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Faces and places: of central (and peripheral) interest

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Early visual cortical areas are organized in retinotopic coordinates. Levy and colleagues now report that category-selective regions show a similar organization, with face-selective areas responding more to central stimuli and place-selective areas responding to peripheral stimuli.

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Primates are highly visual animals, devoting as much as half their cerebral cortex to solving visual problems such as object recognition and visually guided action. In the macaque visual cortex, researchers have discovered and characterized roughly 30 different areas, each with a distinct functional and/or anatomical profile[1]. Yet until the mid-1990s, little was known about the functional organization of human visual cortex. This landscape has changed dramatically with the invention of functional magnetic resonance imaging (fMRI), a powerful tool for the noninvasive mapping of the normal human brain.

Early fMRI investigations in humans located the first few areas of the visual cortical pathway, corresponding to those previously charted in the macaque[2,3]. The inferred homologies between human and macaque visual areas were based largely on a long-known property of visual cortex called ‘retinotopy,’ in which nearby regions in the visual image are represented by nearby regions in the brain, producing a ‘map’ of the visual field in each cortical area. Retinotopic cortex seems to favor polar coordinates, with eccentricity (distance from the center of gaze) mapped onto one cortical axis, and polar angle mapped onto a roughly perpendicular axis.

More recent investigations have identified several higher-level regions of cortex not characterized previously in the macaque. These areas are defined by a distinctive functional profile, such as a selective response to images of faces[4,5] or places[6,7]. A new study by Levy and colleagues[8] in this issue shows that two of these dimensions along which visual cortex is organized—category selectivity and eccentricity bias (a preferential response to either central or peripheral stimuli)—not only co-exist in the same cortical region, but have a systematic relationship to each other. Their findings may have implications for our understanding not only of the functions of these cortical regions, but also of their origins.

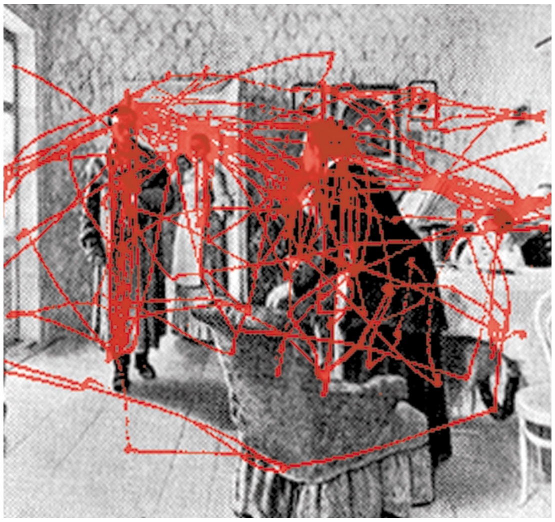

Fig. 1. Eye movement scanpath (in red) of a person viewing a painting by Rein; note the tendency to fixate on the faces. Adapted from Yarbus (*Eye Movements and Vision*, Plenum, New York, 1967).

In the new study, Levy and colleagues first identified regions of cortex that responded more strongly when the subjects viewed faces than when they viewed houses, and other regions with the opposite property. Second, to identify cortical regions that respond differentially to stimuli presented at the center of gaze versus the periphery, the authors scanned subjects while they viewed a set of tiny centrally located images of common objects, or a ring of the same object stimuli around the center of gaze presented at either a medium or large eccentricity. Object size was increased with eccentricity, enabling subjects to identify the objects despite the lower acuity of the peripheral field.

As in earlier reports[4,5,9], Levy and colleagues[8] found stronger responses to faces than houses in two regions: area LO (lateral occipital cortex) and the fusiform face area (FFA)[5]. They also found a third previously described region[6,7] that responded more to houses than to faces. This region included the parahippocampal place area (PPA), which responds to a wide variety of images depicting places, including a maximal response to indoor and outdoor scenes, and a weaker but still strong response to pictures of houses[6].

The new finding[8] is that the face-selective regions responded more strongly to central than to peripheral objects, whereas the house-selective regions had the opposite preference. Thus, category selectivity and eccentricity bias co-exist in the same region of cortex, with face selectivity associated with a center-field bias and place selectivity with a peripheral-field bias.

Levy and colleagues also showed that face and place selectivity is not simply an artifact of the use of small face stimuli and larger house stimuli: face-selective regions responded more strongly to large face images (that extend into the visual periphery) than to small house images (that do not), and house-selective regions prefer the reverse. This result further demonstrates that when category selectivity and visual field biases are pitted against each other, category selectivity wins.

One puzzle raised by these findings is why the center-field bias for face-selective cortex is apparently not mirrored by a similar center-field bias in face discrimination performance (beyond that observed for simpler visual stimuli)[10].

More generally, why should category selectivity and eccentricity bias be associ-

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ated in visual cortex in the first place? A natural interpretation of these results draws on a currently popular view that the cortex is highly plastic, and that its functional organization is shaped substantially by experience. If the stimulus selectivities and receptive field locations of many visual neurons are learned rather than specified innately, the association reported by Levy and colleagues[8] might follow directly from the statistics of everyday perceptual experience. The authors suggest that we generally fix our eyes on faces directly (**Fig. 1**), whereas in place perception more of the relevant visual information comes from the periphery. Thus this association might be a direct mirror of experience.

A strong version of this experiential hypothesis would predict that if a person were raised seeing (or attending to) faces only in the periphery and places only at the center of gaze, his or her cortex might show the reverse of the pattern reported by Levy and colleagues[8]. Such a result might enable us to further determine which dimension—category selectivity or eccentricity bias—is more fundamental in determining the organization of high-level visual cortex. Would the hypothesized face and periphery-selective region of cortex be located in the usual site of the face area, or in the usual site of the (normally place-selective) periphery-biased cortex, or in some new location? Although this particular experiment could never be done, it may be possible to test for sensitivity to experience in adulthood by finding people with unusual visual experience. For example, what happens to the locus of face-selective cortex when central vision is impaired by macular degeneration?

If the experiential hypothesis sounds far-fetched, consider the following strands of evidence. First, after monkeys receive extensive training recognizing originally novel stimuli, some neurons in their visual cortex respond selectively to these learned stimuli[10,11]. Crucially, recent findings suggest that such neurons may respond selectively not only to the trained stimuli, but also to the retinal positions where the stimuli were presented during training, and perhaps even to the exact conjunction of a particular stimulus and the location where it was presented (J.J. DiCarlo and J.H.R. Maunsell, *Soc. Neurosci. Abstr.*, 26, 498.2, 2000). Second, an elegant psychophysical study[12] found that after people are trained to discriminate certain novel visual stimuli presented in fixed retinal locations, performance drops when the same stimuli are subsequently presented at new untrained locations. Why would the visual system use such inflexible and literal representations, rather than extracting representations that are invariant to positional changes? Computational models of object recognition suggest that, counterintuitively, the most effective way to achieve positional invariance may be to store representations of fragments of familiar objects at each spatial position[13].

Despite this evidence in favor of the experiential hypothesis, the ability of visual cortex to learn from experience is highly constrained. For one thing, neuropsychological patients who selectively lose face recognition abilities as a result of focal brain damage are rarely able to relearn this ability, suggesting that the remaining visual cortex (which is adequate for visual recognition of nonface objects) cannot be trained on face recognition in adulthood. Indeed, a study reported at the Cognitive Neuroscience Society meeting last year (R. Le Grand, C. Mondloch, D. Maurer & H.P. Brent, San Francisco, April, 2000) suggested that the development of normal face recognition depends on visual experience extremely early in life. These researchers studied people born with dense bilateral cataracts that precluded pattern vision until surgical correction between two and six months of age. Surprisingly, these people never develop normal configural processing of faces. That is, they are impaired at discriminating between faces that differ in the relative positions of facial features, but unimpaired at discriminating faces on the basis of individual face parts or on either task when the face stimuli are presented upside-down. Thus, pattern vision in the first few months of life is necessary for the development of configural face processing as an adult; years of subsequent visual experience with faces is not sufficient to bring about normal face processing.

Although I have so far emphasized the critical role of experience in the development of visual cortex, Levy and colleagues' findings[8] are also consistent with hypotheses that place a much greater emphasis on innate constraints. After all, it has been true throughout primate evolution that face perception is done best with high-resolution foveal information, and place perception in natural environments usually requires a wide field of view. Thus natural selection may have led to a genetic blueprint not only for specific cortical machinery for face and place perception, but also for the newly reported visual field biases in these areas.

Levy and colleagues' results are also consistent with intermediate hypotheses that incorporate critical instructive roles for both genes and experience. For example, eccentricity biases might be genetically specified, with selectivity for faces or places then developing near the regions that provide their relevant inputs. (Along these lines, it has been argued[14] that cortical regions responsive to tools develop near the visual motion area MT.) Alternatively, cortical neurons originally responsive to one stimulus property may subsequently develop an additional selectivity for a second stimulus property that is experientially associated with the first[15].

In sum, Levy and colleagues' new data are suggestive, but they remain consistent with a wide range of accounts of the origins of the functional organization of high-level visual cortex. The good news is that clever experimentation should enable us to narrow the range of viable hypotheses. Indeed, at the recent meeting of the Cognitive Neuroscience Society (New York, 2001), Malach reported that letter strings (like faces) also activate center-biased regions of visual cortex. Because people have only been reading for a few thousand years—probably not enough time for evolutionary change—this pattern is unlikely to be genetically specified, and is more likely to result from each individual's experience fixating words. Whether center-biased face selectivity and periphery-biased place selectivity arise in the same experiential fashion remains to be determined.

1. Felleman, D. J. & Van Essen, D. C. *Cereb. Cortex* 1, 1–47 (1991).
2. Tootell, R. B., Dale, A. M., Sereno, M. I. & Malach, R. *Trends Neurosci.* 19, 481–489 (1996).
3. Engel, S. A. *et al. Nature* 369, 525 (1994).
4. McCarthy, G., Puce, A., Gore J. & Allison, T. *J. Cogn. Neurosci.* 9, 605–610 (1996).
5. Kanwisher, N., McDermott, J. & Chun, M. *J. Neurosci.* 17, 4302–4311 (1997).
6. Epstein, R. & Kanwisher, N. *Nature* 392, 598–601(1998).
7. Aguirre, G. K., Zarahn, E. & D'Esposito, M. *Neuron* 21, 373–383 (1998).
8. Levy, I., Hasson, U., Avidan, G., Hendler, T. & Malach, R. *Nat. Neurosci.* 4, 533–539 (2001).
9. Gauthier, I., Skularski, P., Gore, J. C. & Anderson, A. W. *Nat. Neurosci.* 3, 191–197 (2000).
10. Rovamo, J., Makela, P., Nasanen, R. & Whitaker, D. *Invest. Ophthalmol. Vis. Sci.* 38, 1029–1039 (1997).
11. Logothetis, N. K. & Pauls, J. *Cereb. Cortex* 3, 270–288 (1995).
12. Nazir, T. A. & O'Regan, J. K. *Spat. Vis.* 5, 81–100 (1990).
13. Ullman, S. & Soloviev, S. *Neural Networks* 12, 1021–1036 (1999).
14. Martin, A., Wiggs, C. L., Ungerleider, L. G. & Haxby, J. V. *Nature* 379, 649–652 (1996).
15. Sakai, K. & Miyashita, Y. *Nature* 354, 152–155 (1991).