

Visual aftereffects: cortical neurons change their tune

Mark Georgeson
School of Life & Health Sciences
Aston University, Birmingham, B4 7ET, U.K.

Georgeson M A (2004) Visual aftereffects: cortical neurons change their tune. (Dispatch) *Current Biology*, 14, R751-R753.

Summary

Recent studies of visual cortex (V1 and MT) show that exposure to a stimulus can change the contrast sensitivity of cells and shift their peak sensitivity to a new orientation or movement direction. In MT these shifts in tuning can correctly predict illusory changes (visual aftereffects) in movement direction, but in V1 the changes are more difficult to interpret.

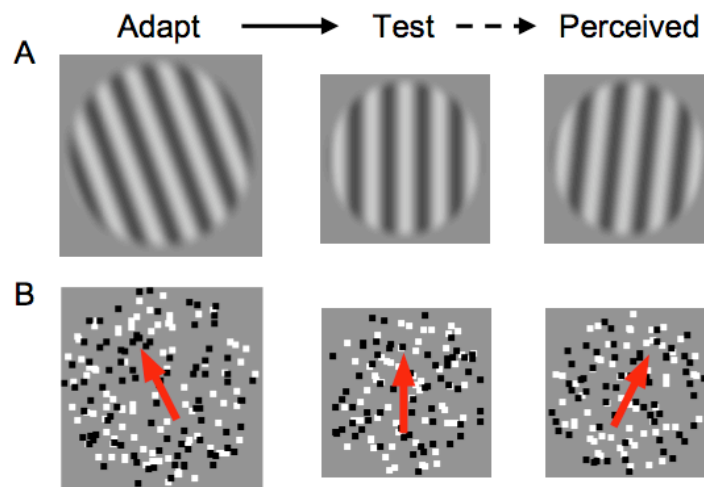


Fig. 1 Visual aftereffects: exposure to a given stimulus pattern (adaptation) leads to a shift in the appearance of other test patterns that are similar along some visual dimension such as orientation or motion direction. A: The tilt aftereffect: adapting to tilted lines makes a vertical test pattern seem tilted a few degrees the other way. B: The directional aftereffect: adapting to dots drifting up and to the left makes a vertically drifting test pattern seem to be drifting up and to the right, by as much as 20 deg^{3,4}.

If you stare at a rotating disc for a little while and then stop the rotation, the disc will appear to be rotating backwards, even though it is actually stationary. Similar illusory movement can be seen after looking at a waterfall, or the credits rolling at the end of a movie. This striking phenomenon – the motion aftereffect – has been known for hundreds of years¹, and is one of many visual aftereffects that have intrigued students and scholars of perception. Aftereffects reveal a gap between appearance and reality, and remind us that what we see is determined by how visual information is coded in the brain, and not simply by how things ‘really are’. Aftereffects provide an opportunity for psychologists and neuroscientists to understand the way in which populations of visually selective cells encode information about visual dimensions such as movement, orientation, size, and colour. For orientation, a few seconds or minutes of exposure to tilted lines will make vertical lines seem tilted the opposite way (Fig. 1A) – the tilt aftereffect². Analogous effects are obtained when the adapting and test patterns are moving in different directions. Adapting to dots or gratings drifting (say) –30 deg from vertical will make vertical movement appear shifted by about +20 deg (Fig. 1B) – the directional aftereffect^{3,4}. The aftereffects are therefore ‘repulsive’:

neighbouring test stimuli appear to be shifted away from the adapter in orientation or direction of movement.

A major goal of research is to understand how and why the response properties of cells in visual areas of the brain change, both during and after a period of exposure to an adapting stimulus, and how these neural changes are related to the perceptual changes experienced in the aftereffects.

Recent studies in the cat and monkey brain⁵⁻⁸ have begun to shed new light on these questions, but also to implicate neural dynamics more complex than we previously supposed.

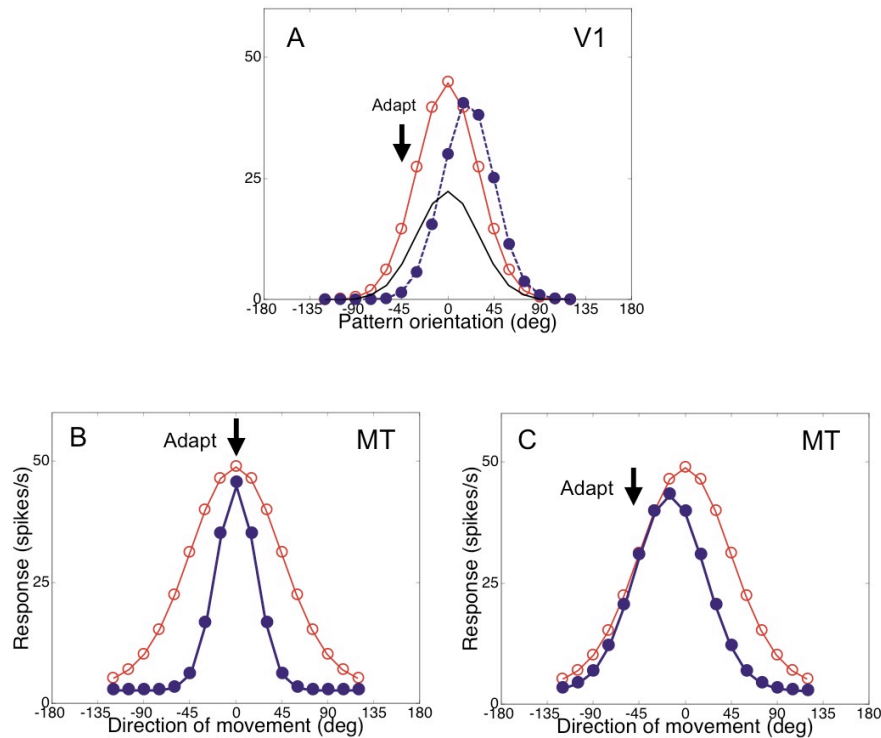


Fig. 2 Re-tuning of visual cell responses after adaptation. A: Schematic response tuning curve (open circles) for an orientation-selective cell in primary visual cortex (V1). After adapting to a given orientation (arrowed), the cell's response might be scaled down equally at all test orientations (black curve). This would be a change in response gain, broadly consistent with the traditional 'fatigue' theory. But experiments in V1 have tended to reveal a 'repulsive' shift in the tuning curve (filled circles), away from the adapting orientation^{5,10}. B: In monkey brain area MT, Kohn & Movshon⁸ found a narrowing of the directional tuning curve (filled circles) after adapting to a grating drifting in the cell's preferred direction. C: Adapting to flanking directions (about 45 deg from the optimal direction) produced 'attractive' shifts of tuning, towards the adapting direction. These attractive shifts may be an important clue to the repulsive nature of the perceptual aftereffects⁸.

Cells in the visual cortex are 'tuned' or selective such that individual cells respond best to a particular orientation and/or direction of motion (Fig. 2A,B; open symbols), and across the population different cells respond best to different orientations and directions of motion. It is the pattern of activation across the population (which cells are most active to a given stimulus?) that is likely to represent the perceived orientation or direction. Twenty or thirty years ago, it seemed reasonable to suppose that when exposed to, say, a pattern moving to the right the cells most responsive to rightward motion would become adapted or de-sensitized, while other cells, less responsive to this stimulus, would be little affected. This attractively simple 'fatigue' model has been at the heart of much thinking about adaptation and aftereffects. It correctly predicts that

individual cells (and the whole observer) should be less sensitive to the adapting stimulus after a period of exposure, and it broadly accounts for the perceptual distortions that result ⁹.

However, it has become increasingly clear that visual cortical cells also adapt in ways not captured by the ‘fatigue’ model. Several studies of V1 cells found that if a cell is exposed to stimulus X (say, a left tilted grating) then its sensitivity and responsiveness to X are indeed reduced (Fig 2A), but its responses to stimulus Y (e.g. a right tilted grating) may be unaffected, or even enhanced (Fig 2A, filled symbols). The adaptation effect can thus be selective at the single-cell level, and the tuning curve of the cell (Fig 2A) may be shifted, not merely scaled down ^{5,6,10}. At first sight, this ‘repulsive’ shift in the tuning curve appears consistent with the ‘repulsive’ character of the perceptual aftereffects. But this correspondence is a false friend: if cells that normally code for leftward tilt become more responsive to vertical (a repulsive shift in tuning), then a vertical test image should surely seem tilted to the left, not the right - just the opposite of what is observed. Thus the reports of shifted tuning in V1 cells are in some respects puzzling and seem to have made it more difficult to understand the tilt aftereffect.

For the aftereffects of motion, primary area V1 may not be the best place to look. The extra-striate cortical area MT is known to be especially concerned with motion coding, in both monkeys¹¹ and humans ¹², and MT is known to play a direct role in motion perception ¹³. To shed new light on the directional aftereffect, Kohn & Movshon ⁸ asked how the direction tuning of MT cells in the monkey is affected by adaptation to moving patterns. The surprising outcome was that responsiveness of MT cells was least affected when they were tested in the adapting direction, but much reduced when the cells were tested in directions about 45-90° from the adapting direction. These differential changes in responsiveness mean that adapting to moving gratings caused substantial alterations in the tuning curves of MT cells. The ‘optimal’ direction for a given cell tended to shift towards the adapting direction (Fig. 2C) – an ‘attractive’ rather than repulsive shift. When the adapting direction was close to the cell’s preferred direction, the cell’s tuning curve became narrower, effectively making the cell more specific to a given direction of motion (Fig. 2B).

Based on these physiological findings, Kohn & Movshon ⁸ modelled the response of the MT cell population in order to predict how the population response – and hence the perceived direction of motion – would shift after adaptation. Their model showed that the attractive shifts in single-cell tuning predict a repulsive perceptual aftereffect very similar in form and magnitude to those measured psychophysically^{3,4}. The logic is roughly this: if a cell normally sensitive to +20 deg becomes most sensitive to 0 deg (‘attracted’ towards a –40 deg adapter) then a 0 deg (vertical) test stimulus will now be seen at +20 deg, because +20 deg is the direction normally signalled when that cell is the most active one. Hence attractive tuning shifts should lead to repulsive aftereffects, as observed.

This leaves us with the puzzle of V1 and the tilt aftereffect. There the evidence favours repulsive tuning shifts^{5,6,10} (the opposite of the observations in MT), but the perceptual tilt aftereffect is also repulsive in the usual way, not attractive. One answer might be that, as with motion and MT, we should look for the neural correlates of the tilt aftereffect in an extra-striate area, such as V4, rather than V1. Secondly, we know that the shifts in tuning are accompanied (or indeed caused) by rather complex changes in gain or responsiveness – a cell may become less sensitive to some stimuli but be unchanged or even more sensitive to others. Kohn & Movshon’s modelling shows that if the gain reductions are large enough, then repulsive aftereffects are predicted even when the tuning shifts are also repulsive. Perhaps the gain reductions in V1 cells are large enough to lead to a repulsive tilt

aftereffect, as in the standard fatigue model, even though the ‘wrong’ shifts of tuning also occur. Thirdly, the tuning shifts in V1 may not be universal⁸; one study found tuning shifts in complex cells but not simple cells¹⁰.

Much remains uncertain about the neural processes underlying adaptation, and how the observed shifts in cell tuning come about. The finding of both reduced and enhanced gain in the same cell for different test stimuli is broadly consistent with other evidence for ‘contextual modulation’, in which the responses of single cells are modulated by excitatory and inhibitory interactions with other cells in the same neighbourhood¹⁴, and by feedback from other cortical areas. In addition, cells may inherit adaptation from the cells that feed them. For example, the finding of spatially localized gain reduction within the receptive field of MT cells⁷ suggests that this aspect of adaptation in MT reflects adaptation in V1 or V2, where receptive fields are much smaller.

Aftereffects are distortions of perception, and so might seem to be maladaptive, but there have been several proposals¹⁵ that adaptation over short time scales may serve to enhance perceptual discriminations and the efficiency of neural coding^{10,16}, and over longer periods may serve to maintain an effective match between sensory coding properties and the statistics of the visual environment (for review see¹⁷). It will take further work to discover whether the adaptive shifts of tuning in V1 and MT, apparently in opposite directions, are both adaptive in functional terms.

References

1. Mather, G., Verstraten, F. and Anstis, S. (eds.) (1998). *The motion aftereffect: a modern perspective* (MIT Press, Cambridge, Mass.).
2. Greenlee, M. W. and Magnussen, S. (1987). Saturation of the tilt aftereffect. *Vis. Res.* *27*, 1041-1043.
3. Levinson, E. and Sekuler, R. (1976). Adaptation alters perceived direction of motion. *Vis. Res.* *16*, 779-781.
4. Schrater, P. R. and Simoncelli, E. P. (1998). Local velocity representation: evidence from motion adaptation. *Vis. Res.* *38*, 3899-3912.
5. Dragoi, V., Sharma, J. and Sur, M. (2000). Adaptation-induced plasticity of orientation tuning in adult visual cortex. *Neuron* *28*, 287-298.
6. Dragoi, V., Sharma, J., Miller, E. K. and Sur, M. (2002). Dynamics of neuronal sensitivity in visual cortex and local feature discrimination. *Nature Neurosci.* *5*, 883-891.
7. Kohn, A. and Movshon, J. A. (2003). Neuronal adaptation to visual motion in area MT of the macaque. *Neuron* *39*, 681-691.
8. Kohn, A. and Movshon, J. A. (2004). Adaptation changes the direction tuning of macaque MT neurons. *Nature Neurosci.* *7*, 764-772.
9. Blakemore, C. and Campbell, F. W. (1969). On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images. *J. Physiol.* *203*, 237-260.
10. Muller, J. R., Metha, A. B., Krauskopf, J. and Lennie, P. (1999). Rapid adaptation in visual cortex to the structure of images. *Science* *285*, 1405-1408.
11. Maunsell, J. H. and van Essen, D. C. (1983). Functional properties of neurons in the middle temporal visual area of the macaque monkey: I. Selectivity for stimulus direction, speed and orientation. *J. Neurophysiol.* *49*, 1127-1147.
12. Heeger, D. J., Boynton, G. M., Demb, J. B., Seidemann, E. and Newsome, W. T. (1999). Motion opponency in visual cortex. *J. Neurosci.* *19*, 7162-7174.
13. Salzman, C. D., Murasugi, C. M., Britten, K. H. and Newsome, W. T. (1992). Microstimulation in visual area MT: effects on direction discrimination performance. *J. Neurosci.* *12*, 2331-2355.
14. Gilbert, C. D. and Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in primary visual cortex of the cat. *Vis. Res.* *30*, 1689-1701.
15. Barlow, H. B. and Foldiak, P. (1989). In *The Computing Neuron*. R. Durbin, C. Miall and G. Mitchison eds. (New York: Addison-Wesley), pp. 54-72.
16. Wainwright, M. (1999). Visual adaptation as optimal information transmission. *Vis. Res.* *39*, 3960-3974.
17. Clifford, C. W. G. (2002). Perceptual adaptation: motion parallels orientation. *Trends Cogn. Sci.* *6*, 136-143.