9.71 Functional MRI of High-Level Vision
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Differential Activation by Convex and Concave Stimuli in Human Parahippocampal Cortex and Lateral Occipital Cortex

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9.71 Experiment Proposal

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Abstract

Previous research suggests the involvement of several ventral temporal brain areas in the processing of specific categories of stimuli. One such region is the Parahippocampal Place Area (PPA), an area within the posterior parahippocampal cortex that responds selectively to visual stimuli conveying information about the layout of local space. Another region, the lateral occipital complex (LOC), responds preferentially to objects and is believed to play a critical role in the processing of object shape. In particular, the LOC seems to be involved in the processing 3-dimensional aspects of objects, rather than their 2-dimensional contours. These results beg the question: if the PPA responds selectively to the 3D layout of scenes and the LOC responds selectively to the 3D layout of objects, what is the difference between scenes and objects such that objects do not recruit preferential activation in the PPA and scenes do not produce preferential activation in the LOC? The current experiment investigates the possibility that the PPA is selectively activated by the concavity of scenes, while the LOC is selectively activated by the convexity of objects. Using stereo to convey the depth information of convex and concave dot arrays, this study tests the hypothesis that the PPA responds more strongly to concave than convex stimuli, and that the LOC responds more strongly to convex than concave stimuli.

Background and Motivation

<u>The PPA</u>

The parahippocampal place area (PPA) is a region within the parahippocampal cortex that has been shown in functional magnetic resonance imaging (fMRI) studies to respond selectively to photographs of scenes such as rooms, landscapes, and city streets compared to photographs of objects, faces, houses, or other kinds of visual stimuli (Epstein & Kanwisher, 1998). The critical factor for this activation appears to be the presence in the stimulus of information about the layout of local space. Evidence in support of this claim includes the finding that the response in the PPA to scenes with spatial layout but no discrete objects was found to be as strong as the response to scenes containing multiple objects. The response to objectless spatial layouts is also more than twice as strong as the response to arrays of multiple objects without three-dimensional spatial context.

The PPA also responds much more strongly to “scenes” made out of Lego blocks (whose geometric structure is similar to a room or street scene, yet is not a real place) than it does to objects made out of Lego materials (Epstein, Harris, Stanley, & Kanwisher, 1999). We can conclude from this that the PPA is responsive to a specific kind of geometric organization in the stimulus--even if the stimulus does not depict a real place in the world. In particular, it responds strongly to depictions of surfaces that in some sense "enclose" the observer and define a space within which one can act. One feature that all such surfaces have in common is concavity. These results reinforce behavioral data from studies on rats (Cheng, 1986; Gallistel, 1990; Margules & Gallistel, 1988) and human infants (Hermer & Spelke, 1994, 1996; Hermer-Vazquez, Spelke,&Katsnelson, 1999).

Several subsequent PPA studies have implicated the PPA in processes involved in navigation, especially the encoding of new perceptual information about the appearance and layout of scenes. An experiment by Epstein & Kanwisher in 2000 found that PPA activity is not affected by the subjects’ familiarity with the place depicted (e.g. a familiar college campus produces as much activation as an unfamiliar college campus). However, within a scan, novel scenes do produce greater activation than repeated scenes. This result cannot be explained solely on the basis of novelty, however, because novel faces did not generate a greater response than repeated faces.

Other evidence in support of the PPA as a topographical information encoding region includes the results of lesions to this area of the brain. Often, damage to the PPA and surrounding regions results in an inability to use salient topographical features such as landscapes and buildings to orient oneself ("landmark agnosia," e.g., Landis et al., 1986; Pallis, 1955) or in a more general inability to learn new topographical information ("anterograde disorientation," e.g., Habib & Sirigu, 1987). Damage to the parahippocampal cortex may also produce deficits for visual materials that conveyed information about the shape of surrounding space. Since this deficit was demonstrated only during a memory encoding test, these data suggest that the PPA may be a learning mechanism specifically dedicated to encoding topographical materials into memory (Epstein et al., 2001).

The LOC

The LOC is defined functionally as the region of occipital and temporal cortex that responds more strongly to objects than to scrambled objects or textures (Malach et al. 1995). The LOC has been shown to respond quite strongly and similarly to all kinds of objects tested so far, from cars to novel three-dimensional (3D) objects that subjects have never encountered before (Grill-Spector et al., 2001).

This study by Grill-Spector et al. found no significant difference in magnitude of the response in this region between common objects and uncommon objects that had clear three-dimensional shape interpretations. A similar result was found by Kanwisher et al. In 1996. Using line drawings, stronger responses were obtained to 3D objects depicted in line drawings, whether familiar or novel, compared to scrambled line drawings, in which no clear shape interpretation was possible. Several more recent studies (Grill-Spector et al., 1998; Grill-Spector, Kushnir, Edelman, Itzchak & Malach, 1998; Murtha, Chertkow, Beauregard & Evans, 1999; Kourtzi & Kanwisher, 2000a; Doniger, Foxe, Murray, Higgins, Snodgrass & Schroeder, 2000) suggest that the entire region, from the lateral occipital cortex to the posterior temporal region, stimuli whose forms depict a distinct shape elicit more activation than control stimuli that do not depict clear shapes.

Results of an adaptation experiment by Kourtzi & Kanwisher in 2001 suggest that neural populations in the LOC represent object shape rather than the low-level features defining the shape. Although this result was important, the question of whether the LOC processes information about visual contours or information about the shape itself was yet to be answered. These two hypotheses at one time seemed difficult to distinguish because contours are always present in images of objects. However, Kourtzi and Kanwisher (2000b) devised an experiment to investigate whether adaptation in the LOC would be observed for objects that have the same shape but different contours and objects that have different shape but share the same contours. They found that when the perceived shape was the same for the two stimuli but the contours were different, adaptation was as strong as for a pair of identical stimuli. In contrast, when the perceived shapes were different but the contours were identical, no adaptation was found. These data suggest that the LOC processes shape information, not just information about the contours that define that shape.

The LOC has been characterized as the main neural locus of visual shape processing. But what about objects that convey depth? After all, many objects in the real world have three dimensions. A recent study by Kourtzi et al. asked whether neural populations in the LOC encode the perceived 3-D shape of objects or simply their 2-D contours. In particular, the experiment tested first for adaptation in the LOC between 2-D silhouettes and 3-D shaded images of objects and then for adaptation in the LOC across changes in the 3-D shape structure of objects (convex versus concave stimuli) compared to changes in their 2-D contours but not the 3-D shape. No adaptation was observed in the LOC for objects that had the same 2-D contours but different perceived 3-D shape structure (convex versus concave objects). In contrast, adaptation was observed in the LOC for images of objects that had the same perceived 3-D shape even when they have different 2-D contours (Kourtzi et al., 2003). They claimed that the sameness of the perceived 3-D shape of objects is necessary and sufficient for adaptation in the LOC.

A recent study by Moore and Engel in 2001 also found increased neural activity in the LOC in response to images of objects perceived as 3D volumes rather than as 2D shapes. These findings are consistent with other recent human fMRI studies that have implicated the LOC in the analysis not only of 2-D but also of 3-D images of objects (Kourtzi and Kanwisher, 2000; Gilaie-Dotan et al., 2001; Moore and Engel, 2001; Kourtzi et al., 2002) independent of the cues that define the object shape (Sary et al., 1993; Mendola et al., 1999; Kourtzi and Kanwisher, 2000). These data suggest that the LOC is involved in processing the three-dimensional features of objects, rather than their two-dimensional contours.

<u>Motivation for Study</u>

Much of the precise mechanisms behind the sensory processing by the PPA and the LOC still remain a mystery. However, data from numerous studies has converged to suggest that the PPA is involved in the processing of the layout of scenes but not objects, while the LOC preferentially processes three-dimensional information about objects, but not scenes. If this is the case, there must be a critical difference between the features of scenes and the features of objects responsible for the fact that of each region discriminates between the two classes of stimuli.

What is this critical difference between scenes and objects? The current study investigates the hypothesis that the concavity of scenes and convexity of objects is responsible for the selective activation of the PPA and the LOC.

Experimental Design

<u>Logic</u>

This experiment will compare the BOLD response produced by concave stimuli to the BOLD response produced by convex stimuli in each region of interest (ROI) to determine whether or not either ROI responds preferentially to one type of stimulus. In each experimental condition, concavity or convexity will be conveyed in depth using stereo. While it is possible to use 2D images to convey depth, stereo more closely resembles the 3D world that humans experience.

<u>Subjects</u>

Ten right-handed students from the Massachusetts Institute of Technology (MIT) will be recruited to participate in this experiment.

<u>Design</u>

This experiment will include two classes of experimental stimuli: convex dot arrays and concave dot arrays. The stimuli in each class will vary in degree of depth and in spacing of the dots.

Scanning sessions will consist of two localizer scans followed by one experimental scan.

The experimental scan will use an event-related design. The scan will consist of one epoch of experimental trials and two 8 s fixation epochs, one at the beginning and one at the end of the scan. Each scan will consist of 90 experimental trials of convex versus concave dot arrays and 18 fixation trials. Each image will be presented for 300 ms with a blank interval 400 ms between images. The stimuli will be counterbalanced for order to ensure that both images appear an equal number of times and each precedes the other equally often.

Data Analysis

For each subject, the BOLD response to concave stimuli will be compared to the BOLD response to convex stimuli in each region of interest.

Twelve coronal-like slices will be used, (as in Kourtzi et al., 2003).

ANOVAs across subjects will be run on the average per cent signal change from fixation produced by each type of stimulus. Data will be analyzed within independently defined ROIs.

Independent localizer scans will be used to define each region of interest (ROI). Localization of the PPA will involve a scenes-versus-objects discrimination task. Localization of the LOC will involve an objects-versus-scrambled line drawings discrimination task. Although the PPA and the LOC are the primary regions of interest, a whole-brain analysis will also be conducted for each subject.

For the PPA localizer scans, photographs of urban scenes, tabletop scenes, and landscapes will be compared to photographs of intact objects. The localizer scan will feature a blocked design with sixteen 16 s stimulus epochs and interleaved fixation periods as described in previous studies (e.g. Kourtzi and Kanwisher, 2000, 2001). Twenty different images of the same type will be presented in each epoch. Each image will be presented for 250 ms with a blank interval of 550 ms between images. Each of the four stimulus types (intact objects and three types of scenes) will be presented in different epochs within each scan, in a design that balances for the order of conditions. The subjects will perform a one-back matching task; i.e. they will be instructed to press a button whenever they see two identical pictures in a row. Two or more consecutive repetitions will in each epoch. This one-back matching task is intended to engage observers' attention on all the stimulus conditions used.

For the LOC localizer scan, grayscale images and line drawings of novel and familiar objects, as well as scrambled versions of each set will be used (as in Kourtzi, 2003). The scrambled images will be created by dividing the intact images in a 20 ◊ 20 square grid and by scrambling the positions of each of the resulting squares. The grid lines will be present in both the intact and the scrambled images.

For the LOC localizer scans a blocked design with sixteen 16-s stimulus epochs and interleaved fixation periods, similar to the PPA localizer scan, will be sued. Twenty different images of the same type will be presented in each epoch. Each image will be presented for 250 ms with a blank interval of 550 ms between images. Each of the four stimulus types (grayscale images and line drawings of objects, as well as scrambled versions of each set) will be presented in different epochs within each scan, in a design that balances for the order of conditions. As in the PPA localizer scan, the subjects will perform a one-back task.

In the PPA localizer scan, the PPA will be defined as the region activated by the scene stimuli. In the LOC localizer scan, the LOC will be defined as the region activated by the non-scrambled objects.

Predictions and Implications
There are several possible outcomes of this experiment.

Possible Result #1

1. No significant difference in BOLD response between convex stimuli and concave stimuli is observed in the PPA. No significant difference in BOLD response between convex stimuli and concave stimuli is observed in the LOC.

PPA LOC

This result does not support the hypothesis. One possible explanation is that neither the PPA nor the LOC is preferentially activated by one class of stimuli over the other. Another possible explanation of this result is that a Type II statistical error occurred (the PPA and the LOC do in fact each respond more strongly to one class of stimuli, but our experiment failed to detect this difference). If this is believed to be the case, one might investigate the possibility that the two classes of stimuli were not distinct enough to recruit selective activation from either area. To test this possibility, the stimuli could be altered by exaggerating the concavity and convexity of the stimuli and the experiment could be rerun.

Possible Result #2

No significant difference in BOLD response between convex stimuli and concave stimuli is observed in the PPA. Convex stimuli produce a greater bold response than concave stimuli in the LOC.

PPA LOC

This result would suggest that the PPA is not selectively activated by concave stimuli. Unlike the previous possible result, this outcome can not be easily explained in terms of inadequately distinct stimuli, since the LOC result demonstrates that the stimuli were distinct enough to recruit selective activation in that region. This outcome also suggests that the LOC is preferentially activated by convex stimuli. This may provide insight into the features of objects responsible for the historical selective activation of the LOC by objects.

Possible Result #3

No significant difference in BOLD response between convex stimuli and concave stimuli is observed in the PPA. Concave stimuli produce a greater bold response than convex stimuli in the LOC.

PPA LOC

This outcome would be difficult to explain. It suggests that the PPA is not selectively activated by either class of stimuli and that the LOC responds more strongly to concave stimuli than convex stimuli. This is counterintuitive, given that objects are convex and the LOC historically has shown a higher BOLD response to objects than to any other class of stimuli. The selective activation in the LOC by concave stimuli can not be attributed to an attentional confound. If it were the result of an attentional confound, one would expect the PPA to be more activated by concave stimuli as well.

Using a region of interest approach and an event-related design already gives this experiment more statistical power and fewer possible confounds than a non-ROI approach and a blocked design. However, if this result were obtained, it is quite possible that some error occurred, either in the experimental trials or in the data analysis. It would be advisable to rerun the experiment. At the very least, one could test additional subjects in order to increase statistical power and possibly overcome some of the 'noise' in the data.

Possible Result #4

No significant difference in BOLD response between convex stimuli and concave stimuli is observed in the LOC. Convex stimuli produce a greater bold response than concave stimuli in the PPA.

PPA LOC

As in the case of the previous result, this outcome would be difficult to explain. It is feasible that the LOC would not respond more strongly to one class of stimuli than another. This simply suggests that some other feature of objects is responsible for recruiting selective activation in the LOC. However, it would be difficult to explain a result in which the PPA is more activated by convex stimuli than concave stimuli, given that the PPA responds preferentially to scenes and scenes are concave. As in the last possible result, one should consider the possibility that an error occurred in the experimental run or in the analysis of the data.

<u>Possible Result #5</u>

> No significant difference in BOLD response between convex stimuli and concave stimuli is observed in the LOC. Concave stimuli produce a greater bold response than convex stimuli in the PPA.

PPA LOC

This outcome supports part of the hypothesis: that concave stimuli produce a greater PPA response than do convex stimuli. This may give insight into the features of a scene that are responsible for selectively activating the PPA. An attentional confound is unlikely, as such a confound would likely produce a greater activation by concave stimuli in both regions, not just the PPA. Also, an attentional confound is also unlikely given that the stimuli share all features in common except the feature that we are testing (concavity versus convexity). This result does not support the claim that the LOC is more strongly activated by convex stimuli than concave stimuli. Given the PPA result, it is unlikely that this result was due to a confound.

<u>Possible Result #6</u>

> Convex stimuli produce a greater bold response than concave stimuli in the PPA. Convex stimuli produce a greater bold response than concave stimuli in the LOC.

This result is similar to the last one in that it supports part of the hypothesis and fails to support the rest. It suggests that convex stimuli produce a greater LOC response than do concave stimuli. This may give insight into the features of an object that are responsible for selectively activating the LOC. This result does not support the claim that the PPA is more strongly activated by concave stimuli than convex stimuli. In fact, it produces a response that is quite different from that which is expected and intuitive. Under some circumstances, it is reasonable to hypothesize that a greater response in both regions to one class of stimuli is due to the fact that those stimuli were more salient or complex (a confound). However, given the similarity of the stimuli in this experiment, such an explanation is not likely to be true.

<u>Possible Result #7</u>

> Convex stimuli produce a greater bold response than concave stimuli in the PPA. Concave stimuli produce a greater bold response than convex stimuli in the LOC.

PPA LOC

This unexpected outcome is doubly difficult to interpret. It contradicts both parts of the hypothesis and suggests that either the hypothesis is completely wrong, or the experiment and/or analysis of the data was flawed.

<u>Possible Result #8</u>

> Concave stimuli produce a greater bold response than convex stimuli in the PPA. Concave stimuli produce a greater bold response than convex stimuli in the LOC.

PPA LOC

This result would support the first portion of the hypothesis: that PPA response is higher to concave stimuli than to convex stimuli. However, it challenges the experimenter to explain why the same result was found in the LOC. As previously mentioned, the features of these stimuli are so similar that it is unlikely that the concave stimuli could be considered more salient or more complex than the convex stimuli. Given the PPA results, it would be reasonable to hypothesize that some feature other than convexity is responsible for selective LOC activation by objects.

Possible Result #9

> Concave stimuli produce a greater bold response than convex stimuli in the PPA. Convex stimuli produce a greater bold response than concave stimuli in the LOC.

PPA LOC

This is the optimal result, and the only one that supports the hypothesis in its entirety. The fact that concave stimuli produced more activation than convex stimuli in the PPA and less activation than convex stimuli in the LOC (and vice versa for convex stimuli) suggests that there was no attentional confound.

Conclusion

The current study investigates the mechanisms responsible for the selective activation of the PPA and the LOC. As such, it is at the intersection of two important lines of research, each of which has broad and far-reaching implications. The PPA is believed to be critically involved in processes necessary for human navigation, including the encoding of spatial information into memory. Insight into the functions of the LOC is equally valuable. Understanding the mechanisms by which the LOC processes object shape information is critical to the development of a full theory of object recognition. This alone has important implications, especially to the future of artificial intelligence. Previous research has addressed the question of what kinds of stimuli activate each of these important regions. The current study investigates 'why.'

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