter string, were filled in, and performed a one-back same/different discrimination on the imagined shape. Thus, participants had to compute global shape using the spatial relationships between component parts, analogous to the processes hypothesized for uHS in our model (see above). Participants were trained on this task, the day before the fMRI scan for the task. No time limit was set for this and no instructions were provided regarding the method of memorization, to allow for spontaneous use of individually preferred strategies. We first asked participants to memorize the lettered matrix and then, to test for accurate memorization, asked them to identify the four-letter sequences that formed all the horizontal rows, vertical columns, 2×2 squares, and diagonal lines. They next had to describe the shapes represented by the four-letter sequences, read aloud by the experimenter, for all the horizontal rows, vertical columns, and the 2×2 squares in the four corners of the grid (note

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