(Reprinted from Nature, Vol. 278, No. 5707, pp. 850-852, April 26 1979)

Pattern-selective adaptation in visual cortical neurones

PROLONGED viewing of a grating pattern produces striking 'after-effects', involving changes in the detectability, apparent size, orientation and contrast of subsequently viewed gratings[1-3]. Studies of perceptual after-effects have been used to infer properties of neurones in the human visual cortex[2,4,5] similar to those pattern-selective neurones whose sensitivities have been directly measured in the visual cortex of cats and monkeys[6,7]. Such inferences are based on two assumptions: first, that perceptual changes result from changes in the distribution of activity within the responding population of neurones; second, that the effect of adaptation on each neurone of the population is to reduce its sensitivity uniformly to all stimuli. The experimental results reported here support the first but challenge the second assumption, as they show that after adaptation to a particular grating the sensitivity of a single neurone to that grating may be reduced more than its sensitivity to other gratings.

We recorded the activity of single neurones in the portion of the striate cortex representing the central visual field in young adult cats anaesthetised with nitrous oxide, using methods described in detail elsewhere[8]. The after-effects of prolonged stimulation by grating patterns were examined in 20 cells in five cats. Initially, we explored the receptive fields of each neurone with bars, edges and spots, and as a result classified them as simple, complex or hypercomplex[6,7]. The face of a display oscilloscope, which subtended a circle 10° in diameter at the cat's eye, was then centred on the receptive field (in the dominant eye); the other eye was covered.

The luminance of the oscilloscope screen (which was kept at a space average of 6 cd m^{-2} throughout) could be spatially modulated by signals from a computer to produce sinusoidal gratings. These are patterns of light and dark bars whose luminance profile perpendicular to the bars is a sine wave; their spatial frequency is the number of cycles that subtend one degree of visual angle, and their contrast is the difference between the maximum and minimum luminance divided by twice the mean luminance. All the gratings moved steadily in a direction orthogonal to their bars at 2 Hz (so that two cycles crossed any point on the screen in 1 s). The computer controlled the orientation, direction of movement, spatial frequency and contrast of the grating, and also, within the limits of the 10° field, its spatial extent. While presenting grating patterns, the computer counted action potentials and compiled them into average response histograms; these were saved on disk for later analysis.

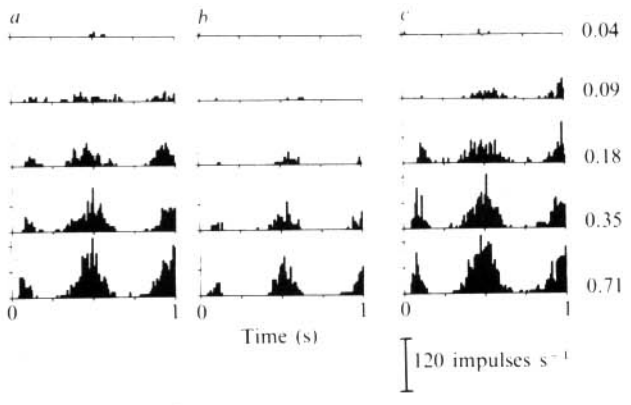

Fig. 1 Responses of a simple cell to gratings of different contrast, obtained before (*a*), during (*b*) and after (*c*) a period of adaptation. *a* Shows averaged responses to gratings of 0.75 c deg^{-1}, moving at 2 Hz in the optimal direction, presented at the five contrasts indicated on the right. Each grating was presented 20 times, each time for two stimulus cycles; each histogram thus shows the response to the passage of two bars of the grating across the receptive field. *b* Shows the responses to the test stimuli while the neurone was fully adapted to the same grating presented at high contrast (0.71). Each test stimulus was preceded by a presentation of the adapting stimulus. *c* Shows responses to the same test stimuli, measured in an experiment begun 12 min after the end of the adaptation experiment.

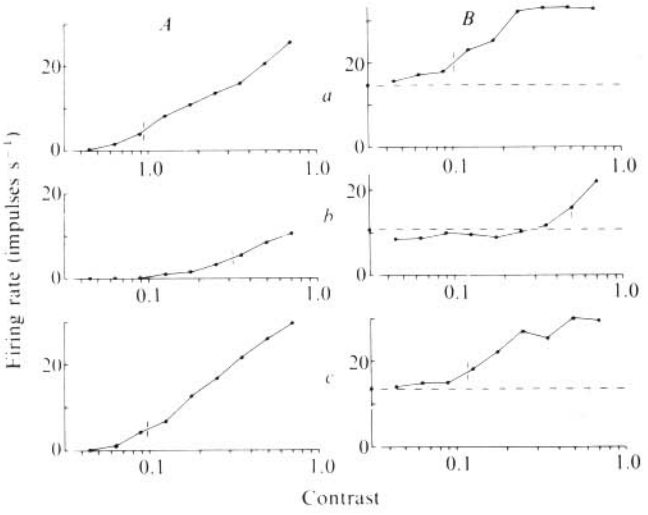

Fig. 2 The effect of adaptation on contrast–response relations. *A*, Results of the experiment partially illustrated in Fig. 1. *a* Shows the contrast–response relationship measured before adaptation, *b* shows the relationship while the cell was fully adapted, and *c* shows it after a 12-min recovery period. *B*, Results of a similar experiment on a complex cell; the spatial frequency of all gratings was 2.0 c deg^{-1}, and they moved at 2 Hz. Horizontal dashed lines indicate spontaneous activity. As in *A*, the three graphs show measurements made before (*a*), during (*b*) and after (*c*) adaptation. The vertical bar on each graph indicates the contrast necessary to elicit a criterion response of 5 impulses s^{-1} above spontaneous firing. Comparison of these criterion contrasts provides a useful index of adaptation; within limits, the choice of criterion does not strongly affect the index obtained. Here and in Fig. 3, the response plotted is the average discharge rate elicited by the stimulus. This is the natural measure of the response of complex cells, which do not give modulated responses to most gratings; simple cells do give modulated responses but as they generally lack maintained discharge, measures of modulated or unmodulated responses are very well correlated (see Fig. 1).

For each neurone we first established the spatial frequency, orientation, extent and direction of movement of the optimal grating; then, using optimal stimuli, we measured the relationship between response and stimulus contrast. Figure 1*a* shows the results of a set of such measurements. In this and all other experiments, the stimuli were presented in blocks. Within a block, each stimulus was presented once for 1 s, during which two cycles of the grating crossed the receptive field. The order of presentation within a block was random and different within each block, of which there were normally 20 in an experiment.

The contrast–response relationship was then determined again, while the neurone was fully adapted to a high-contrast grating. Each block of this 'adaptation' experiment began with a 32- or 64-s presentation of the adapting grating; each test stimulus after the first was preceded by a 4- or 8-s topping-up presentation of the adapting stimulus[2]. Figure 1*b* shows the results of an experiment in which the adapting stimulus was of optimum spatial frequency and orientation. A comparison of these responses with their counterparts in Fig. 1*a* shows clearly that prolonged stimulation by a high-contrast grating greatly reduced the strength of responses. In separate experiments we established that the initial period of adaptation used was sufficient to produce the maximum reduction in sensitivity, and that the topping-up period was sufficient to maintain it.

Figure 1*c* shows the results of measurements begun 12 min after adaptation, by which time responses had fully recovered. In all cases, except three where the unit was lost, we verified that

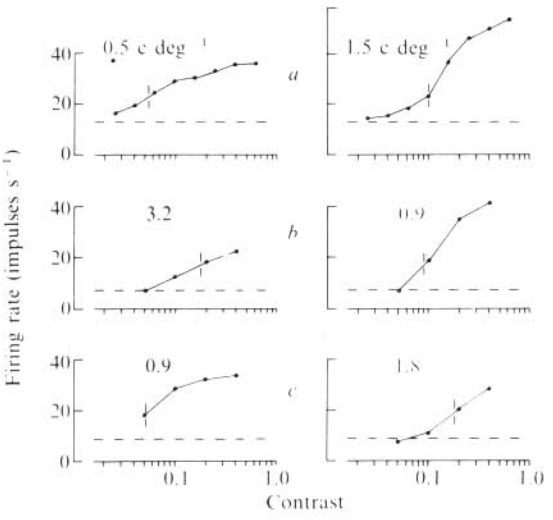

Fig. 3 The spatial frequency selective nature of adaptation. In these experiments, on a complex cell, test gratings of 0.5 and 1.5 c deg^{-1} were used. *a* Shows the contrast–response relationship for both spatial frequencies, measured before adaptation. *b* Shows the results of an adaptation experiment in which the adapting grating had a contrast of 0.71 and a spatial frequency of 0.5 c deg^{-1}. *c* Shows the results of a similar experiment in which the adapting grating had a contrast of 0.71 and a spatial frequency of 1.5 c deg^{-1}. The vertical bars on each graph, as in Fig. 2, indicate the contrast needed to elicit a criterion response (here, 10 impulses s^{-1} above spontaneous level). Each adaptation experiment was followed by a period of recovery, during which we verified that responses had returned to pre-adaptation levels. The ratios of the post-adaptation and pre-adaptation contrasts needed to elicit the criterion response are shown on each of the four lower graphs; values greater than 1 indicate an elevation of this 'threshold', values less than 1 a reduction.

within 5–15 min after the end of adaptation, responses were similar to those observed before adaptation.

Figure 2*A* shows the full results of this experiment, which was carried out on a simple cell, and Fig. 2*B* shows the results of a similar experiment on a complex cell. For both neurones, Fig. 2 shows the contrast–response relationship measured before adaptation (*a*), while the cell was fully adapted (*b*) and after a period of recovery (*c*). For both neurones, adaptation raised the contrast required to produce a given response by a factor of about four, and recovery returned it to very nearly its former value. Although the changes brought about by adaptation are apparently very similar in form for the two units when expressed in this way, the extent to which the response to a grating of fixed contrast is reduced by adaptation may be a poor guide to the extent of this adaptation. Thus, in the case of the complex cell, adaptation produces a much smaller reduction in the response to high-contrast stimuli than it does to ones of lower contrast. Increase in the contrast required to produce a given response (that is, reduction in sensitivity) seems to be the appropriate measure of adaptation.

To ascertain how great a change in sensitivity is brought about by an adapting stimulus, one must compare responses to stimuli of different contrasts presented before, during and after adaptation. Adaptation brought about clear reductions in sensitivity in 19 of the 20 neurones we studied; the remaining unit, a monocularly driven neurone with unusually broad orientation selectivity, showed no reliable effects. Spontaneous activity was not always depressed by adaptation.

We were especially interested to know whether the reduction in sensitivity that followed adaptation was confined to stimuli of the same spatial frequency as the adapting pattern; we examined this question in experiments where the spatial frequencies of the test and adapting patterns were varied. The graphs in Fig. 3*a* show contrast–response relationships for a complex cell, obtained with gratings of 0.5 and 1.5 c deg^{-1}; vertical bars mark the contrast needed to produce a response of 10 impulses s^{-1}. The graphs in Fig. 3*b* show the same relationships obtained during adaptation to a grating of 0.5 c deg^{-1}. Responses to gratings of this spatial frequency were much reduced by adaptation (the contrast required to produce a response of 10 impulses s^{-1} was elevated by a factor of more than three), whereas responses to gratings of 1.5 c deg^{-1} were hardly affected. The graphs in Fig. 3*c* show the results of a complementary experiment, in which the spatial frequency of the adapting grating was 1.5 c deg^{-1}. In this case, sensitivity for test gratings of 0.5 c deg^{-1} was unaffected, whereas sensitivity for gratings of 1.5 c deg^{-1} was much reduced. The effect of adaptation on this neurone cannot be explained by a uniform change in sensitivity; some spatial frequency selective mechanism must be involved. We observed behaviour of this kind in all seven complex neurones in which we studied the spatial frequency selectivity of adaptation; of three simple cells, one seemed to show spatial frequency selective adaptation, one definitely did not, and the third gave variable results.

Our experiments confirm two earlier reports that the behaviour of cortical neurones may be altered following a period of prolonged stimulation[9,10]. However, it is necessary to measure sensivitity in order to characterise the changes adequately; alterations in spontaneous activity, or in responses to high-contrast stimuli, provide an incomplete description of the effects of adaptation.

Our most surprising observation is that the loss of sensitivity in cortical neurones can be specific to the adapting stimulus. Our observations on complex cells might be explained by supposing that each complex cell is excited by a group of simple cells having different frequency selectivities. However, because the spatial frequency selectivity of complex cells is little different from that of simple cells[11], and because we have observed frequency-selective adaptation in a simple cell, this is not a convincing argument. Alternatively, adaptation in both simple and complex cells might result from changes in the afferent relay from the lateral geniculate nucleus. Again, this seems unlikely, as the spatial frequency selectivity of cortical neurones is far greater than that of geniculate neurones[12], and also as we have found in separate experiments that the responses of geniculate cells are unaffected by adaptation. We are left with the suggestion that some pattern-selective, perhaps inhibitory, cortical mechanism is involved.

Our observed frequency-selective loss of sensitivity is inconsistent with some models of perceptual after-effects[2,5]. Although our experiments do not question the idea that human perceptual adaptation reflects adaptation in cortical neurones, they do limit the inferences about the properties of these neurones that may be based on adaptation experiments in man.

This research was supported by grants to J.A.M. from NIH (EY 2017) and NSF (BNS 76-18904). Alloferin was supplied by Roche. J.A.M. is an Alfred Sloan Research Fellow.

J. ANTHONY MOVSHON
PETER LENNIE*

Department of Psychology,
New York University,
New York, New York 10003

Received 19 September 1978; accepted 13 March 1979.

*Permanent address: Laboratory of Experimental Psychology, University of Sussex, Brighton, UK.

1. Gibson, J. J. & Radner, M. *J. exp. Psychol.* **20,** 453–467 (1937).
2. Blakemore, C. & Campbell, F. W. *J. Physiol., Lond.* **203,** 237–260 (1969).
3. Blakemore, C. & Sutton, P. *Science* **166,** 245–247 (1969).
4. Sutherland, N. S. *Q. Jl exp. Psychol.* **13,** 222–228 (1961).
5. Coltheart, M. *Psych. Rev.* **78,** 114–121 (1971).
6. Hubel, D. H. & Wiesel, T. N. *J. Physiol., Lond.* **160,** 106–154 (1962).
7. Hubel, D. H. & Wiesel, T. N. *J. Physiol., Lond.* **195,** 215–243 (1968).
8. Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. *J. Physiol., Lond.* **283,** 53–66 (1978).
9. Maffei, L., Fiorentini, A. & Bisti S. *Science* **182,** 1036–1038 (1973).
10. Vautin, R. & Berkley, M. *J. Neurophysiol.* **40,** 1051–1065 (1977).
11. Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. *J. Physiol., London* **283,** 101–120 (1978).
12. Cooper, G. F. & Robson, J. G. *IEEE NPL Conf. Proc.*, 134–143 (1968).

Printed in Great Britain by Macmillan Production Ltd., Basingstoke, Hampshire