bacteria thus yielded an electron donor–acceptor couple required to stimulate sulphate reduction. Sulphate-reducing bacteria were thus apparently much less numerous in shales, but abundant and electron-donor-limited in sandstones.

The known interdependence of fermenters and sulphate-reducing bacteria suggested that a relatively complex microbial community was present. Organisms with other metabolic capabilities (such as methanogens and acetogens) could also be important in this system. No methane production could be measured in the sandstone–shale slurries, but acetate was produced in all incubations (Fig. 3), with the amount of acetate being far greater in sandstone slurries amended with shale than in incubations receiving only sandstone or shale. Pure cultures of both acetogenic and sulphate-reducing bacteria were also isolated from the rock material on the basis of their ability to grow by using hydrogen as the electron donor (L.R.K., unpublished results), providing further evidence for the existence of these processes in the sandstone units.

These results suggest an explanation for the presence of spatially discrete microbial ecosystems at sandstone–shale interfaces which are fuelled by organic matter deposited during the Cretaceous period. A similar model has been proposed for unconsolidated clay/sand aquifers of the late Cretaceous period[14–16]. Our results build on this previous work, but in addition demonstrate that organic material can diffuse from shales to sandstones in consolidated rock, creating isolated microbial communities that exist in a narrow band near this interface. Such microbial communities are probably not unique to this Cretaceous lithologic system: they may exist near many other formations where biodegradation of organic carbon was constrained following deposition, and where adjacent higher-porosity sediments can help migration of microbial energy sources (see ref. 17, for example). Successional events could then select for the metabolic capacity to use the nutrients diffusing from adjacent sediment layers. Our results have far-reaching implications, in that they suggest that there are large areas of undiscovered biomass growing on ancient nutrient-rich deposits within isolated subsurface sedimentary rocks. They also explain the long-term survival of microbial communities in the subsurface and justify searching for microbial life in unexplored environments. □

Methods

Radioisotope imaging of sulphate-reduction activity. All manipulations were done in an anaerobic glove box under a nitrogen:hydrogen (5% H_2) headspace. Rock cores were fractured to reveal a new face, and $^{35}SO_4^{2-}$ (10 μCi per core) was applied to the core face by dripping 100 μl of 100 μM Na_2SO_4 solution on to it. After pretreatment of silver foils (8 cm × 8 cm) by washing consecutively with ethanol, acetone and hexane, the surface was oxidized in concentrated nitric acid. Foils were then washed in water, rewashed with the solvents, dried and autoclaved. The foil was then placed on the core face; the rock core was reassembled along fracture lines, clamped in position and incubated for 6 weeks. The foil was then washed with water to remove sulphate and the labelled sulphide adhering to the foil surface was analysed by radio-image analysis (Packard Instruments).

Analyses. To measure sulphate reduction, serum bottles were incubated with 5 ml filter-sterilized groundwater (obtained from the Cubero sandstone formation and amended with 10 μCi $Na_2^{35}SO_4$, resazurin (1 mg l^{-1}), NH_4Cl (20 mg l^{-1}) and K_2HPO_4 (10 mg l^{-1}) and adjusted to pH 7.6 by the addition of CO_2 to the headspace) and 0.75 g of ground sediments from 213 m depth or 1.5 g of sediments from 247 m. Original sulphate in these incubations was ~3.0 mM. To be certain that contamination of sediments did not occur from the surface of cores that had been exposed to drilling fluids, sediments were ground by drilling from the centre of the newly exposed face of the core with a sterile masonry drill bit; in this way, the grinding process did not pick up any rock from near the surface of the core. This experiment was repeated with sediments ground using a mortar and pestle rather than a drill bit, with similar results (data not shown). No activity was detected in autoclaved controls. Fluorescent microspheres were used as tracers during the drilling of these samples. No contamination of the 213-m sample could be detected. Slurry

subsamples (0.5 ml) were periodically removed and Cr(II)-reducible sulphur (sulphides, pyrite and sulphur) were measured using a modification of the procedure of Fossing and Jorgensen[18]. The sample was added directly to a stoppered 120-ml serum bottle containing 5 ml 1 M Cr(II)Cl$_2$ and 2.5 ml concentrated HCl. A 5-ml test tube containing 2.5 ml 10% zinc acetate was also in the bottle to act as a trap for volatilized sulphide. After a 3-day incubation, the trap was removed and the radioactivity counted. This technique traps sulphur from sulphides and pyrite with almost 100% efficiency[19]. Acetate was determined using a Dionex ion chromatograph (Dionex Instruments, CA). TOC was determined by difference from measurements of total and carbonate carbon. Total carbon was determined by combustion using a Leco carbon analyser, and carbonate carbon by digestion and titration (Method ASTM 513 Section G).

1. Pederson, K. *Earh-Sci. Rev.* **34**, 243–260 (1993).
2. Beeman, R. E. & Suflita, J. M. *Microb. Ecol.* **14**, 39–54 (1987).
3. Balkwill, D. L., Fredrickson, J. K. & Thomas, J. M. *Appl. Environ. Microbiol.* **55**, 1058–1065 (1989).
4. Amy, P. S., Haldeman, D. H., Ringelberg, D. B., Hall, D. H. & Russell, C. *Appl. Environ. Microbiol.* **58**, 3367–3373 (1992).
5. Lipman, C. B. *Science* **68**, 272–273 (1928).
6. Turner, H. G. *Science* **76**, 121–122 (1932).
7. Farrell, M. A. & Turner, H. G. *J. Bacteriol.* **23**, 155–162 (1932).
8. Fredrickson, J. K. & Phelps, T. J. in *Manual of Environmental Microbiology* (eds Knudsen, G., Stetzenbach, L., McInerney, M. M. & Walter, M.) 526–540 (Am. Soc. Microbiol., Washington, 1996).
9. Fredrickson, J. K. *et al. Geomicrobiol. J.* (in the press).
10. Kauffman, E. B. in *Treatise on Invertibrate Paleontology A* (eds Robinson, R. A. & Teichart, C.) 418–487 (Geol. Soc. Am., Boulder and Univ. of Kansas, Lawrence, 1979).
11. Pegram, P. thesis, New Mexico Inst. Mining and Technol. (1995).
12. Chambers, L. A. & Trudinger, P. A. *Geomicrobiol. J.* **1**, 249–293 (1979).
13. Sharma, P. K. & McInerney, M. J. *Appl. Environ. Microbiol.* **60**, 1481–1486 (1994).
14. McMahon, P. B. & Chapelle, F. H. *Nature* **349**, 233–235 (1991).
15. McMahon, P. B., Chapelle, F. H., Falls, W. F. & Bradley, P. M. *J. Sedim. Petrol.* **62**, 1–10 (1992).
16. Chapelle, F. H. & Lovley, D. R. *Appl. Environ. Microbiol.* **56**, 1865–1874 (1990).
17. McKinley, J. P. *et al. Geomicrobiol. J.* **14**, 23–39 (1997).
18. Fossing, H. & Jorgensen, B. B. *Biogeochemistry* **8**, 205–222 (1989).
19. Ulrich, G. A., Krumholz, L. R. & Suflita, J. M. *Appl. Environ. Microbiol.* **63** (in the press).

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Visual decomposition of colour through motion extrapolation

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The perception of yellow has played a central role in distinguishing two main theories of colour vision. Hering proposed that yellow results from the activation of a distinct retinal–neural mechanism, whereas according to the Young–Helmholtz–Maxwell view, yellow results from the combined activation of red and green cone mechanisms[1]. When red and green images are presented separately to corresponding retinal locations in the two eyes, the resulting sensation is yellow[1,2]. As the pathways from the two eyes do not converge until the cortex, this suggests that yellow can indeed arise from the central combining of separate red and green channels[2]. I now show that the reverse process can also occur; the visual system can decompose a 'yellow' stimulus into its constituent red and green components. A 'yellow' stimulus was created by optically superimposing a flashed red line onto a moving green bar. If the bar is visible only briefly, the flashed line appears yellow. If the trajectory of the green bar is exposed for sufficient time, however, the line is incorrectly perceived to trail the bar, and appears red. Motion processing occurs in the cortex rather than the retina in primates, and so the ability of motion cues to affect the perception of colour is consistent with the Young–Helmholtz–Maxwell notion of a 'central synthesis' of yellow.
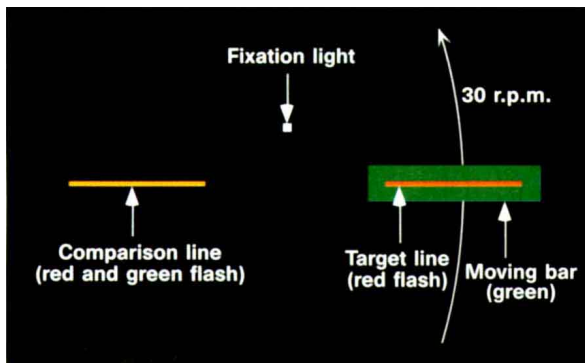
Figure 1 The physical display. Background luminance was 0.00 cd m^{-2}. A comparison line (red + green components) and a target line (red) were simultaneously flashed for 2 ms. The intensity of the comparison line's green component and the intensity of the green bar could be varied. The red target line and the red component of the comparison line were identical and invariant. Arbitrary intensities of the green bar and the comparison line's green component are shown. All coloured stimuli were produced with broadband filters. The green filter had zero transmittance cut-offs at 492 and 580 nm (peak 528 nm); the red filter had a cut-off at 592 nm (peak > 660 nm). For further filter specifications, see ref. 29. The fixation light was located 0.48° above the midpoint between the lines.

It is predominantly believed that colour and motion are processed by independent neural channels[3-6], but there are findings that the motion system can be stimulated by borders defined solely by chromatic contrast[7]. Humans can use colour to reliably distinguish the movement direction of very briefly exposed stimuli, further supporting the view that colour can independently contribute to motion perception[8]. The following display describes a previously unknown interaction between the mechanisms of colour and motion.

A green bar moved on a circular path on a dark background, while two lines, a comparison and a target, were flashed simultaneously for 2 ms. The target line was red and its flash was superimposed on the green bar (Fig. 1). Observers changed the colour of the comparison line to match that of the target line. The comparison line had a red component that was identical to the target line, and a green component that could be adjusted by the observer from zero intensity (resulting in a red comparison line) to maximum (resulting in a green–yellow comparison line). A green and a red filter (transmittance peaks 528 nm and >660 nm, respectively) were used to produce the coloured stimuli.

Initially, the green bar was exposed at the location of the red target line so briefly that it appeared motionless. The comparison line was fixed at the green-yellow colour (maximum intensity of the green component) in this 'brief exposure' condition, and the bar intensity was changed until observers indicated a colour match between the lines (Fig. 2a). This bar intensity, determined for each observer, was next used in the 'extended exposure' condition in which the full trajectory of the bar was exposed (Fig. 2b). Observers now adjusted the colour of the comparison line to match that of the target line. Were the observers' matches based on the spectral composition of the target line, the comparison line's green component should have been set to the same value in the brief and extended exposure conditions. In other words, the green components of the comparison lines in Fig. 2a, b should have been set to the same (maximum) value. However, in the extended exposure condition the comparison line's green component was set to one fifth its maximum value. Thus, despite equal quantal absorption in the cones, the colour of the target line was perceived as green–yellow with brief exposure, and as reddish with extended exposure of the bar. Figure 3 shows data for three observers. In addition, observers reported on the perceived location of the target line relative to the bar. Consistent
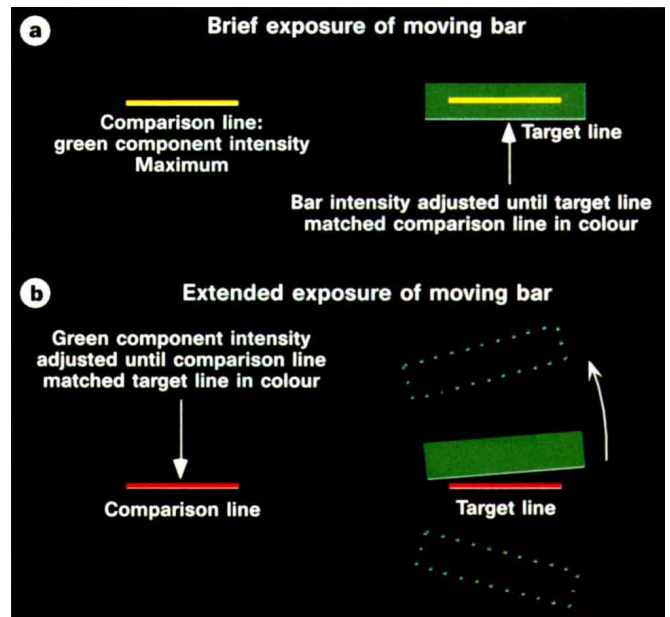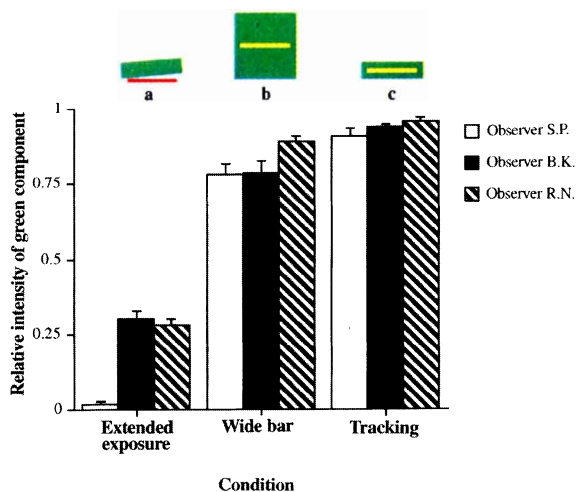

Figure 2 The brief- and extended-exposure conditions. **a**, In the brief-exposure condition, the comparison line's green component was fixed at its maximum intensity. The intensity of the green bar was changed until the observer reported that the colour of the target line matched that of the comparison line. With brief exposure, observers perceived the target line to be superimposed on the bar and its colour to be yellow. **b**, In the extended-exposure condition, the intensity of the green bar was fixed. Observers changed the intensity of the comparison line's green component until the colour of the comparison line matched that of the target line. With extended exposure, the target line appeared on the dark background, spatially lagging behind the green bar, and its colour appeared red. Note that in the experiment the spectral composition of the target line, and the target line's physical position relative to the bar, were identical in **a** and **b**.

with previous findings[9,10], the target line appeared to be superimposed on the bar in the brief-exposure condition (Fig. 2a), and on the background, trailing the bar, in the extended-exposure condition (Fig. 2b).

Could the bar's perceived motion *per se* have caused the target line to appear red, or is the perceived separation between the target line and the bar crucial? The smaller dimension of the bar was scaled up by a factor of ten so that the target line would appear superimposed on the bar, even while the bar was seen in motion. The colour matches obtained in this 'wide-bar' condition show only a slight tendency of the target line to appear red (Fig. 3), which suggests that the significant factor is the apparent non-overlap of the line and the bar. The wide-bar condition also eliminates the potential factors of chromatic adaptation[11] such as stray light from the green bar producing adaptive effects that dominate its colour mixing effects[12], and unmeasured eye-drifts causing prolonged retinal stimulation by green light.

The primate visual system is characterized by significant transit delays of neural signals between the photoreceptors and higher cortical areas. As a result, a moving object's retinal image location should lead the object's neural representation in any retinotopically organized cortical map. However, it has been suggested that an 'early' visual operation, mathematically akin to extrapolation, corrects for cortical lag and restores position correspondence between different processing levels for predictably moving objects[10,13]. There is evidence suggesting that a mechanism for motion extrapolation might be present even in other animals, such as frogs[14]. As a result of motion extrapolation, the retinotopic site in the cortex maximally activated by a moving object at any given instant is the same as would be activated by a stationary object

Figure 3 Three observers, two experienced (B.K and R.N.) and one naive (S.P.), participated. The average bar intensity that produced a colour match between the lines in the brief-exposure condition for S.P., B.K. and R.N. was 1.41, 1.91 and 1.25 cd m^{-2}, respectively. The maximum intensity of the comparison line's green component, which caused the line to appear green-yellow, is represented as '1' on the ordinate. The average intensity of the green component set by the observers, in the extended-exposure, wide-bar, and tracking conditions, is reported as a proportion between 0 and 1. In the 'extended-exposure' condition (motion visible) the value of the comparison line's green component set by the observers was, on average, one fifth its maximum value. The 'wide-bar' condition (motion visible) tested the role of motion *per se* in causing the red appearance of the target line. The 'tracking' condition, which restored alignment between the moving green bar and the flashed target line, tested the role of spatial separation. In both the 'wide-bar' and 'tracking' conditions the green bar was sensed as moving, but the target line appeared to overlap the bar. These conditions produced only a small shift in the appearance of the target line towards red, suggesting that spatial separation was the crucial factor. Inset **a**, the observers' percept in the 'extended-exposure' condition–the target line appeared red and not to overlap the green bar. Inset **b**, the percept in the 'wide-bar' condition–the target line appeared yellow and to overlap the bar. Inset **c**, the percept in the 'brief-exposure' and 'tracking' conditions – the target line appeared yellow and to overlap the bar in both.

located where the moving object is at that instant. In contrast, a brief flash is unpredictable and the nerve impulses triggered by the flash arrive in the cortex after the expected delay. Thus, at a given time the flash and the moving object stimulate separate retinotopic locations in the cortex, with the moving object in a leading position. This is the basis of the observers' perception that the moving bar leads the flashed target line.

This extrapolation and delay hypothesis has further support in that smooth pursuit of the moving item restores its alignment with the flashed item (R.N., manuscript in preparation). The retinal displacement of a flashed object, while the eyes are tracking, will be insignificant—0.8-μs flashes have produced comparable results. It is known that eye position and perceived location of retinally stable objects, like ordinary after images, are perfectly correlated. What about flashed objects? The extrapolation and delay hypothesis assumes identical processing of flashed and moving items during smooth pursuit and fixation. However, eyes in pursuit can rotate significantly in the time it would take photoisomerizations triggered by the flash to culminate in cortical signals[15]. It is suggested that, like after images, flashed objects are also seen in the direction in which the eyes point. As the eyes, by definition, always point towards the tracked object, the flash appears to overlap the moving object. A further prediction of this hypothesis, that a flashed object should appear displaced in the direction of pursuit relative to a stationary target, has been experimentally verified.
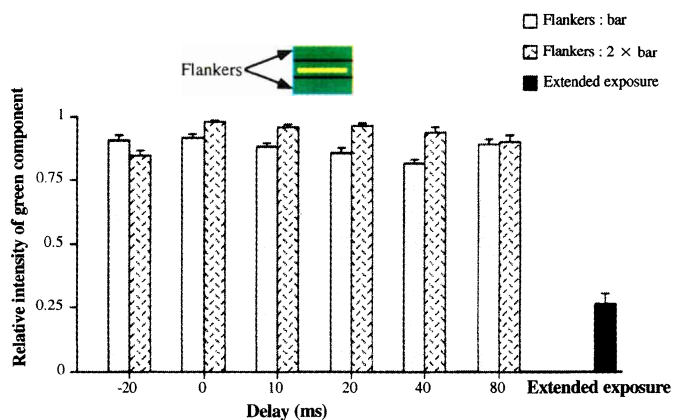
Figure 4 Abscissa, time delays between the flash of the lines and the flash of the flanker masking bars. A negative delay indicates that the flankers were flashed before the lines. Several delays were used to ensure that at least one delay would significantly reduce the original bar's visibility. The observer, as before, matched the colour of the two lines. The height of the data bars corresponds to the intensity of the comparison line's green component that produced a colour match for observer R.N. The right-most data bar corresponds to the extended exposure condition with no flankers. Relative to the extended exposure condition, the other data bars show a relatively small decrease in the intensity of the comparison line's green component. Other observers gave similar results. Each flanking bar in the inset is as wide as the original bar.

The perceived overlap of the flashed target line and the moving green bar obtained with pursuit eye movements was used to test whether the apparent separation between these items is necessary for the colour effect. In the 'tracking' condition, observers were instructed to smoothly pursue the bar and report the location and the colour of the target line. Observers reported the target line to be centred precisely on the bar, and its colour to be yellow (Fig. 3). This outcome further reinforces my finding that the apparent separation of the bar and the target line is critical for the target line's red appearance, and that motion *per se* is not sufficient. The target line's red appearance in the extended-exposure condition may be an instance of the phenomenon of colour constancy[16,17] in which the bar's antecedent colour signals are used to discount its spectral contribution. However, this would predict a similar outcome in the wide-bar and tracking conditions as well, which is not observed.

Flashed and moving items differ in another important way. The visibility of a flashed stimulus persists beyond the physical flash by about 120 ms (refs 18, 19), whereas the 'smear' due to the gradual decay of neural activity left behind by a moving object is not visible to observers. The mechanisms specialized to detect motion also reduce motion smear[20,21]. The green bar signals motion with extended exposure but not with brief exposure. Arguably, the green bar's prolonged visibility in the brief-exposure condition could bias the perceived colour of the target line towards green. Thus, a persisting green bar of lower intensity might produce the same colour shift in the target line as a green bar of higher intensity that does not persist. As the bar intensity in the brief exposure (Fig. 2a) and extended exposure (Fig. 2b) conditions is the same, the colour of the target line could be biased towards red in the latter condition. If this hypothesis is correct, then a similar bias should be observed if the visibility of the bar is reduced by a visual mask[22] in place of motion. A mask consisting of two green bars, presented with a delay of ~40 ms after a target bar, significantly reduces the target bar's visibility[23,24]. The brief exposure condition was modified so that masking bars were presented at several delays to ensure that

the original bar's visibility would be sufficiently reduced for at least one of these delays[25] (Fig. 4). Although the mask was effective, it produced only a slight shift in the target line's colour towards red (Fig. 4), so failing to support the persistence explanation.

Further experiments will reveal the neural basis of this colour phenomenon, which cannot have a retinal origin as the primate retina is unable to distinguish the direction of movement of a target[26]. The effect is probably a by-product of motion extrapolation, which could be accomplished by cortical neurons that demonstrate 'predictive remapping'. For these neurons, the response latency for a target entering the cell's receptive field from some other location is lower than the latency for a target with an abrupt onset in that cell's receptive field[27]. At a given instant, two sets of active cells of this type, one stimulated by a moving object and the other by a retinally superimposed flash, will thus code non-overlapping retinotopic locations. Given the reported interaction between colour and motion, I suggest that some cells that demonstrate predictive remapping are also stimulated by colour input. Finally, my findings not only support the Young–Helmholtz–Maxwell view of colour vision, but also suggest that retinally overlaid red and green signals yield the perception of yellow if, and only if, these signals originate from the same retinotopic locations in the cortex. □

Methods

A d.c. motor connected to a speed controller revolved a green bar ($1.59° \times 0.20°$) anti-clockwise on a circular path (diameter, $7.63°$) at 30 r.p.m. (instantaneous speed, $11.46° \mathrm{s}^{-1}$). Two horizontal lines (length, $1.27°$), separated by $0.91°$, were flashed simultaneously for 2 ms at 0.5 hertz. A mirror-type beam-splitter was used to present the flashed lines in the optical plane of the bar. The flash was synchronized with the bar so that the target line was superimposed on the bar. Observers used a chin rest to view the display binocularly through natural pupils. Ambient room lights were turned on about once every 10 s for a comparable period in order to maintain the observer's light adaptation level and pupil size.

Brief-exposure condition. The bar was visible only through a $1.59° \times 0.20°$ window. The duration of visibility was $\sim$17.45 ms. The colour of the comparison line was held constant at green–yellow. On ten trials the experimenter adjusted the bar's intensity until the observer indicated that the target line matched the comparison line in colour. The average of the bar intensities for each observer was used in all conditions tested.

Extended-exposure condition. The complete trajectory of the green bar was visible. The bar's intensity was set at a value that produced a colour match of the lines in the brief-exposure condition. On ten trials the observer adjusted the intensity of the comparison line's green component to achieve a colour match between the lines.

Wide-bar and tracking conditions. A wide bar ($1.59° \times 2.0°$) was used to test the contribution of motion per se to the colour effect (see text). In the tracking condition, observers used smooth-pursuit eye movements to follow the bar of original size ($1.59° \times 0.20°$).

Persistence reduction through visual masking. Introduction of a visual mask in the brief exposure condition required an additional viewing channel which involved several changes in the optical arrangement. Consequently, the brief and extended exposure conditions were repeated. The mask consisted of two flanking bars, abutting the original bar with no gap or overlap, flashed for 10 ms. Each flanking bar was either $1.59° \times 0.20°$ or $1.59° \times 0.40°$. The intensity of the flanking bars was equated to that of the original bar by using modified 'minimally distinct border' technique[28].

1. Hurvich, L. M. & Jameson, D. The binocular fusion of yellow in relation to color theories. *Science* 114, 199–202 (1951).
2. Hecht, S. On the binocular fusion of colors and its relation to theories of color vision. *Proc. Natl Acad. Sci. USA* 14, 237–241 (1928).
3. Zeki, S. M. The functional organization of projections from striate to prestriate visual cortex in the rhesus monkey. *Cold Spring Harb. Symp. Quant. Biol.* 40, 591–600 (1975).
4. Livingstone, M. S. & Hubel, D. H. Psychophysical evidence for separate channels for the perception of form, color, movement, and depth. *J. Neurosci.* 7, 3416–3468 (1987).
5. Ramachandran, V. S. & Gregory, R. L. Does colour provide an input to human motion perception? *Nature* 275, 55–56 (1978).
6. Cavanagh, P., Tyler, C. W. & Favreau, O. E. Perceived velocity of moving chromatic gratings. *J. Opt. Soc. Am.* 1, 893–899 (1984).
7. Saito, H., Tanaka, K., Isono, H., Yasuda, M. & Mikami, A. Directionally selective response of cells in the middle temporal area (MT) of the macaque monkey to the movement of equiluminous opponent color stimuli. *Exp. Brain Res.* 75, 1–14 (1989).
8. Cropper, S. J. & Derrington, A. M. Rapid colour-specific detection of motion in human vision. *Nature* 379, 72–74 (1996).
9. MacKay, D. M. Perceptual stability of a stroboscopically lit visual field containing self-luminous objects. *Nature* 181, 507–508 (1958).
10. Nijhawan, R. Motion extrapolation in catching. *Nature* 370, 256–257 (1994).
11. Hurvich, L. M. *Color Vision* (Sinauer, Sunderland, Massachusetts, 1981).
12. Walraven, J. Spatial characteristics of chromatic induction; the segregatin of lateral effects from straylight artefacts. *Vision Res.* 13, 1739–1753 (1973).
13. Khurana, B. & Nijhawan, R. Extrapolation or attention shift? *Nature* 378, 565–566 (1995).
14. Aho, A.-C., Donner, K., Helenius, S., Olesen Larsen, L. & Reuter, T. Visual performance of the toad (*Bufo bufo*) at low light levels: retinal ganglion cell responses and prey-catching accuracy. *J. Comp. Physiol.* 172, 671–682 (1993).
15. Richards, W. Visual suppression during passive eye movement. *J. Opt. Soc. Am.* 58, 1159–1160 (1968).
16. Land, E. H. & McCann, J. J. Lightness and the retinex theory. *J. Opt. Soc. Am.* 61, 1–11 (1971).
17. Gilchrist, A. The perception of surface blacks and whites. *Sci. Am.* 24, 88–97 (1979).
18. Efron, R. The minimum duration of a perception. *Neuropsychologia* 8, 57–63 (1970).
19. Hogben, J. H. & Di Lollo, V. Perceptual integration and perceptual segregation of brief visual stimuli. *Vision Res.* 14, 1059–1069 (1974).
20. Burr, D. Motion smear. *Nature* 284, 164–165 (1980).
21. Morgan, M. J. Perception of continuity in stroboscopic motion: A temporal frequency analysis. *Vision Res.* 19, 491–500 (1979).
22. Kahneman, D. Method, findings, and theory in studies of visual masking. *Psychol. Bull.* 70, 404–425 (1968).
23. Alpern, M. & Rushton, W. A. H. The specificity of the cone interaction in the after-flash effect. *J. Physiol.* 176, 473–482 (1965).
24. Yellott, J. I. & Wandell, B. A. Color properties of the contrast flash effect: Monoptic vs dichoptic comparisons. *Vision Res.* 16, 1275–1280 (1976).
25. Di Lollo, V. & Hogben, J. H. Suppression of visible persistence as a function of spatial separation between inducing stimuli. *Percept. Psychophys.* 41, 345–354 (1987).
26. Hubel, D. H. & Wiesel, T. N. Receptive fields and functional architecture of monkey striate cortex. *J. Physiol. (Lond.)* 195, 215–243 (1968).
27. Duhamel, J.-R., Colby, C. L. & Goldberg, M. E. The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255, 90–92 (1992).
28. Boynton, R. M. in *Visual Psychophysics and Physiology* (eds Armington, J. C., Krauskopf, J. & Wooten, B. R.) 193–207 (Academic, New York, 1978).
29. Zeki, S. The representation of colours in the cerebral cortex. *Nature* 284, 412–418 (1980).

Adaptation of retinal processing to image contrast and spatial scale

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Owing to the limited dynamic range of a neuron's output, neural circuits are faced with a trade-off between encoding the full range of their inputs and resolving gradations among those inputs. For example, the ambient light level varies daily over more than nine orders of magnitude[1], whereas the firing rate of optic nerve fibres spans less than two[2]. This discrepancy is alleviated by light adaptation[3]: as the mean intensity increases, the retina becomes proportionally less sensitive. However, image statistics other than the mean intensity also vary drastically during routine visual processing. Theory predicts that an efficient visual encoder should adapt its strategy not only to the mean, but to the full shape of the intensity distribution[4–6]. Here we report that retinal ganglion cells, the output neurons of the retina, adapt to both image contrast—the range of light intensities—and to spatial correlations within the scene, even at constant mean intensity. The adaptation occurs on a scale of seconds, one hundred times