

Vision: In the Brain of the Beholder

Dispatch

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It is commonly thought that neural activity in the visual cortex reflects retinal input. Recent studies, however, suggest that patterns of cortical activity are mostly intrinsically generated, and that visual input exerts but a modulatory influence.

At first glance, it seems obvious that what the visual cortex does is an analysis of the information conveyed by the retinal images in the two eyes. One would therefore expect that there should be a rather strict relationship between retinal input and the output of the visual cortex – the spiking activity of its neurons. But researchers in the field know that many neurons display a high variability of response when the same stimuli are shown repeatedly. This variability is attributed to the spontaneous activity of cortical neurons, which in turn is usually dismissed as ‘noise’. A recent study by Fiser *et al.* [1], however, provides evidence that spontaneous activity may shape the response to sensory stimuli, which systematically improves during early postnatal development.

That spontaneous activity might not be as random as previously thought has been demonstrated in a number of studies of its spatio-temporal pattern at various levels of the visual pathway. Patterns of locally correlated bursting activity were originally discovered in the developing retina, where they became known as retinal waves [2]. Later they were also observed in the lateral geniculate nucleus [3] and the primary visual cortex, V1 [4,5]. Interestingly, correlated spontaneous activity in V1 exhibits a similar kind of patchy organization as exhibited by horizontal intracortical connections [5], and periodic fluctuations in correlated activity match with periodic changes in ocular dominance [6].

Even more surprising than the mere presence of spatio-temporal patterns in spontaneous activity was the finding that those patterns often match those observed in response to actual visual stimuli. Using voltage-sensitive dye imaging, Kenet *et al.* [7] recorded and compared patterns of spontaneous activity and those elicited with full-field gratings of various orientations (Figure 1). Spontaneous activity patterns were highly dynamic, but at any moment in time they often corresponded quite closely to an orientation map in response to visual stimulation. This finding raises the question, addressed by Fiser *et al.* [1], whether spontaneous activity is not just ‘noise’ but plays an important role in how neurons respond during natural viewing.

Fiser *et al.* [1] studied the primary visual cortex of awake, freely viewing ferrets by means of implanted micro-electrode arrays [8]. They recorded neural

activity from three age groups: at postnatal day (P) 30–32, just after eye-opening; at P44–45, when orientation selective responses have matured; and in adult animals (P83–90). Each animal was tested under three randomly interleaved viewing conditions: complete darkness; dynamic random noise; and a movie of natural scenes (Figure 2A). As one might have expected, both random noise and moving natural images increased neuronal responses and the percentage of time that neurons were active compared with the darkness condition, which served to measure spontaneous activity. Also, activity under all three conditions increased in the two weeks after eye-opening, but remained stable thereafter.

The critical question is, how did the firing patterns, in space and time, compare with the image statistics, or in other words, how strong was the causal relationship between the visual stimuli and the neuronal responses? Surprisingly weak, is the answer. Typical neurons in the primary visual cortex respond well to moving edges, contours and high contrasts, but not much to homogeneous surfaces of low contrast, and these responses have long been modelled successfully using so-called ‘linear filters’, both for laboratory stimuli [9] and natural visual stimuli [10]. Using linear filters derived from neuronal responses in ferret V1, Fiser *et al.* [1] could accurately predict what firing patterns should look like if they resulted solely from the visual stimuli being placed within the neurons’ receptive fields. They could then compare the neurons’ actual responses with both the predicted responses and the spontaneous firing patterns observed in complete darkness.

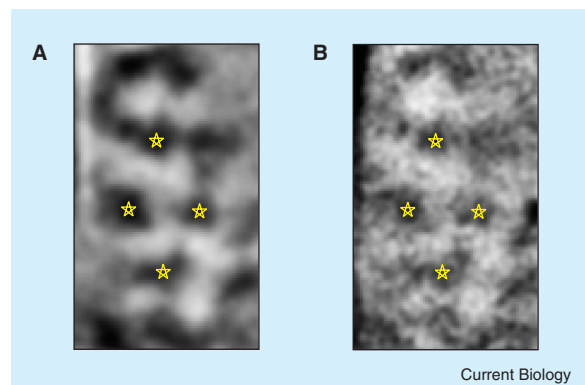


Figure 1. Similar patterns of visually evoked and spontaneous activity in cat primary visual cortex.

(A) A typical orientation map obtained by optical imaging [15] in response to a drifting grating. In this case, responses to presentation of a horizontal grating were divided by responses to an otherwise identical vertical grating. Responses were summed over several frames and a number of repeat presentations; dark areas signify a strong response to the horizontal stimulus. (B) Spontaneous activity pattern as it may be seen in an individual image frame in the absence of any visual stimulus. Patterns are often similar to ones observed with visual stimulation, but change very rapidly. Here, stars mark patches that respond preferentially to horizontal contours, as seen in (A).

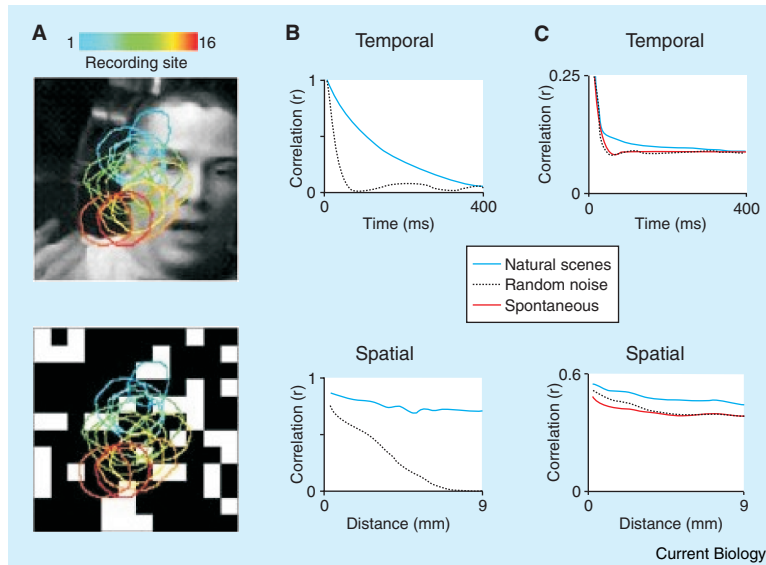


Figure 2. Statistical properties of two visual stimuli and of spontaneous and evoked activity patterns in ferret visual cortex.

(A) Illustration of two individual frames from a natural-scenes movie (top) and a random-noise movie (bottom) used for stimulation of visual cortical neurons. Coloured outlines indicate receptive fields of neurons recorded at sites 1–16 of the implanted array (colour code at top). (B) Expected temporal and spatial correlation functions of neuronal activity elicited by natural scenes and random noise, respectively, if activity were fully predictable on the basis of applying linear filters to the visual input. Correlations should decrease much more gradually with time and distance during viewing of natural scenes as opposed to random noise. (C) Actual temporal and spatial correlation functions of cortical activity in adult ferret V1 during viewing of natural scenes and random noise, and in complete darkness. Note the similarity of correlation functions under all three conditions. (Adapted from [1].)

At the time of eye-opening (P30–32), visual cortical activity was dominated by slow, irregular bursts lasting for several hundred milliseconds, and no differences were observed between spontaneous activity patterns and those elicited by visual stimuli, although of course the image statistics differed drastically. In natural scenes, but not in random noise, individual pixels tend to change slowly in time, and neighbouring pixels tend to be similar, resulting in extensive temporal and spatial correlations (Figure 2B). After two weeks of visual experience (P44–45), spontaneous firing patterns had changed considerably, but so had responses to random noise or natural scenes. The most significant development was the shortening of bursts, eliminating temporal correlations beyond 100 milliseconds: for natural images, these decreased slightly less sharply than for random noise or in darkness. Spatial correlations between responses of different neurons recorded at different sites at the same time remained identical under all three conditions.

Maturation to a near-adult state (P83–90) was characterized by a further decrease in temporal correlation for all three stimulus conditions, while the difference between responses to natural scenes on the one hand and spontaneous responses and those to random noise on the other hand increased further. In fact, the temporal modulation of responses to natural scenes had come close to reflecting the statistical properties of the visual stimulus (Figure 2C, top). Similarly, spatial correlations were increased, for more widely separated recording sites, during viewing of natural scenes compared with the other two conditions, in line with the fact that long-range correlations in images containing larger objects are high compared with random noise or darkness (Figure 2C, bottom). Nevertheless, even in the mature visual cortex all three correlation functions remained similar, and overall activity in response to natural scenes

exceeded spontaneous rates by just 23%. So it is more accurate to say that visual stimuli modulate neuronal activity in V1, rather than that they elicit it.

If spontaneous firing forms such a large part of the total cortical activity, and therefore consumes so much of the brain's energy budget [11], one has to assume that it is in itself important for sensory processing, and perhaps question the classical view of the visual cortex as a mere analyser of retinal input. This notion assumes that increasingly complex information is extracted from the retinal images at successive stages of the visual pathway, and is eventually brought together to form a representation of the visual world. An alternative hypothesis proposes that vision is an inferential process, in which prior knowledge of the make-up of the visual environment determines neuronal activity and, consequently, what we see or do not see [12].

It has been shown that Bayesian inference is an optimal method to extract information on the nature of a visual stimulus from the firing of a population of cortical neurons [13], but so far we can only speculate whether the brain itself uses this method. If it does, then information is primarily present within the visual system, and only secondarily in the retinal input [12], counterintuitive as this may sound. The firing of a group of neurons then indicates the probability of a certain visual stimulus being present, based on what they 'know' about the visual world. Evidence is just beginning to emerge that the ability of the human visual system to discriminate orientations is indeed influenced by prior expectation when stimuli are presented in an orderly sequence [14]. In this context, what we consider spontaneous activity may well reflect the expectations or 'knowledge' of the brain about the visual world.

References

1. Fiser, J., Chiu, C., and Weliky, M. (2004). Small modulation of ongoing cortical dynamics by sensory input during natural vision. *Nature* 431, 573–578.

2. Meister, M., Wong, R.O., Baylor, D.A., and Shatz C.J. (1991). Synchronous bursts of action potentials in ganglion cells of the developing mammalian retina. *Science* 252, 939-943.
3. Weliky, M., and Katz, L.C. (1999). Correlational structure of spontaneous neuronal activity in the developing lateral geniculate nucleus *in vivo*. *Science* 285, 599-604.
4. Tsodyks, M., Kenet, T., Grinvald, A., and Arieli, A. (1999). Linking spontaneous activity of single cortical neurons and the underlying functional architecture. *Science* 286, 1943-1946.
5. Chiu, C., and Weliky, M. (2001). Spontaneous activity in developing ferret visual cortex *in vivo*. *J. Neurosci.* 21, 8906-8914.
6. Chiu, C., and Weliky, M. (2002). Relationship of correlated spontaneous activity to functional ocular dominance columns in the developing visual cortex. *Neuron* 35, 1123-1134.
7. Kenet, T., Bibitchkov, D., Tsodyks, M., Grinvald, A., and Arieli, A. (2003). Spontaneously emerging cortical representations of visual attributes. *Nature* 425, 954-956.
8. Chiu, C., and Weliky, M. (2004). Multi-electrode recording from the developing visual pathway of awake behaving ferrets. *J. Neurosci. Meth.* 136, 55-61.
9. Jones, J.P., and Palmer, L.A. (1987). An evaluation of the two-dimensional Gabor filter model of simple receptive fields in cat striate cortex. *J. Neurophysiol.* 58, 1233-1258.
10. Weliky, M., Fiser, J., Hunt, R.H., and Wagner, D.N. (2003). Coding of natural scenes in primary visual cortex. *Neuron* 37, 703-718.
11. Attwell, D., and Laughlin, S.B. (2001). An energy budget for signaling in the grey matter of the brain. *J. Cereb. Blood Flow Metab.* 21, 1133-1145.
12. Young, M.P. (2000). The architecture of visual cortex and inferential processes in vision. *Spat. Vis.* 13, 137-146.
13. Oram, M.W., Földiák, P., Perrett, D.I., and Sengpiel, F. (1998). The 'Ideal Homunculus': decoding neural population signals. *Trends Neurosci.* 21, 259-265.
14. Guo, K., Nevado, A., Robertson, R.G., Pulgarin, M., Thiele, A., and Young, M.P. (2004). Effects on orientation perception of manipulating the spatio-temporal prior probability of stimuli. *Vision Res.* 44, 2349-2358.
15. Zepeda, A., Arias, C., and Sengpiel, F. (2004). Optical imaging of intrinsic signals: recent developments in the methodology and its applications. *J. Neurosci. Meth.* 136, 1-21.