

Haptically evoked activation of visual cortex

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Introduction

Thanks to the acceleration of research into multi-sensory processing in recent years, the idea that the brain is organized around parallel processing of separate sensory inputs is giving way to the concept of a ‘metamodal’ brain [1] organized around particular tasks in a modality-independent fashion. For example, it is now apparent that many cortical areas previously thought to be specialized for processing specific aspects of visual input are also activated during analogous haptic or tactile tasks. In this chapter, we review the circumstances in which haptic or tactile tasks are associated with visual cortical activity and what this means for our internal representation of the external world, i.e., how information about objects and events in the external world is stored in memory. By ‘haptic’, we mean tasks involving active motor exploration of stimuli, whereas ‘tactile’ refers here to tasks in which stimuli are applied to the passive finger or other skin surface.

Visual cortical involvement in touch

Gratings and dot-patterns

The first indication that tactile input could activate extrastriate visual cortex came from our positron emission tomographic (PET) study [2]. In this study, participants had to discriminate the orientation of gratings presented to the immobilized right index fingerpad. In a control task, participants discriminated the width of the grooves on the gratings. A contrast between

these tasks revealed activity that was selective for tactile discrimination of grating orientation in the left extrastriate visual cortex, at a focus close to the parieto-occipital fissure. This same focus is known to be active during both visual grating orientation discrimination [3] and spatial imagery [4]. We therefore concluded that activation of this focus during tactile discrimination of grating orientation reflected spatial processes that are common to vision and touch [2]. This study suggested, for the first time, that task-selective visual cortex responds to a tactile analog of the relevant visual task and that visual cortical activity might be independent of the sensory modality in which a task is presented.

A subsequent functional magnetic resonance imaging (fMRI) study confirmed this left parieto-occipital activation during tactile discrimination of grating orientation when contrasted with discrimination of grating groove width, and also revealed additional activations on this contrast in the right postcentral sulcus (PCS) and the left anterior intraparietal sulcus (aIPS) [5]. Another fMRI study also found left-lateralized activity in the aIPS during discrimination of grating orientation on a contrast with discrimination of small changes in grating location [6], whereas a third study in which the control task was discrimination of grating roughness revealed a right-lateralized PCS-aIPS complex that was selectively active during grating orientation discrimination [7]. This last study, moreover, demonstrated multi-sensory task-related activity in the right aIPS, which was also activated by visual discrimination of grating orientation compared to discrimination of grating color.

Transcranial magnetic stimulation (TMS) studies have shown that these tactually-evoked visual

cortical activations reflect functional involvement in tactile perception, rather than being an epiphenomenal byproduct. TMS involves the application of a magnetic pulse to the scalp that can temporarily disrupt the function of the immediately underlying cortex, producing a 'virtual lesion' [8]. If TMS over a particular area results in impaired task performance, we can infer that the targeted area is necessary for task performance [9]. Applying single-pulse TMS to the left parieto-occipital region found by Sathian and colleagues [2], 180 ms after tactile stimulus onset, significantly impaired tactile discrimination of grating orientation, but not grating groove width [10]. TMS at other sites did not affect performance on either task. In another study, repetitive TMS (rTMS) was used in a study of subjective estimates of tactile interdot distance and roughness [11]. The psychometric functions differ for these two kinds of estimates: perceived interdot distance increases monotonically as physical interdot distance increases up to 8 mm, while perceived roughness peaks around 3 mm. This dissociation was reflected in the rTMS effects: rTMS over medial occipital cortex disrupted estimates of tactile distance but not roughness, whereas the reverse was true for rTMS over primary somatosensory cortex. Furthermore, a congenitally blind patient with bilateral occipital lesions was impaired at estimating tactile interdot distances but not roughness [11]. However, a corresponding fMRI study failed to show a similar dissociation: activity in primary visual cortex was weak and non-selective, distance-selective activity was found only in the left IPS, and no roughness-selective activation was found [12]. The reasons underlying this disparity between the fMRI study and the corresponding TMS/lesion studies are not clear at this time.

Shape

Several cortical areas have been implicated in visuo-haptic shape processing, principally the lateral occipital complex (LOC). The LOC is a

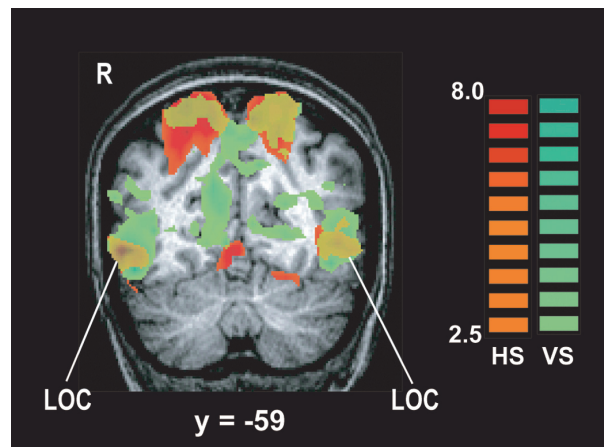


FIGURE 1.

Brain regions showing selective activity for perception of visual shape (VS, green) and haptic shape (HS, red) displayed on a coronal slice through the brain image (the Talairach y-coordinate for this slice is shown). Bisensory (visuo-haptic) overlap of shape-selectivity (yellow) can be seen in the lateral occipital complex (LOC, identified by pointers) and also in the intraparietal sulcus (at the top). The brain is shown in radiologic convention in which the right hemisphere (R) is on the left. The color t-scales reflect the statistical significance of shape-selectivity, in each modality, relative to the control condition (texture perception). Based on the data of Stilla and Sathian [15].

visually shape-selective area in the ventral visual pathway [13] that is also shape-selective during haptic perception of 3-D objects [14–16] (Fig. 1). This bisensory shape processing is confined to a sub-region of the LOC, termed LOTv [17]. The LOC is active even during tactile processing of 2-D forms, as contrasted with both gap detection [18] and bar orientation [19]. The overlap of visual and haptic shape-selective activity in LOTv suggests the possibility of a shared representation of shape. The finding that the magnitudes of visually- and haptically-evoked shape activations are significantly correlated across subjects in the right but not the left LOC [15] suggests that the site of a shared representation across vision and touch might be the right LOC. The LOTv appears