

Motion perception is learned, not innate

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Visual cortex neurons are arranged into maps according to their response selectivity. Ocular dominance and orientation selectivity maps can develop without visual experience. Unexpectedly, the direction selectivity map requires visual input during a critical period, as later visual experience cannot rescue the direction selectivity map in dark-reared ferrets.

The nature-versus-nurture debate has been hotly contested ever since John Locke first pondered the question of whether a blind person, upon restoration of sight, would be able to distinguish between a cube and a sphere just by looking, without resorting to touch. The empiricists (Locke among them) suggested not, because the subject lacked the requisite experience. Nativists like Kant insisted the answer was yes, because such basic concepts were thought to be innate. In modern neuroscience terms, they would have expected to find neurons somewhere in the visual cortex responding selectively to cubes or spheres even in individuals without prior exposure to those stimuli.

A paper by Li *et al.*¹ in this issue suggests that the primary visual cortex is not innately equipped to perceive the direction of moving objects. Rather, neurons develop the ability to discriminate between opposite directions of motion during a sensitive period early in life, following exposure to appropriate visual stimulation. In other words, nurture is critical for motion perception. Why is this newsworthy? It is because the finding comes as a big surprise after decades of research into visual cortex development, which has resulted in a general consensus that basic response characteristics of neurons are innate, albeit modifiable by post-natal experience².

Since Hubel and Wiesel first described receptive field properties of neurons in the primary visual cortex (V1) in the 1960s, research into developmental plasticity has tended to concentrate on binocularity (or ocular dominance) and orientation selectivity. Hubel and Wiesel³ had already noted that even in the visual cortex of very young, visually naive kittens, some neurons had adult-like response qualities. Many studies

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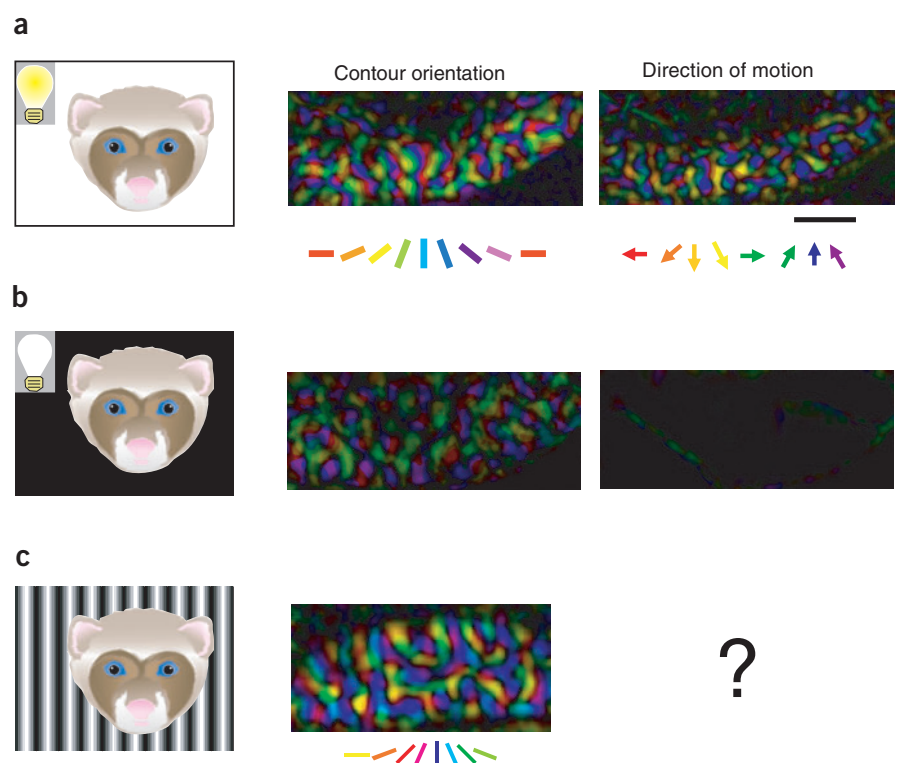


Figure 1 Nature and nurture in development and plasticity of orientation and direction maps in the primary visual cortex. Animals were reared in different visual environments (left panels) either from birth or from a later time, and the effects of rearing conditions on functional cortical maps were visualized by optical imaging. To obtain maps for contour orientation preference (center panels), animals were shown gratings in a range of orientations. Each pixel of the cortical surface map is pseudocolor coded according to the orientation that elicited the strongest response (color bars). Maps for direction-of-motion preference (right panels) are obtained by presenting gratings moving in a range of different directions and color coding the cortical surface according to which direction yielded the strongest response (color arrows). Scale bar, 2 mm. (a) Animals growing up in a normally lit visual environment show clear maps for both orientation and direction. (b) Animals reared in the dark from before natural eye opening until early in the critical period still have orientation maps, but have no direction maps at all¹. (c) Animals that are first dark reared and then 'stripe reared'—that is, exposed to an environment in which only one contour orientation is present—still have reasonably normal orientation maps, albeit with the experienced orientation over-represented¹⁰. It would be fascinating to see direction maps from animals reared in an analogous environment in which everything moved in one particular direction. This could be achieved by placing animals inside a rotating drum painted with vertical stripes¹².

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since then have confirmed that, at or before eye opening (depending on species), afferents from the two eyes are at least partially segregated into ocular dominance columns^{4,5} and that before the onset of the critical period of visual cortical plasticity, neurons are weakly grouped into orientation columns according to their preferred orientation⁶. Intrinsic factors seem to be responsible for the generation and the individual layout of these columnar patterns or maps.

Visual experience, however, is involved in maintaining and refining cortical maps. Closure of one eye leads to shrinkage of that eye's ocular dominance columns and expansion of the other eye's representation⁷. Ocular dominance columns are less distinct in dark-reared cats than in light-reared cats⁸. Prolonged dark rearing causes the early orientation preference maps to degrade and to disappear^{6,9}; rearing in a striped environment results in an increase of the cortical territory dedicated to processing the orientation of the stripes over columns processing other orientations¹⁰.

Parameters other than ocular dominance and orientation preference are characteristic of V1 neurons, for example, spatial frequency selectivity (relating to the spatial detail they can resolve) and direction selectivity, whose developmental plasticity has so far received less attention for various reasons. First, it is notoriously difficult to record the activity of single neurons extracellularly from very young animals, and second, recordings of small numbers of cells may not be representative. Finally, the grouping of neurons according to their spatial frequency or direction preference is much weaker than that for ocular dominance and orientation preference. Li and colleagues, in their study of ferret V1, used a functional brain imaging technique that overcomes these problems. In optical imaging of intrinsic signals¹¹, the surface of the cortical area under study is exposed and illuminated with red light. Depending on the distribution of local neural activity, some parts of the cortical surface absorb more of the incoming light than others. This is primarily because active neurons consume more energy and the necessary oxygen is provided by hemoglobin in nearby microcapillaries. Deoxyhemoglobin absorbs more red light than oxyhemoglobin, making regions of relatively increased activity appear darker than surrounding tissue. This technique is very sensitive, can be used on very young animals and allows researchers to map an area of cortex without sampling bias.

Li and colleagues used drifting gratings (stripe patterns) to visualize maps of orientation and direction preference in the visual cortex of young ferrets, starting before eye opening. They found well-defined orientation maps from

the earliest ages that they studied, confirming earlier work in ferrets⁹ as well as cats⁶. In contrast, direction maps only began to emerge after eye opening—that is, after the onset of visual experience—and reached mature strength a full two weeks later. Another standard test of whether a cortical map depends on visual experience is to rear animals in complete darkness. This procedure did not eliminate orientation maps for several weeks (although they did get weaker), but it completely prevented direction maps from forming (Fig. 1).

Furthermore, the role of experience in map development can be demonstrated by removing animals from the dark and exposing them to a normally lit environment. In this situation, orientation maps quickly recover their full strength, as long as light rearing is introduced at some point during the critical period. In contrast, Li *et al.* found that direction maps formed only if dark rearing was terminated within a week of eye opening, but not later. Together, these results suggest that early visual experience right after eye opening is necessary for the development of motion sensitivity in the primary visual cortex and that later experience cannot substitute for it.

One could also interpret these results as evidence that the critical period for motion sensitivity is earlier and/or shorter than the more familiar critical periods for ocular dominance and orientation selectivity. A similar conclusion was drawn based on single-cell recordings¹² from kittens reared in a rotating drum in which the direction of rotation was reversed at a range of ages. A change of direction later than five weeks of age led to a preponderance of cells preferring the direction of movement that the animals had experienced initially, not that seen last. In contrast, reverse lid suture at the same age leads to most cells being dominated by the initially closed eye¹³.

In addition to the nature-versus-nurture debate, the study by Li *et al.* provides an opportunity to re-examine another bone of contention among developmental neuroscientists. This is whether experience is 'instructive' or 'selective' in shaping cortical responses. Instruction refers to a process whereby activity is necessary to establish or modify a neuronal structure or functional property, and activity levels or patterns are directly related to the shape that this structure or function takes. Selection means that activity is necessary to maintain a particular structure or response and its absence causes a degeneration or passive loss of responsiveness². Stripe rearing has an instructive effect on V1 orientation columns: orientation preferences of neurons are modified so that they respond best to the experienced orientation. However, a fairly large percentage

of cells remain selective for orientations never experienced by the stripe-reared animals¹⁰. Because V1 is a *tabula rasa* at eye opening with respect to direction tuning, instructive and selective processes would predict very different outcomes of rearing ferrets in drums rotating in a fixed direction¹². The former would cause virtually every neuron in the cortex to respond to the experienced direction, whereas the latter would cause only cells whose intrinsic direction preference matched the experienced direction to respond at all.

Another question thrown up by the work of Li *et al.* is what happens in V1 at the time of eye opening that makes further dark rearing (or lid suture) detrimental to visual cortex function? And are these changes triggered by the eye opening itself, or are they preprogrammed to occur around that time? We know that the day of eye opening is by no means the first time a ferret has any visual experience. Ferret kits can certainly see something through their closed eyelids, as evidenced by neuronal responses to traditional grating stimuli¹⁴ as well as natural scenes¹⁵. Until a few days after eye opening, this degraded visual input is not harmful; thereafter it is⁹. The very early visual experience through closed eyes may even be of special significance to the development of motion sensitivity, as dark rearing during that period results in abnormal receptive field properties of LGN neurons¹⁵ that could account for the failure of direction selectivity to develop in those animals. The study by Li *et al.* clearly demonstrates that a narrow time window may be essential for sensory experience to shape certain aspects of cortical development: you use it, or you lose it.

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