

Commentary

Visual scenes and cortical neurons: What you see is what you get

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To even the casual observer, it cannot be doubted that animals are highly adapted to their environments. The long necks of giraffes help them to gather food from high in the trees and a cheetah's speed helps it to capture prey. But over the last several years, studies of visual information processing have taken this sort of insight to levels that are not as inherently obvious. When we examine a visual scene, there are certain features that attract our attention, such as the face of a friend or an oncoming car. But to identify these objects, neural circuits in the visual system must extract relevant cues from the available visual information. For example, the outline of the oncoming car can be defined by the organization of oriented edges within the visual field. Information theory now is being used to define what cues are available within visual scenes. It is believed that neural circuits in the visual system should be adapted to take advantage of these cues (for review see refs. 1 and 2).

This approach has met with some success. Notably, there is a close correspondence between the components found in natural scenes and the visual stimuli that optimally excite a certain class of visual cortical neurons called simple cells (3–6). Analyses of these components reveal “edge filters” bearing a striking similarity to the receptive fields of neurons in primary visual cortex, as first described by Hubel and Wiesel in the early 1960s (7, 8). In this issue of the *Proceedings*, Coppola *et al.* (9) describe studies of the oriented contours found in visual scenes. They report that there is an overrepresentation of vertical and horizontal contours, not only in visual scenes containing man-made objects, but also in “natural” scenes (see also ref. 10). Relating their findings to studies of orientation selective neurons in visual cortex and how orientation selectivity emerges during development, they point out how this approach can provide insight not only into how the visual system is organized, but also into the developmental and evolutionary forces that might give rise to that organization. The observations help to explain the overrepresentation in visual cortex of neurons that respond selectively to vertical or horizontal contours (11–14), and they suggest mechanisms for the emergence of this bias.

One of the more compelling features of the organization of the visual system is the “functional architecture” of visual cortex. Hubel and Wiesel (8) established that neurons in the primary visual cortex respond best to light or dark bars and are particular about both the orientation of this stimulus and the eye through which it is viewed. Furthermore, these ocular dominance and orientation preferences are mapped systematically across the cortical surface (functional architecture). Columns running perpendicular to the cortical surface contain neurons with similar orientation and ocular preferences (orientation and ocular dominance columns).

The discovery of this functional organization provided an experimental framework for addressing the age-old nature versus nurture question. What features of the functional architecture appear innately and to what extent can they be altered by visual experience? One might expect that a question

first asked more than 20 years ago would be pretty well settled by now, but as is often the case in the nature versus nurture debate, finding the answer is not straightforward. Wiesel and Hubel established rather quickly and elegantly that the ocular dominance of cortical neurons can be affected dramatically by visual experience (for review see ref. 15). But more recent observations show that macaque monkeys already have adult-like ocular dominance columns at the time of birth (16). So even though visual experience can influence the development of these columns, their basic organization appears to emerge innately, before visual experience.

Understanding the role of visual experience in orientation column development has been more difficult. This difficulty arises largely from the greater difficulty in manipulating the orientations of contours visualized by a developing animal. Studies addressing this question have used “stripe rearing.” Animals were raised under conditions where only a small subset of all possible orientations were visualized. Microelectrode recordings of the receptive fields of cortical neurons in these animals showed that the majority of recorded neurons responded preferentially to the experienced orientations (17–19). These observations suggested that neurons that normally might have developed selectivity for one orientation had shifted their preference to some other orientation—chalk one up to nurture. But later studies found that, under these rearing conditions, many neurons became unresponsive to visual stimuli (20). This finding suggested that neurons had not shifted their orientation preference, but rather neurons that had an initial preference for the deprived orientations had become unresponsive.

Also on the side of nature, even the earliest studies of Wiesel and Hubel had suggested the presence of orientation columns in cats whose eyes had not yet opened (21). A number of more recent studies using modern, optical imaging techniques to map out the organization of orientation columns over large areas of cortex also provide strong evidence for an innate component to the organization of orientation columns (22–26). Most notably, the visual cortex of developing ferrets has more territory containing neurons selective for vertical or horizontal orientations than oblique angles and this bias is already present shortly after or sometimes even before the eyes first open (26). The findings of Coppola *et al.* (9) suggest a mechanism by which such an innate preference might come about. An abundance of vertical and horizontal contours in manmade scenes could have an experience-dependent influence on the orientation preference of neurons, but it would seem that such scenes have not been around long enough to provide an evolutionary advantage and thus select for animals with an innately specified preponderance of neurons preferring the cardinal axes. The observation that natural scenes also contain more horizontal and vertical contours, however, raises the possibility that this bias could be the basis for such a selective advantage.

As is usually the case in the nature versus nurture debate, it would appear that the answer will be “some of each.” There

is evidence that the organization of orientation columns, including an overrepresentation of the cardinal axes, is at least in part specified innately. Furthermore, natural scenes have a bias in their distributions of oriented contours that could provide a selective advantage for this innate predisposition. But unlike ocular dominance columns, for which experimental studies show that an experience-dependent component clearly exists, there are no experimental observations of orientation column development that necessarily reveal an influence of experience. Interestingly, Coppola *et al.*'s observations may suggest an experimental resolution to the problem. If an animal was raised in a typical caged environment containing primarily horizontal and vertical contours, but not deprived of other orientations, there should be more cortical territory responsive to these contours, just as in normal animals. But now, if the entire visual scene was rotated optically, there would be preferential experience at the corresponding oblique angles. If the percentage of cortical neurons devoted to processing those angles was increased, the result finally might demonstrate an experience-dependent influence.

1. Atick, J. J. (1992) *Network* **3**, 213–251.
2. Ruderman, D. L. (1994) *Network* **5**, 517–548.
3. Olshausen, B. A. & Field, D. J. (1996) *Nature (London)* **381**, 607–609.
4. Olshausen, B. A. & Field, D. J. (1997) *Vision Res.* **37**, 3311–3325.
5. Bell, A. J. & Sejnowski, T. J. (1997) *Vision Res.* **37**, 3327–3338.
6. van Hateren, J. H. & van der Schaaf, A. (1998) *Proc. R. Soc. London B*, in press.
7. Hubel, D. H. & Wiesel, T. N. (1959) *J. Physiol.* **148**, 574–591.
8. Hubel, D. H. & Wiesel, T. N. (1962) *J. Physiol.* **160**, 106–154.
9. Coppola, D. M., Purves, H. R., McCoy, A. N. & Purves, D. *Proc. Natl. Acad. Sci. USA* **95**, 4002–4006.
10. Switkes, E., Mayer, M. J. & Sloan, J. A. (1978) *Vision Res.* **18**, 1393–1399.
11. Pettigrew, J. D., Nikara, T. & Bishop, P. O. (1968) *Exp. Brain Res.* **6**, 373–390.
12. Mansfield, R. J. W. (1974) *Science* **136**, 1133–1134.
13. Leventhal, A. G. & Hirsch, H. V. B. (1980) *J. Neurophysiol.* **43**, 1111–1132.
14. Orban, G. A. & Kennedy, H. (1981) *Brain Res.* **208**, 203–208.
15. Wiesel, T. N. (1982) *Nature (London)* **299**, 583–591.
16. Horton, J. C. & Hocking, D. R. (1996) *J. Neurosci.* **16**, 1791–1801.
17. Hirsch, H. V. B. & Spinnelli, D. N. (1970) *Science* **168**, 869–871.
18. Blakemore, C. & Cooper, G. F. (1970) *Nature (London)* **228**, 477–478.
19. Pettigrew, J. D. (1974) *J. Physiol.* **237**, 49–74.
20. Stryker, M. P., Sherk, H., Leventhal, A. G. & Hirsch, H. V. B. (1978) *J. Neurophysiol.* **41**, 896–909.
21. Hubel, D. H. & Wiesel, T. N. (1963) *J. Neurophysiol.* **26**, 994–1002.
22. Kim, D.-S. & Bonhoeffer, T. (1994) *Nature (London)* **370**, 370–372.
23. Godecke, I. & Bonhoeffer, T. (1996) *Nature (London)* **379**, 251–254.
24. Weliky, M. & Katz, L. C. (1997) *Nature (London)* **386**, 680–685.
25. Crair, M. C., Gillespie, D. C. & Stryker, M. P. (1998) *Science* **279**, 566–570.
26. Chapman, B., Stryker, M. P. & Bonhoeffer, T. (1996) *J. Neurosci.* **16**, 6443–6453.