Cognitive Neuroscience: Scene Layout from Vision and Touch

Parahippocampal and retrosplenial cortices respond strongly to visual scenes. A new study shows that these regions also activate when scenes are perceived haptically — even in the blind.

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Functional magnetic resonance imaging (fMRI) studies have identified several regions of the human brain involved in the perception of navigationally-relevant stimuli [1–3]. For example, a region in posterior parahippocampal cortex known as the parahippocampal place area (PPA) responds strongly when subjects view scenes (landscapes, cityscapes, rooms) but only weakly when they view non-scene objects such as vehicles, tools, bodies, and faces. A similar pattern of scene-preferential response has been observed in a retrosplenial/ medial-parietal region known as the retrosplenial complex (RSC). Although these data, along with concomitant neuropsychological findings [4], strongly suggest that these brain areas might encode spatial information useful for navigation, this principle has not been firmly established, and the precise function of these regions remains a topic of much debate.

Consider, for example, the PPA. The original report on this region hypothesized that the PPA responds preferentially to scenes because it codes the spatial layout of the local environment, as defined by major barriers and affordances (such as walls and pathways), information that is conveyed by scenes but is not typically conveyed by single, standalone objects [5]. This idea was further supported by findings that the PPA is highly sensitive to the geometric structure of a stimulus; for example, it responds more strongly to 'scenes' made out of Lego blocks than to 'objects' constructed from the same materials [6]. However, because these earlier studies only examined fMRI response to *visually* presented scenes, it was not clear that the PPA encoded *spatial* information available from a scene, rather than nonspatial visual qualities.

A new paper by Wolbers *et al.* [7], in this issue of *Current Biology*, makes some progress in resolving this issue.

The key innovation is that subjects in the experiments perceived scenes haptically (without vision) before they perceived them visually. The authors constructed 27 'scenes' and 27 'objects' from Lego blocks. On each haptic trial, subjects explored four scenes or objects by touch for 12 seconds each and then reported whether a fifth item (also explored solely by touch) matched any of the four preceding sample items. To encourage subjects to perceive the scenes as navigable layouts, toy furniture items were placed in the sample scenes — however, because no objects were placed in the match scenes, subjects had to base their judgment on the geometry of the walls rather than the furniture. Following the haptic run, subjects performed the same task visually, with faster presentation times and no haptic exploration. fMRI data were collected whilst subjects performed both tasks.

In both the haptic and visual runs, the PPA and RSC responded more strongly to Lego scenes than to Lego objects. This suggests that these regions encode spatial information that is obtainable through both vision and touch. An alternative explanation, however, might be that subjects were forming mental images of the scenes during the haptic runs. Wolbers *et al.* [7] ruled this account out in two ways. First, they examined functional connectivity between the PPA and early visual areas in occipital cortex. These regions were functionally coupled during visual perception of scenes but not haptic perception, arguing against visual recoding of scenes during the haptic runs. Second, they repeated the haptic version of the experiments in seven blind subjects (including three blind from birth). Remarkably, the PPA and RSC exhibited preferential response to scenes even in these subjects, who could not have been forming mental images.

These findings are consistent with other recent work suggesting that PPA

and RSC encode spatial aspects of scenes. Two fMRI studies [8,9] found that multivoxel patterns in the PPA were more similar for scenes sharing the same spatial geometry (open or closed) than for scenes with different geometry, even when the scenes in question are drawn from different categories [8] and differ in visual details [9]. Along the same lines, a study examining fMRI adaptation effects in PPA and RSC found evidence for *boundary extension*, which is the tendency to see a repeated scene image as being more 'close up' than the original [10]. This phenomenon is usually taken to indicate encoding of spatial layout that extends beyond the arbitrary edges of the image — the second presentation is judged to be more constrained than the first because this extended layout is not fully depicted in the image [11]. Interestingly, boundary extension has been observed for haptically-perceived scenes in behavioral studies and has even been reported in a deaf and blind subject [12], thus providing another line of evidence for the existence of a modality-independent representation of scene layout. Finally, recent studies indicate that the PPA is sensitive to spatial quantities such as size and distance, responding more strongly to larger [13] and more distant [14] items. This might have been a factor in the current experiment: although the Lego scenes and Lego objects were roughly the same size, the subjects were encouraged to treat the scenes as life-size rooms, whereas no similar rescaling cues were given for the objects.

Many questions remain about the exact nature of the spatial codes revealed by these experiments. In the case of the PPA, the current results are most naturally interpretable in terms of coding of the geometric structure defined by the Lego 'walls', but they do not preclude the possibility that the region may encode a less detailed spatial coordinate frame that is anchored to the walls but might equally well be anchored to a landmark object with quite different intrinsic geometry. In the case of RSC, previous studies have implicated the region in the coding of directional information that allows a navigator to orient herself in the wider environment [15–17]. Thus, activation in RSC in the current study might reflect the setting up of an orientational axis for each scene, but

this remains to be proven. It is worth noting that these results implicating PPA and RSC in the coding of spatial information do not exclude the possibility that these regions might also encode nonspatial information, such as color, texture, or statistical summaries of visual features, which might give important cues for scene recognition. Nor do they preclude the possibility that PPA and RSC might encode a broader set of spatial relationships that would fall under the more general rubric of "contextual associations" rather than just spatial layout alone [18].

Finally, an especially intriguing aspect of the current findings is the observation of scene-selective responses in blind subjects, including three participants blind from birth. These subjects have never perceived a scene through sight, so they must have become accustomed to learning about scene geometry through other routes. Do blind navigators use auditory cues to perceive the structure of a room? Or do they use idiothetic cues to keep track of locations within the room, building up a representation of spatial layout over time [19,20]? Answering these questions is important not only for understanding navigation in the blind, but also

for understanding the spatial representations common to blind and sighted navigators.

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Olfactory Neuroscience: Beyond the Bulb

High-resolution tracing of projections from the olfactory bulb to its cortical targets revealed coarse topography and stereotypy in some areas but highly distributed, combinatorial connectivity in others. These results provide a basis for understanding innate and associative olfactory processing and perception.

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Although the cerebral cortex is overwhelmingly complex, many sensory cortices are spatially organized by simple topographic principles. The mammalian visual cortex, for example, contains a map of visual space that is established through a series of precise topographic connections from the eye. Similarly, orderly projections set up maps of stimulus features in other sensory cortices. However, topographic maps are not omnipresent — the visual

cortex of turtles, for example, lacks a precise two-dimensional map of visual space [1]. Four recent studies [2–5] now report that topography is not a prominent feature of projections from the first processing center in the olfactory system, the olfactory bulb, to higher brain areas in the mouse. Projections to two cortical targets, the anterior olfactory nucleus (AON) and the cortical amygdala, are topographically organized at coarse, but not at fine, spatial scales. No topography whatsoever was found in projections to piriform cortex, the

largest target area. These results provide a hard anatomical foundation for understanding the organization of higher olfactory brain areas — and ample food for thought.

From the Olfactory Bulb to Higher Brain Areas

Input to the olfactory bulb from the nose terminates in a stereotyped array of glomeruli. Within each of the approximately 2000 glomeruli of the rodent olfactory bulb, thousands of sensory neurons expressing the same odorant receptor converge onto approximately 20–50 principal neurons, the mitral/tufted (MT) cells. Odors are represented by the activation of distributed combinations of glomeruli. Glomerular activation patterns can be biased towards subregions of the olfactory bulb by particular molecular features, but nearby glomeruli frequently respond to chemically different sets of odorants