Scene Areas in Humans and Macaques

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In this issue of *Neuron*, Kornblith et al. (2013) identify two regions in macaque occipitotemporal cortex that encode both spatial and nonspatial aspects of visual scenes and might be the homolog of the human parahippocampal place area.

A central finding of human cognitive neuroscience is that specific regions of visual cortex respond preferentially to certain ecologically important stimulus categories. For example, the fusiform face area (FFA) responds more strongly to faces than to nonface objects during fMRI, and the parahippocampal place area (PPA) responds more strongly to scenes (landscapes, cityscapes, rooms) than to nonscenes. Recent studies have identified a macaque homolog of the FFA, which has allowed the region to be explored using neurophysiological techniques. In contrast, only one previous study has identified a PPA homolog in macaques (Nasr et al., 2011), and no neurophysiological recordings have been made from this region.

This lacuna has now been filled by Kornblith et al. (2013), with potentially important consequences for our understanding of the neural basis of scene recognition and spatial cognition. Using a combination of neuroimaging (fMRI) and microstimulation, Kornblith et al. (2013) identify two scene regions in the macaque brain, which they label the lateral place patch (LPP) and the medial place patch (MPP). The LPP is located in the occipitotemporal sulcus just anterior to V4, while MPP is located in the medial parahippocampal gyrus. These locations are close to what would be expected given the location of the human PPA.

LPP was identified using a standard fMRI localizer technique, directly analogous to the technique typically used to define the PPA in humans. Monkeys were scanned while fixating and passively viewing scenes, objects, and textures. The scenes were all indoor locations, some of which were familiar to the monkeys (e.g., views of the laboratory and

their home cages) and some of which were unfamiliar. fMRI response in the LPP was greater during viewing of scenes than during viewing of objects and texture patterns. MPP, on the other hand, did not show a consistent preferential response to scenes in the fMRI signal but was identified as one of several regions that activated during microstimulation of the LPP. Given the potential homology to the human PPA, it too was targeted for further investigation.

Recordings made from neurons in the LPP and MPP indicated that these regions do indeed process information about scenes: firing rates were higher in both regions when monkeys viewed scenes than when they viewed other stimuli. Response to scenes was over twice the response to nonscenes in 46% of visually responsive LPP neurons and 27% of visually responsive MPP neurons. Furthermore, analysis of the population code indicated that both LPP and MPP discriminated between individual scenes significantly better than they discriminated between individual objects. Thus, not only do LPP and MPP respond more strongly to scenes than nonscene objects, they also represent scenes with greater accuracy. This suggests that these regions are truly specialized for scene processing.

There are many similarities worth noting between these macaque scene areas and the human PPA. First, the PPA responds strongly to images of both familiar and unfamiliar locations, with a slight but significant advantage for the familiar locations. Although not emphasized by Kornblith et al. (2013), their figures tell a similar story: LPP responds equally strongly (in both fMRI and single neuron response) to familiar and unfamiliar locations, implicating it in perceptual analyses

that do not rely on long-term memory. MPP, on the other hand, shows an advantage for the familiar locations, suggesting that it may have a more mnemonic role. Second, the PPA responds strongly to both empty rooms and rooms filled with furniture and objects; moreover, these responses are reduced by scrambling the spatial arrangement of the extended surface boundaries in the rooms (Epstein and Kanwisher, 1998). fMRI response in the LPP replicates these results. Third, previous work using fMRI adaptation has found that the PPA is relatively insensitive to the exact retinal position of a stimulus, showing reduced response when a scene is repeated even when the repetition is in the opposite visual field of the first presentation (MacEvoy and Epstein, 2007). Consistent with this finding, neurons in LPP responded to visual stimulation in both visual fields. Finally, a multivoxel pattern analysis (MVPA) study found that fMRI activation patterns in PPA elicited by photographs of scenes were similar to those elicited by line drawings of the same scenes (Walther et al., 2011). This point is even more impressively made here by showing that a classifier trained on the neuronal responses in LPP to photographs could distinguish between the corresponding line drawings and vice versa.

So, are the LPP/MPP and PPA the same thing? One clear difference is that the PPA is a single coterminous region, whereas the LPP and MPP are physically separated. However, recent work suggests the possibility of subdivisions within the PPA. A retinotopic mapping study identified not one but two such maps in the PPA (Arcaro et al., 2009). In addition, a recent functional connectivity study found that fMRI activity in posterior PPA was more strongly coupled to activity in
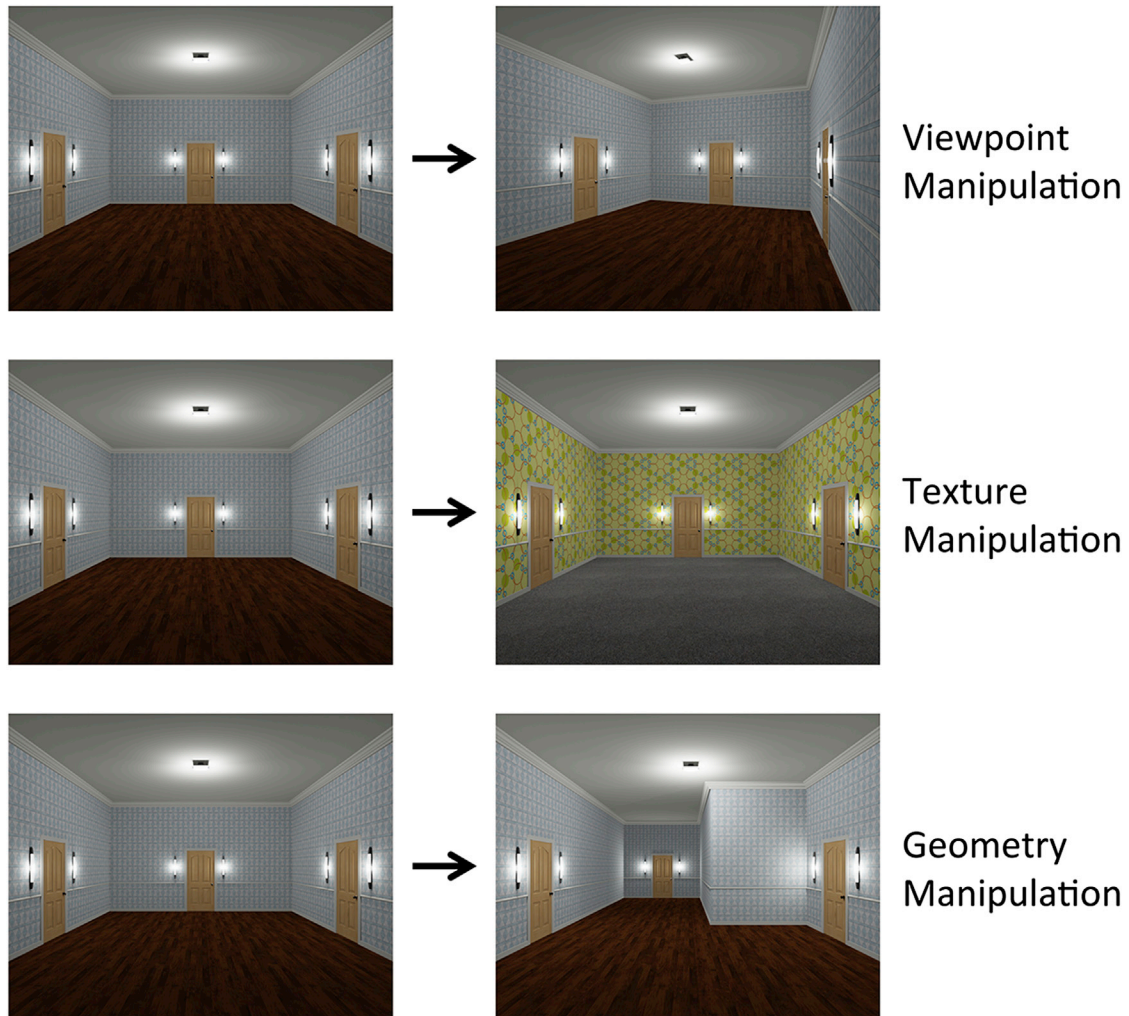
Figure 1. Three Possible Manipulations of a Scene
Kornblith et al. (2013) examined viewpoint and texture manipulations. The effect of changing geometry has yet to be explored.

occipital lobe visual regions, while activity in anterior PPA was more strongly coupled to activity in parietal lobe regions implicated in spatial processing (Baldassano et al., 2013). Although these divisions need to be further explored, it is possible that human PPA is a compound of two functionally differentiable regions that are physically split into LPP and MPP in the macaque.

In addition to establishing this possible homology, Kornblith et al. (2013) also explore questions about the kind of information coded by macaque scene regions. Although some progress has been made in this direction in humans using fMRI adaptation and MVPA, the current study goes further, with some intriguing results. For example, the stimuli that most

strongly activate the scene-selective neurons in LPP and MPP appear to have a common visual feature: long, straight contours. Although the response in LPP (but not MPP) to the nonscene stimuli (objects and textures) that contained long, straight contours was still lower than the response to scenes, this finding is suggestive about the types of low-level features that might be used for scene perception. Another even more important observation is that LPP and MPP neurons respond to both spatial and nonspatial features of scenes. This was established by examining neuronal response to a synthetic room presented stereoscopically, shown with different wall textures ("wallpaper") and objects, and from different viewing angles and distances.

Neuronal firing rates in LPP and MPP were modulated by all of these factors, with the strongest modulations caused by differences in texture.

This last result deserves some comment. Early work on the PPA suggested that it was especially concerned with processing the spatial layout of scenes. Results from some recent studies have supported this idea (Kravitz et al., 2011; Park et al., 2011). However, other studies have found evidence that the PPA codes nonspatial aspects of scenes such as texture and objects (Cant and Xu, 2012; Harel et al., 2013). Kornblith et al. (2013)'s finding that viewpoint, depth, texture, and object can all be decoded based on multiunit responses in LPP (with somewhat weaker

performance in MPP) is broadly consistent with these human fMRI results, indicating representation of both spatial and nonspatial features in the PPA. Nevertheless, the finding that LPP and MPP response is dominated by texture, rather than by spatial features (i.e., viewpoint and depth), is at first glance surprising. However, there are two things worth keeping in mind when interpreting this result. First, as Kornblith et al. (2013) note, texture, unlike viewpoint and depth, may be an important cue for conveying a scene's identity. As such, it is possible that the monkeys encoded scenes with different textures as different "places" but encoded scenes from different views and distances as different visual instantiations of the same place. Second, as Kornblith et al. (2013) also note, manipulations of viewpoint and depth are not manipulations of the spatial layout of the scene per se (see Figure 1). Indeed, all of the room stimuli used in this experiment had the same intrinsic geometry (i.e., were the same "shape"). Thus, the question of how LPP and MPP neurons respond to changes in the spatial structure of the scene itself has yet to be explored.

Beyond these issues, Kornblith et al. (2013)'s results open the possibility of addressing a number of important topics using the same techniques. To give one example, recent studies suggest that the PPA responds preferentially not just to scenes but also to nonscene objects that act—or have the potential to act—as landmarks (Troiani et al., 2012). Objects encountered at navigational decision points (e.g., intersections) elicit greater PPA response than objects encountered at navigationally unimportant locations (Janzen and van Turennout, 2004). Likewise, objects that are physically large, immovable, and define the

space around them elicit more PPA activity than do objects that are smaller, movable, and spatially ambiguous (see Mullally and Maguire, 2011, for one example). Thus, the PPA responds to objects that make good landmarks either because of their locations or because of their intrinsic qualities. Future studies might explore response of LPP and MPP neurons to object-like landmarks. It would be especially interesting to know whether the same neurons that encode scenes also encode these landmarks, or whether scenes and object-like landmarks are coded by different neuronal populations.

The scene areas outside of the LPP and MPP are also ripe targets for future investigation. In humans, the PPA is one of three scene-responsive regions: the other two are the retrosplenial complex (RSC) in the parietaloccipital sulcus and the occipital place area near the transverse occipital sulcus (OPA/TOS). Kornblith et al. (2013) observe scene-preferential response in anterior parietaloccipital sulcus (APOS), which may be the homolog of human RSC, and also in V3A/DP, which may be the homolog of OPA/TOS. Nasr et al. (2011) also found robust scene-selective response in the monkey at approximately the same locations and argued for the same homologies. In contrast to the PPA, which has primarily been implicated in coding of the immediate scene, RSC appears to encode spatial information that allows the local scene to be situated within the broader navigable environment (Epstein, 2008). Thus, neuronal recordings from APOS have the potential to illuminate not only scene recognition but also spatial navigation.

In sum, Kornblith et al. (2013) demonstrate that the scene network in humans has a direct homolog in macaques. This finding is consistent with the ecological

importance of scenes as the visual stimulus that is most relevant for spatial navigation. Like us, monkeys must recognize scenes because they need to know where they are in the world, and like us, they appear to have cortical machinery specialized for this task.

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