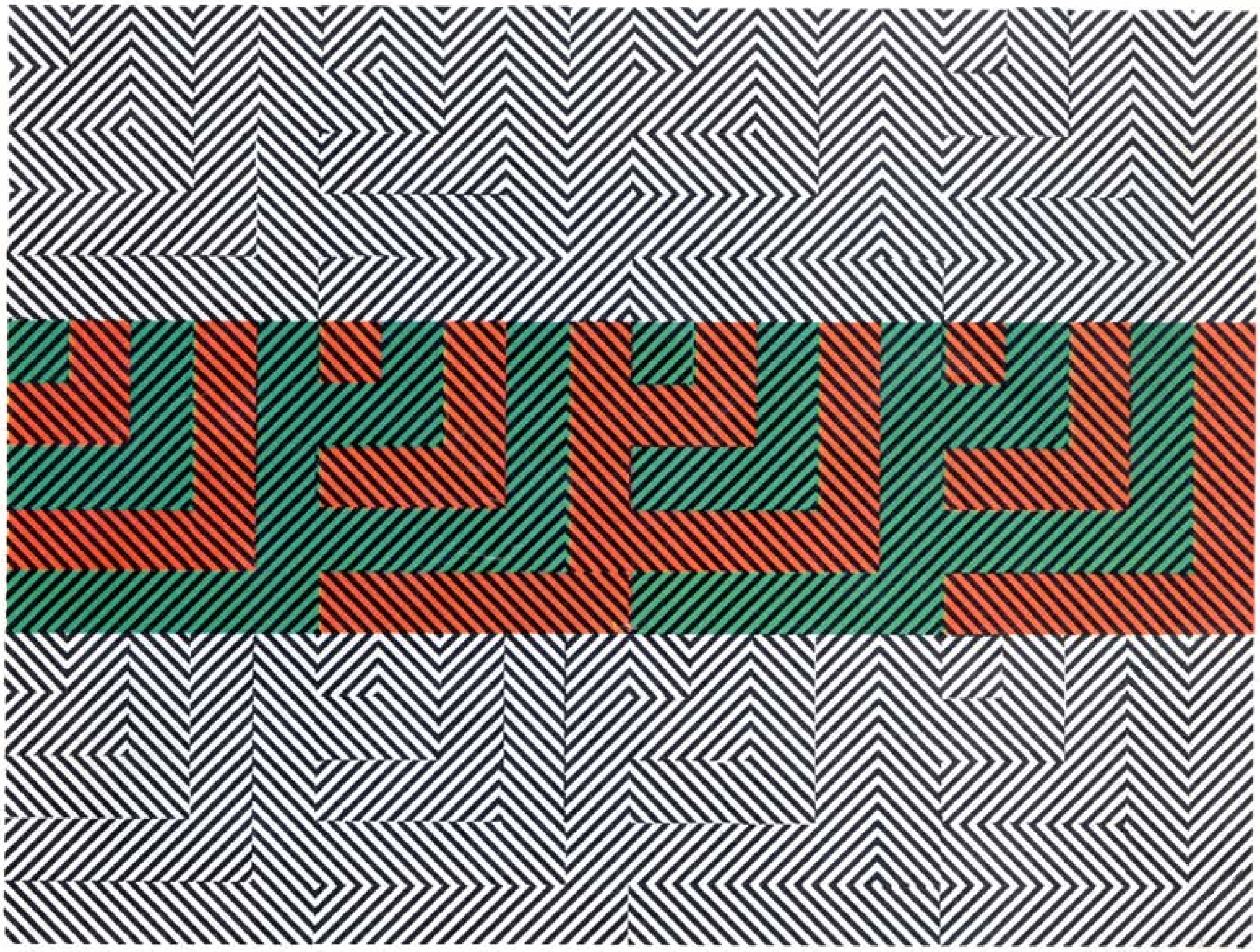
new scientist

21 February 1974
Vol 61 No 886
Weekly 18p
Australia 40 cents/
Canada 60 cents/
New Zealand 40 cents/
South Africa 40 cents/
USA (by air) $1.00/
BF 36/FF 3/DM 2.80/
hfl 1.75/skr 3.00/
Spain 30 pts/



A new visual experience

After-effects and the brain

After-effects and the brain

Psychologists stick microelectrodes into animals' brains to discover the secrets of the nerve tissue's activity. But the functioning of human brains can be exposed more indirectly by studying the curious phenomena known as perceptual after-effects

Dr John Mollon is a researcher in the department of experimental psychology, Cambridge, and he recently convened a meeting of the British Psychological Society on perceptual after-effects.

J. B. S. Haldane once reported that after he had spent ninety minutes in an atmosphere containing an excess of carbon dioxide he had the illusion of smelling ammonia. If one listens for some time to white noise from which a narrow band of frequencies has been removed one will afterwards hear for a few seconds a faint tone that corresponds to the missing frequencies. If you draw thick radial lines about 45 degrees apart on a paper disc, allow the disc to rotate on a record-player at 33 rev. min and fixate the centre for about a minute, then any textured surface that you look at immediately afterwards will dramatically appear to rotate in the opposite direction.

Such phenomena as these, long of interest to experimental psychologists, are known as perceptual after-effects. If any one of our senses is exposed for some time to a stimulus that is unchanging in a particular attribute (such as colour, direction of movement, temperature), then our subsequent perception of that attribute, or our capacity to detect it, is briefly altered. Interest in these curious phenomena has recently revived and it is significant that much of the experimental work has been done in physiological, rather than psychological, laboratories. What has seduced sensory physiologists from their rightful trade?

In the case of animals it is possible, with very fine electrodes, to record the responses of individual nerve cells and it has become clear that sensory systems contain many specialised mechanisms that are apparently designed to extract particular features or attributes of the external stimulus (see "Why we see what we see", by Colin Blakemore, New Scientist, vol 51, p 614). The visual system, for example, could be regarded as several sense-organs rather than one, for experiments on animals have shown it to contain individual nerve cells that respond only to edges of a particular orientation, or only to movement in a particular direction, or only to a particular colour, or only to stimuli at a given distance from the eyes. Often the specificity is to conjunctions or disjunctions of the attributes of the stimulus.

How to produce a perceptual after-effect from the cover-design

Place the cover upright in good illumination. From a distance of about two feet, gaze at the red and green pattern for about three minutes. Do not let your eye rest on any one point for very long and try to look equally often at red and green areas.

If then you look at one of the uncoloured patterns, you should see illusory colours that vary according to the orientation of the tilted lines: where the lines are tilted to the right you will see pinks and where they are tilted to the left you will see pale greens. Don't expect the illusory hues to be very strong: the effect is scientifically, rather than phenomenally, striking. Try tilting the cover, or your head, 90 degrees to one side: the apparent colours should exchange positions.

One of the most remarkable aspects of the phenomenon is its persistence. Try testing yourself again after half an hour. If you gaze at the coloured figure for rather longer than three minutes—for, say, quarter of an hour—you may produce an effect that survives for days or weeks.

To obtain the basic effect some readers will need to look at the coloured pattern for a little longer than three minutes, some for a little less. Since the phenomenon, once established, is very stable, it does no harm to glance occasionally at the uncoloured patterns.

There is every reason to suppose that man's sensory systems are organised in the same way, but here we must use the methods of the experimental psychologist. Can sensory after-effects help us to discover the sensory dimensions that are important to our own sense-organs and to our own brain? Can they reveal, in other words, which attributes of a complex stimulus are singled out for neural analysis? If one suspects that a particular attribute of the stimulus is subject to specialised analysis, then the principle is to try to fatigue, or "adapt", selectively the neural mechanism tuned to detect that particular attribute. At its most naked, and within the privacy of the laboratory, the argument runs "If you can adapt it, it's there".

It was the validity of this argument that was discussed at a symposium held recently in London by the British Psychological Society. Let us first consider some examples of adptation and after-effect that were examined during the symposium and which do reveal some possibly unexpected properties of perceptual systems.

Colin Blakemore, of the Cambridge Physiology Department, suggested that there may be neural channels in the visual system that are tuned to the *spatial frequency* of the stimulus. (The gratings of Figure 1A differ in "spatial frequency".) By following the instructions in Figure 1 you should be able to adapt selectively these putative channels in your own visual system and so change the apparent density of the test patterns (Figure 1B). Nerve cells—neurones—tuned to particular spatial frequencies have in fact been discovered in the visual systems of animals. Yet what would be their rôle in perceptual analysis? Some believe that these analysers of spatial frequency are directly responsible for pattern recognition and that, in engineering terms, the visual system performs a spatial Fourier-analysis of the retinal image. On the other hand, the density of texture of a surface (and that is what spatial frequency may amount to) may be on a par with colour: especially in mammals that do not enjoy colour vision, density of texture may be important in the separation of figure from ground and of one object from another, a separation that is a preliminary to the perception of form. In addition, *gradients* of texture density are critical to our judgements of distance.

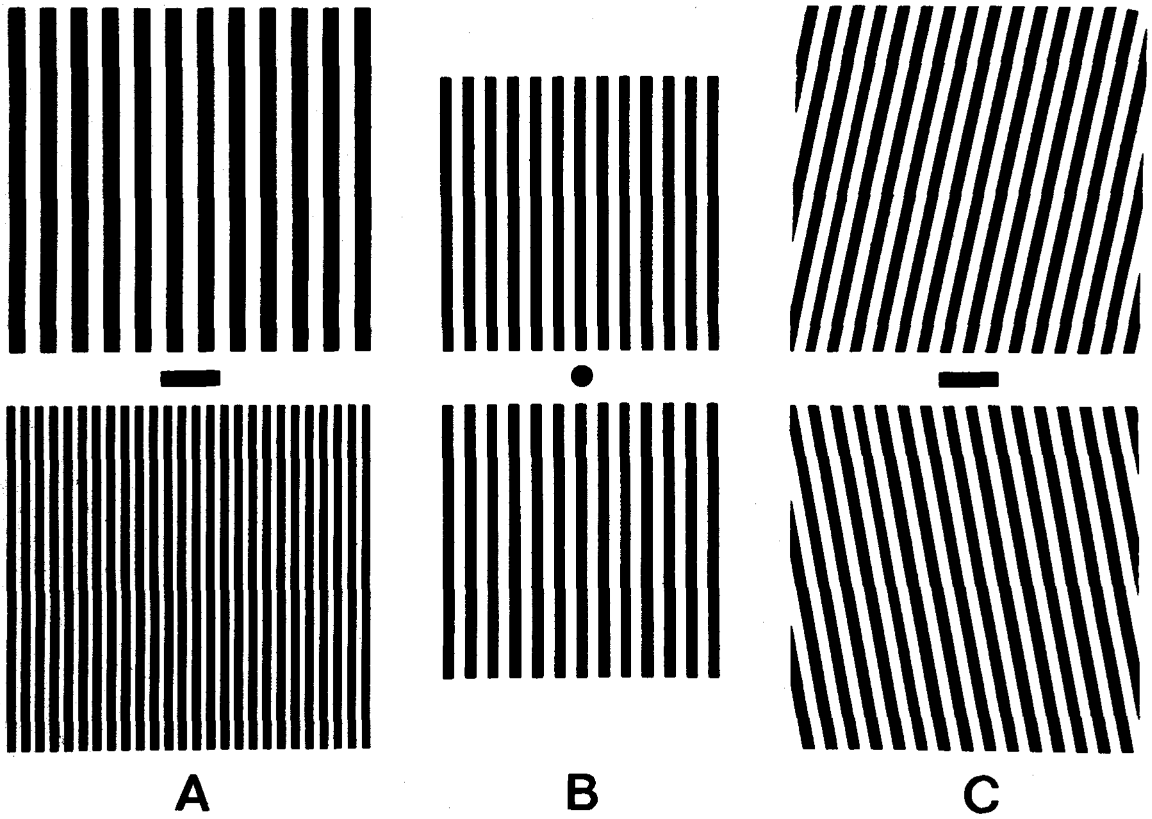


Figure 1 To obtain an after-effect of spatial frequency, move away from the page until the finest grating is still just clearly resolvable and gaze for about one minute at the horizontal bar of Figure A. Keep your eye moving to and fro along the bar in order to avoid producing an ordinary after-image. Then switch your gaze rapidly to the central spot of Figure B. For a moment the upper grating of B will look denser while the lower grating will appear coarser. To obtain the tilt after-effect, gaze for about 30 seconds at the central horizontal bar of Figure C, again moving your eye along the bar. Then look rapidly at the central spot of Figure B. For a moment the vertical bars of Figure B will appear tilted in directions opposite to those of the adapting gratings in Figure C. If you have difficulty in securing either effect, try adapting for longer periods or try viewing from a different distance

Using Figure 1C you can also experience one of the most celebrated of all visual after-effects: J. J. Gibson's "tilt after-effect". Long before it was possible to record from the mammalian visual system with microelectrodes and thus before it was known that there are neurones that respond only to bars or edges in particular orientations, Gibson drew upon the tilt after-effect to argue that the orientation of a line should be regarded as a simple sensory quality, comparable, in fact, to brightness and to colour.

If we judge by our knowledge of visual pattern-recognition, relatively little is known of the acoustic features that are critical in the identification of complex sounds; and much auditory research has been concerned with peculiarly unnatural stimuli, pure sinusoidal waves of unchanging frequency. However, in the auditory system of the cat there are individual neurones that respond only to a particular direction of change of frequency (that is, either to rising or to falling pitch) or only to a sound that is modulated in frequency (that is, to a sound that would be subjectively heard as a warble). R. H. Kay, of the physiology department of Oxford University, described at the recent meeting how adaptational techniques may reveal similar neural channels in man. If an observer listens for some time to an adapting tone that varies sinusoidally in frequency, then immediately afterwards his capacity to detect a weak modulation at the same frequency will be reduced: the modulation must be about three times deeper than it normally has to be if he is to report whether the tone is varying or not. This is true only if the modulation frequencies of the adapting and testing tones are the same or very similar. The channels that are being adapted are apparently quite narrowly tuned to the frequency of modulation, but are not critically concerned with the "carrier" frequency, the frequency around which the tone is modulated. From further experiments, Kay and his collaborators conclude that an important factor in adapting the channels is rate of change of frequency, for, at low modulation-frequencies, similarity of the modulating waveform is important. The detectability of a sinusoidal modulation of frequency is lowered by adaptation to triangular wave modulation at the same frequency, but not by adaptation to square-wave modulation; and sinusoidal modulation of amplitude does not affect the detectability of frequency-modulation.

Peter Bailey, of the Queen's University, Belfast, has asked whether the adaptational method can disclose the features that we use in discriminating the sounds of speech. As stimuli he used artificially-generated syllables, each consisting of a consonant and a vowel: Figure 2 helps to explain how they were constructed. The syllables /ba/ and /da/ differ in *place of articulation,* that is, in the place along the vocal tract where constriction occurs (for /ba/ it is at the lips, and for /da/, behind the teeth). Physically the two syllables differ in the direction in which their higher component frequencies are changing during the first few milliseconds after onset (see Figure 2A). Bailey generated a series of stimuli, numbered 1 to 10 in the diagram. It is a remarkable characteristic of speech perception that a physical continuum of this kind is not perceived as continuous: in fact, our identification switches abruptly from /ba/ to /da/ around the middle of the range. In Bailey's experiment the adapting stimulus was drawn from one or other end of the series of stimuli and was played 40 times to the subject. After adaptation to /ba/ an intermediate stimulus was more likely to be perceived as /da/, and vice versa. What exactly is being adapted? It does not seem to be an abstract mechanism detecting "place of articulation", for adaptation to /ba/ has only a slight effect on the perception of an intermediate syllable in the range /bɛ/ to /dɛ/. The neural detector that is being adapted must be concerned with changes only in a specific range of frequencies.

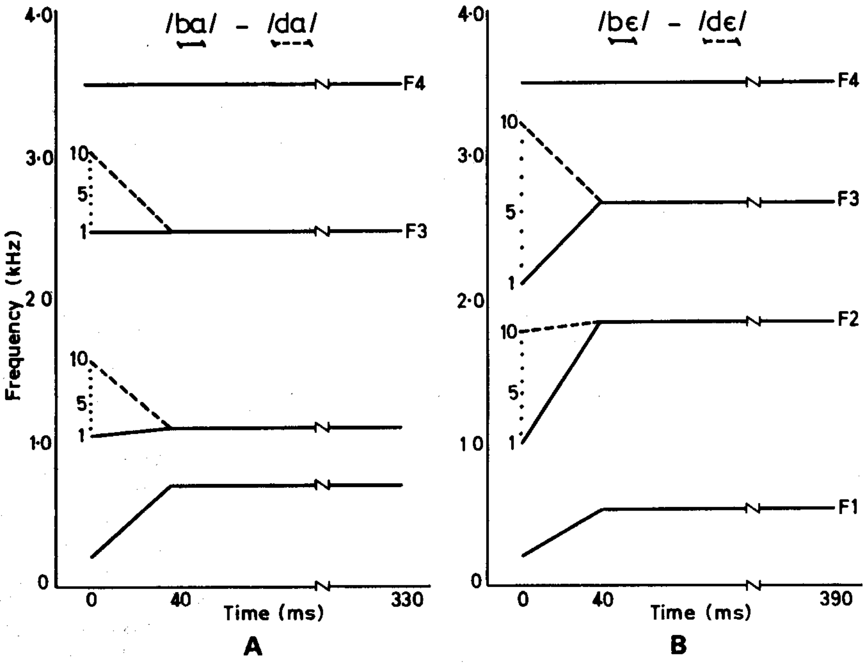


Figure 2 Schematic representation of the artificial syllables used in Bailey's experiment. The left-hand diagram shows the four main frequency-bands ("formants") that make up the speech sounds we perceive as /ba/ and /da/; the right-hand figure corresponds to /bɛ/ and /dɛ/. How we perceive the initial consonant depends on the direction in which frequency is changing during the first few milliseconds

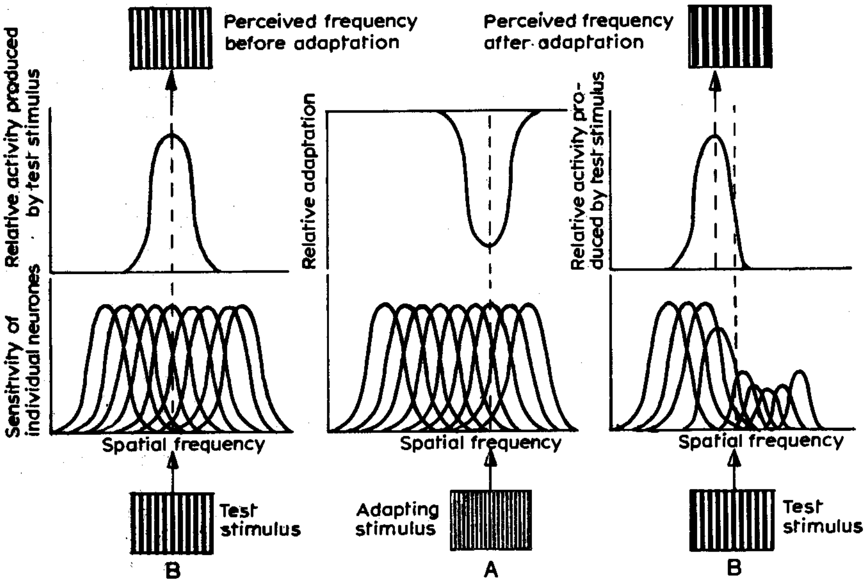


Figure 3 Qualitative model of how after-effects occur when coding is by place. The details are explained in the text

Can after-effects tell us more than that something exists to be adapted? Cautiously interpreted, they may reveal details of neural organisation, of how a particular attribute of the stimulus, such as colour or direction of movement, is represented in the brain. Psychologists believe that there are two principal ways in which information is transmitted in sensory systems. First, different values on a stimulus dimension may be represented by which of a set of neurones is active: thus different neurones may correspond to different spatial frequencies or to sounds of different pitch. This kind of coding is known as *coding by place.* Secondly, different values on a sensory dimension may be represented by the frequency of nerve impulses in a single neurone. This representation is known as *frequency coding.*

It is on the basis of these two types of neural representation that we can best classify and explain after-effects. Figure 3, which is based on a hypothesis first introduced by Georg von Békésy in 1929, shows how aftereffects may arise when coding is by place. We would take the dimension of spatial frequency as an example. We must first make the assumptions that the neurones representing different values on the dimension have overlapping sensitivities and that decisions by later mechanisms are based on the position of peak activity in this series. Prolonged exposure to a particular value on the dimension (A in the Figure for example) will depress the corresponding neurones to an extent that is inversely related to their response to the adapting stimulus. If we now present a test stimulus (B) that lies to one side of A, the activity it produces must be weighted by the adaptation left by A. So the peak of activity produced by B, and thus perhaps its phenomenal appearance, will be displaced away from A. If, however, the test stimulus is coincident with A, it will not be displaced (provided there are no asymmetries in the tuning curves of individual neurones in the series). Thus stimulus dimensions coded by place will show the "distance paradox": the maximum after-effect will be for stimuli some distance along the dimension from the adapting stimulus. Appropriate measurements are available for the Blakemore-Sutton effect of Figure 1A and indeed distortion is greatest for test gratings lying one half to one octave either side of the adapting frequency. If an after-effect shows a "distance paradox", then that sensory dimension is probably coded by place.

If coding is by frequency and the same nerve cells are always involved, then adaptation at any point on the sensory dimension will reduce sensitivity at all points on the dimension. But here we must introduce a further subdivision of after-effects. Some sensory dimensions, such as temperature (warm-cold), brightness-darkness, direction of movement and direction of curvature, are bipolar or oppositional: the continuum has a central null-point at which neither of the complementary or antagonistic qualities is present. It is such dimensions that give rise to some of the most intriguing of after-effects, the class properly called "negative after-effects": if, for example, one gazes for a short time at bars moving left and if they are then suddenly stopped, they will appear to move right. Moreover, in contrast to what happens in the case of dimensions coded by place, the perceived attribute will change during the adapting period itself: colours will come to look less saturated, warm water will feel less warm and curved lines will look less curved. Figure 4 shows schematically how this type of after-effect may arise for the case of movement.

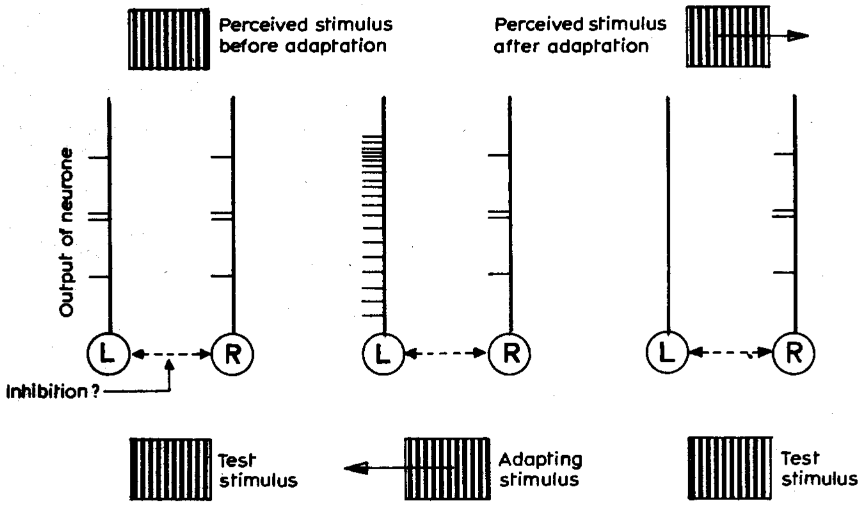


Figure 4 Exner's explanation of the after-effect of seen movement. Before adaptation both neurones are spontaneously active; after adaptation only R is active

Hypothesis can be found quite explicitly as early as 1894 in the writings of the neglected but extraordinarily prescient psychophysiologist, Sigmund Exner. The figure shows two neurones, L and R, one sensitive to movement to the left, the other sensitive to movement to the right. We have to assume that when their outputs are equal the brain takes the stimulus to be stationary. During prolonged stimulation by stimuli moving to the left, the response of neurone L slowly wanes. When stimulation ends the neurone will be depressed for several seconds and an imbalance in the spontaneous activity of L and R may be treated by the brain as movement to the right. Alternatively, L and R may be linked by mutual inhibition and, after adaptation, R may be transiently released from the inhibition of L. This kind of mechanism is called an "opponent-process" system.

There are difficulties. First some sensory dimensions, such as tilt or the velocity of visual movement, behave in some ways as if they were coded by place but also have oppositional qualities; and colour is almost certainly coded by place and by opponent processes at different levels of the visual system. Second, a neurone can be adapted even if it does not itself respond to the adapting stimulus. For instance, David Tolhurst, of the Cambridge physiology department, has found evidence that the physiological basis of after-effects is not the simple fatigue of the stimulated neurone but rather the active inhibition by that neurone of itself and of neurones tuned to adjacent points on the same sensory dimension.

Most curious of all are the "contingent" after-effects. The first was introduced by Celeste McCollough in 1965 and they have since multiplied with eponymous promiscuity. The reader is invited to try out the McCollough effect for himself, following the instructions given on page 479. This mysterious effect cannot be explained by ordinary after-images, since any particular point on the retina has been stimulated equally by red and green light during the period of adaptation. The illusory hues are "contingent": that is, they are seen only when grids of appropriate orientation are present in the visual field. Analogous after-effects of colour have been found that are contingent on direction of movement, on spatial frequency, on sense of curvature and possibly even on shape. It has been argued that these contingent after-effects reveal analysing mechanisms with multiple specificity. At the BPS meeting Professor Ray Over, from the University of Queensland, discussed how the McCollough effect might be explained in terms of individual nerve cells that respond to stimuli of a particular orientation and of a particular hue. During the adapting period there occurs a selective adaptation of neurones specific, for example, to green bars tilted 45 degrees to the right and of others specific to red bars tilted to the left. We have to assume that the apparent colour of a grating normally depends on the relative activity of orientation-detectors tuned to different colours. When the cells specific to green bars tilted right are depressed by adaptation, a black and white grating tilted right will appear pink. Professor Over argued that the detectors specific to both orientation and colour do not receive inputs from both eyes. For, if adaptation is confined to one eye, the McCollough effect is not seen when the other eye is tested (the reader may wish to check the truth of this for himself); and indeed, contradictory McCollough effects can be simultaneously established in the two eyes.

The number and complexity of contingent after-effects and their strange persistence suggest that they are in some ways more akin to the phenomena of conditioning than to sensory adaptation. If we do not have neurones specific to colour and orientation before we look at the cover, perhaps we do when we have finished.