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Selectivity for large nonmanipulable objects in scene-selective visual cortex does not require visual experience

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ABSTRACT

The principles that determine the organization of object representations in ventral temporal cortex (VTC) remain elusive. Here, we focus on the parahippocampal place area (PPA), a region in medial VTC that has been shown to respond selectively to pictures of scenes. Recent studies further observed that this region also shows a preference for large nonmanipulable objects relative to other objects, which might reflect the suitability of large objects for navigation. The mechanisms underlying this selectivity remain poorly understood. We examined the extent to which PPA selectivity requires visual experience. Fourteen congenitally blind and matched sighted participants were tested on an auditory size judgment experiment involving large nonmanipulable objects, small objects (tools), and animals. Sighted participants additionally participated in a picture-viewing experiment. Replicating previous work, we found that the PPA responded selectively to large nonmanipulable objects, relative to tools and animals, in the sighted group viewing pictures. Importantly, this selectivity was also observed in the auditory experiment in both sighted and congenitally blind groups. In both groups, selectivity for large nonmanipulable objects was additionally observed in the retrosplenial complex (RSC) and the transverse occipital sulcus (TOS), regions previously implicated in scene perception and navigation. Finally, in both groups the PPA showed resting-state functional connectivity with TOS and RSC. These results provide new evidence that large object selectivity in PPA, and the intrinsic connectivity between PPA and other navigation-relevant regions, do not require visual experience. More generally, they show that the organization of object representations in VTC can develop, at least partly, without visual experience.

Introduction

The functional organization of object representations in the human visual cortex, especially the ventral temporal cortex (VTC), has been the focus of much recent research. Functional neuroimaging studies have provided evidence that different object domains evoke distinct responses in VTC. For example, specific regions of VTC respond selectively to particular object categories, such as faces, bodies, words, or places (Bracci et al., 2010; Chao et al., 1999; Cohen and Dehaene, 2004; Downing et al., 2001, 2006; Epstein and Kanwisher, 1998; Kanwisher, 2010; Kanwisher et al., 1997; Peelen and Downing, 2005).

A particularly strong type of categorical selectivity is observed with scene stimuli. Compared to pictures of faces, common objects or scrambled pictures, pictures of scenes or places elicit stronger activation in a region in the parahippocampal gyrus (the parahippocampal place area, PPA), along with two additional regions in the retrosplenial complex (RSC) and the transverse occipital sulcus (TOS) (e.g., Epstein and Kanwisher, 1998; Goh et al., 2004). These findings motivated hypotheses about the function of PPA, including that it processes peripheral visual information, certain geometrical features about openness or closeness, or spatial properties (e.g., Kravitz et al., 2011; Levy et al., 2001; Park et al., 2011; Ross and Oliva, 2010). Interestingly, a series of recent studies showed that PPA activity is also modulated by the type of objects, preferring objects that are part of a scene (e.g., buildings, Maguire et al., 2001), large (Konkle and Oliva, 2012; Mullally and Maguire, 2011; Troiano et al., in press), with strong contextual associations (e.g., Bar and Aminoff, 2003), or those that more easily evoke a sense of space or place (Mullally and Maguire, 2011).

The degree to which visual object properties underlie the observed object categorical effects in PPA remains debated. One type of proposal is that the preference for scenes and some types of objects is driven by its sensitivity to certain visual aspects that are shared between scenes and these objects, e.g., peripheral visual information being more important (e.g., Konkle and Oliva, 2012). Alternatively, it might be because these regions are at least partly engaged in the more abstract interpretation of the stimulus, and the selectivity reflects how strongly the objects imply a scene/place and information useful for spatial navigation (e.g., Troiano et al., in press). In the

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present study we tested congenitally blind participants to investigate whether knowledge of visual object properties is required for object category selectivity in the PPA.

While the potentially relevant object properties driving PPA, such as size, are predominantly obtained through the visual modality in normal circumstances, they can nonetheless be obtained through other modalities. Save et al. (1998) reported that early blind rats exhibited place cell firing activities highly similar to sighted rats. In humans, Wolbers et al. (2011) reported that both blind and sighted participants showed stronger PPA activation when they explored Legos as a scene layout compared to when they explored the stimuli as objects, suggesting that PPA's engagement in scene processing can develop without visual experience.

Other aspects of object categorical distributions in VTC have also been shown to be independent of visual experience. Pietrini et al. (2004) reported category-related fMRI response patterns for faces and manmade objects in VTC in congenitally blind participants during tactile object recognition. Reich et al. (2011) found that congenitally blind individuals show selective fMRI responses to Braille word stimuli in a region in left VTC that closely corresponds to the "visual word form area" in sighted individuals. Mahon et al. (2009) observed a preference for inanimate over animate objects in the medial portion of bilateral VTC in both sighted and three congenitally blind participants performing an auditory size judgment task.

In the present study, we investigated whether the selectivity for large nonmanipulable objects in PPA requires previous visual experience. We compared PPA responses to objects that are large and typically nonmanipulable/nonportable, relative to small manipulable objects (tools) and animals in sighted and congenitally blind participants. Both participant groups listened to the names of these objects, and sighted participants additionally viewed pictures. If the selectivity to large nonmanipulable objects in PPA was driven primarily by certain visual properties specifically associated with these objects, we expect that congenitally blind participants would show different (i.e., weaker, null, or disordered) patterns in comparison to the sighted participants. If, however, such selectivity in PPA originated from non-visual processes such as multi-modal spatial navigation, we expect that congenitally blind participants would develop PPA selectivity patterns similar to sighted participants. Furthermore, to better understand the role of visual experience in shaping PPA's functional profile, we explored the intrinsic functional connectivity pattern of PPA using resting-state fMRI in both participant groups, aiming to examine whether the spontaneous functional network associated with PPA is affected by visual experience.

Methods

Participants

Sixteen congenitally blind and seventeen sighted adults were scanned and paid for participation in the study. All blind participants reported that they lost their vision since birth, ten due to major retinal damage and six not knowing the exact pathology. Seven of them had faint light perception but could not recognize any pattern. Two blind individuals were excluded from the data analysis because the MRI scans discovered unknown old brain lesions. One sighted participant was discarded from the experimental data analysis due to excessive head motion during the experimental run. The remaining fourteen blind and sixteen sighted participants were matched on gender distribution (blind: seven females; sighted: seven females), handedness (all right handed), age (blind: mean = 45, SD = 10, range = 26–60; sighted: mean = 38, SD = 12, range = 18–60; $t(28) = 1.6$, $p = .11$) and years of education (blind: mean = 11, SD = 2, range = 9–12; sighted: mean = 11, SD = 2, range = 9–12; $t(28) < 1$). They were all native Mandarin Chinese speakers. None suffered from psychiatric or neurological disorders, had ever sustained head injury, or were on any psychoactive medications. All participants completed a written informed consent approved by the institutional review board of Beijing Normal University (BNU) Imaging Center for Brain Research.

Materials and procedure

Congenitally blind and sighted participants performed an auditorily-presented task. In the same session we also included a picture-viewing task in which the sighted participants viewed the same objects as the items used in the auditory experiment. In a separate session, carried out at a later time, a scene localizer task was administered to four of the sighted participants to functionally localize the parahippocampal place area (PPA) in the sighted group.

Experiment 1 — Size judgment

The participants were asked to perform size judgments on the objects that were referred to by the auditory words. There were three object categories — tools (e.g., 斧子 axe), large nonmanipulable objects (e.g., 帆船 sailboat) and animals (e.g., 青蛙 frog), each comprised of 30 items (see complete list in Supplementary Appendix). Tools included kitchen utensils, farm implements, weapons and other common indoor tools. Animals included mammals, birds, insects and reptiles. Following Mahon et al. (2009), large nonmanipulable objects included furniture (8, e.g., couch), appliances (6, e.g., refrigerator), vehicles (3, e.g., truck), buildings (3, e.g., castle) and other common objects (10, e.g., blackboard). All stimuli were disyllabic words and were matched across conditions on word frequency (log; tools: mean = .75, SD = 0.4; large nonmanipulable objects: mean = .77, SD = 0.6; animals: mean = .73, SD = 0.4; $F(2, 87) < 1$), familiarity (tools: mean = 5.5, SD = 1.1; large nonmanipulable objects: mean = 5.4, SD = 1.0; animals: mean = 5.1, SD = 0.7; $F(2, 87) = 1.1$, $p = .30$) and imageability (tools: mean = 6.7, SD = 0.4; large nonmanipulable objects: mean = 6.7, SD = 0.3; animals: mean = 6.7, SD = 0.2; $F(2, 87) < 1$). The familiarity and imageability ratings were collected from a group of 32 (16 for each rating) college students, who did not participate in the fMRI experiments, using a seven-point scale (seven for most familiar and most imageable). Each word was recorded digitally (22,050 Hz, 16 Bit) by a female native Mandarin speaker.

In the scanner, stimuli were presented binaurally over a headphone in blocks of five words, all from the same category. The participants were instructed to think about the size of the first item of the group, and to compare the subsequent items to the first one. If all of the five objects had roughly the same size, the participants responded by pressing a button with the index finger of the left hand; if at least one of the last four objects was different in size from the first one, the participants pressed a button with the right index finger. A response cue (auditory tone, duration 200 ms) was presented after the offset of the last item of the block, and the participants were asked to respond after hearing this response cue. Each of the five trials in a block lasted 2 s and the last trial was followed by a 4 s silent period for response. Thus, each block lasted 14 s, and was separated by a 14 s period of silence between blocks.

Each item was presented twice during the experiment and was grouped with different words for the two presentations. There were four runs: each lasted 4 min and 40 s and had 10 blocks. The first block of each run was used for practice. The order of blocks was constant for each participant and was pseudo-randomized with the restriction that no two consecutive blocks were from the same category.

Experiment 2 — Picture viewing

A passive picture-viewing task was conducted with the sighted individuals, using the items from the three main categories (tools, large nonmanipulable objects, and animals) in Experiment 1. Black and white photographs ($400 * 400$ pixels, visual angle $10.55° \times 10.55°$) were used in this experiment.