

allometric consequence of increasing body size expressed in a hominid with a pattern of gait widely divergent from that of the African apes.

On the other hand, because of the unique proportions of Lucy's limbs relative to each other, the biomechanical requirements of this gait pattern differed somewhat from those for living people. It is possible that Lucy's limb proportions correspond to a different, perhaps broader, locomotor repertoire than is the case today. If, as claimed above, this difference does not lie in the bipedal gait pattern evidenced by the pelvic and hindlimb adaptations, contra Jungers it might be productive to focus on the unique aspects of the australopithecine forelimb.

I thank D. C. Johanson, J.-L. Heim and C. K. Brain for permission to study the original specimens, E. Trinkaus for permission to examine his casts of the Shanidar specimens, R. C. Bailey, N. R. Peacock and members of the Harvard Ituri Project for providing the Efé height and weight data, and L. Schepartz for measuring the Amerind sample. This work was supported in part by NSF grant BNS 76-82729.

Received 21 March; accepted 4 May 1983.

1. Jungers, W. L. *Nature* **297**, 676-678 (1982).
2. Johanson, D. C. & Edey, M. A. *Lucy, the Beginnings of Humankind* (Simon & Schuster, New York, 1981).
3. Senut, B. *Am. J. phys. Anthrop.* **56**, 275-284 (1981).
4. Lovejoy, C. O. *Yrb. phys. Anthrop.* **17**, 147-161 (1974).
5. Johanson, D. C. *et al. Am. J. phys. Anthrop.* **57**, 403-451 (1982).
6. Reed, C. A. & Falk, D. *Fieldiana, Geol.* **33**, 423-44 (1977).
7. Mann, G. V., Roels, O. A., Price, D. L. & Merrill, J. M. *J. chron. Dis.* **15**, 341-371 (1962).
8. Genovés, S. *Am. J. phys. Anthrop.* **26**, 67-77 (1967).
9. Toerien, M. J. S. *Afr. J. med. Sci.* **19**, 97-104 (1954).
10. Matiegka, J. *Die Bambuti-Pygmäen vom Ituri* (ed. Schebesta, P.) 321-353 (Mem. Inst. R. Colon. Belge, In-4, (1938).
11. Flower, W. H. *J. R. anthrop. Inst.* **18**, 3-18 (1888).
12. Broek, A. J. P. Z. *Morph. Anthrop.* **38**, 121-169 (1940).
13. Shruballs, F. C. *The Uganda Protectorate* Vol. 2 (ed. Johnson, H.) 559-565 (Hutchinson, London, 1902).
14. Bakonyi, M. *Contribution a L'Étude du Squelette des Pygmées (Ba)Mbuti de L'Ituri (Zaire)* (Université de Genève, 1976).
15. Schultz, A. H. *Hum. Biol.* **2**, 303-428 (1930).
16. Olivier, G. *Practical Anthropology* (Thomas, Springfield, 1969).
17. Yamazaki, N., Ishida, H., Kimura, T. & Okada, M. *J. hum. Evol.* **8**, 337-349 (1979).

## Rapid motion aftereffect seen within uniform flickering test fields

M. Green\*, M. Chilcoat† & C. F. Stromeyer III‡

\* Psychology Department, Erindale College, University of Toronto, Mississauga, Ontario, Canada L5L 1C6

† School of Optometry, University of California, Berkeley, California 94720, USA

‡ Division of Applied Sciences, Pierce Hall, Harvard University, Cambridge, Massachusetts 02138, USA

Prolonged viewing of a moving pattern selectively elevates the threshold for a pattern moving in the same direction<sup>1</sup> and induces the classical motion aftereffect (MAE). The aftereffect is seen as a slow drift<sup>2</sup> in the opposite direction, which is visible even with the eyes shut<sup>2,3</sup> or while viewing a uniform field<sup>3,4</sup>. However, as we report here, a strikingly different aftereffect is seen when the test field is uniform and sinusoidally flickered: the field is filled with rapid motion in the direction opposite the adapting motion. This flicker MAE has distinct properties: the adapting grating must be of low spatial frequency; the effect is promoted by high contrast and high temporal frequencies of both adapting and test stimuli; and the aftereffect does not transfer interocularly. In all these respects the flicker MAE differs from the traditional MAE. Motion detectors have been identified in human vision by the threshold detectability<sup>5,6</sup> and discriminability<sup>6</sup> of moving patterns and by selective adaptation. The flicker MAE selectively taps a class of transient motion mechanisms that are selective for rapid motion and low spatial frequency. Uniform flicker is an effective stimulus for these mechanisms. It thus appears that the human visual system contains at least two distinct classes of mechanisms for sensing motion.

Stimuli were displayed on a cathode ray tube (CRT) that had a 6 deg diameter field of constant mean luminance (45 cd m<sup>-2</sup>) with dark surround. The observer stared at a central fixation point and saw a vertical sinusoidal grating that moved rightwards at a rate expressed in Hz. Periodically the adapting grating was replaced by spatially uniform sinusoidal flicker, whose rate (in Hz) was typically the same as that of the adapting grating. The observer pressed a button the instant that the rapid leftward motion aftereffect disappeared from the flickering field. This duration provided a measure of aftereffect strength. Most measurements were done with four to six observers; the results shown here for one or two observers are typical.

For a better impression of the aftereffect, consider the following. The observer adapted to a high-contrast, vertical grating of 0.4 cycle per deg moving rightwards at 8 Hz. The grating filled a 25 deg diameter field, of constant mean luminance. When the adapting grating was turned off, spatially uniform test flicker was presented in only the central 5° of the field. The observer reported that the rapid motion aftereffect was seen only in this central area. However, the aftereffect was seen over the entire field when the flickering region was increased to 25 deg diameter. Thus, the rapid motion aftereffect is seen only on flickering regions, and a very large flickering field may elicit the aftereffect.

Measurements with the 6 deg field demonstrate that the aftereffect is produced only with low spatial frequencies. Figure 1a shows that the aftereffect decreases as the spatial frequency of the adapting grating increases to 3.0 cycles per deg. When the adapting pattern was raised to the next step (4.2 cycles per deg), observer M.C. saw no aftereffect and M.G. saw a fleeting effect that was too brief to measure. The adapting and test rates were 8 Hz, and each adapting grating was 1.3 log units above threshold. Varying the adapting spatial frequency did not seem to change the appearance of the aftereffect, but only affected its duration. The aftereffect is thus obtained only by adapting to patterns below about 4 cycles per deg. This conclusion is reinforced by magnitude estimates<sup>7</sup> of the initial vividness of the aftereffect. The 0.38 cycles per deg adapting pattern produced the most vivid aftereffect, and vividness decreased as the adapting pattern was raised to 3 cycles per deg.

We next measured the effect of temporal frequency with the adapting pattern at 0.38 cycles per deg. Figure 1b shows that the aftereffect is greatest at the highest rates used, 8 and 16 Hz. The adapting and test rates were the same. Very weak effects were obtained when the adapting pattern was 8 Hz and the test

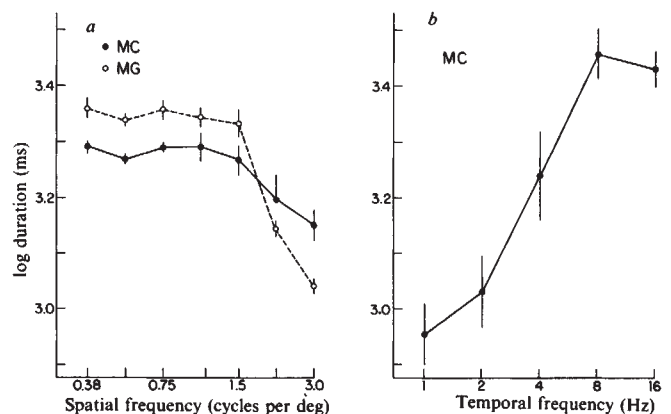
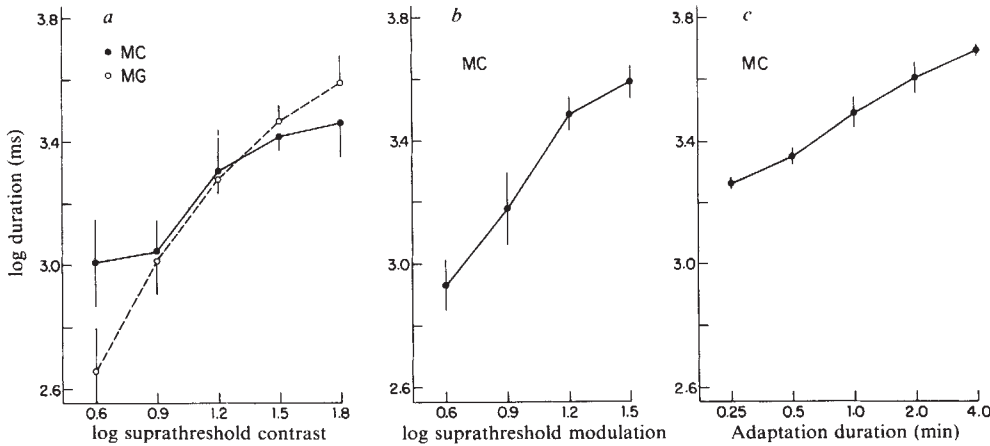


Fig. 1 Duration ( $\pm 1$  s.d.) of flicker MAE—the rapid motion seen on a uniform flickering field after adapting to a rightward-moving grating. In *a*, the spatial frequency of the adapting grating was varied. The rate of motion of the adapting grating and the flicker rate of the test field was 8 Hz. Adapting and test stimuli were set 1.3 log units above threshold. Observers M.C. and M.G. adapted to the moving grating for periods of 15 and 30 s, respectively. In *b*, the moving adapting grating was held at 0.38 cycle per deg, and the rate of motion of the adapting grating was varied. The adapting and test rates were the same. Stimuli were 1.3 log units above threshold, and the adapting period was 90 s.



**Fig. 2** Duration of flicker MAE. The moving adapting grating was 0.38 cycle per deg; the adapting and test rates were 8 Hz. In *a*, the contrast of the adapting grating was varied. The adapting period was 15 s, and the test flicker was 1.1 log units above threshold. In *b* the amplitude of the test flicker was varied. The adapting period was 90 s and the adapting grating was 1.8 log units above threshold. In *c*, the duration of the adapting period was varied. Adapting and test patterns were 1.3 log units above threshold.

1 Hz or vice versa. Thus, for a strong aftereffect, rapid rates are needed in both adapting and test phases.

Further measurements examined the effect of stimulus contrast. The optimum adapting spatial frequency (0.38 cycle per deg) and adapting and test rates (8 Hz) were used. Figure 2*a* shows that the aftereffect increases as the adapting contrast is raised to the highest level used, 64 times the threshold. Figure 2*b* shows that the aftereffect also increases with the amplitude of the test flicker. Magnitude estimations for two observers showed that the initial vividness of the aftereffect was greater when the test flicker was 1.5 log units above threshold as opposed to 1.2 log units. This result was obtained with adapting spatial frequencies from 0.38 to 3 cycles per deg. The increasing strength of the aftereffect with high test amplitudes is surprising as the traditional MAE is strongest with low test contrasts<sup>8</sup>.

The flicker MAE is also distinguished from the traditional MAE by its duration. The latter may last 20 s<sup>9</sup>, several minutes<sup>10</sup> or longer<sup>11</sup>. The flicker MAE is quite ephemeral. Long adaptation periods were used to maximize the aftereffect. The aftereffect lasted less than 5 s after 4 min adaptation (Fig. 2*c*), and the effect was extended to only 7 s with 10 min adaptation (data not shown).

We were unable to obtain interocular transfer of the flicker MAE when the moving adapting grating was presented to one eye and the flickering test field was presented to the other eye with a mirror haploscope and two CRTs. Both the flicker and traditional MAEs were seen, however, when the adapted eye simultaneously viewed a stationary grating and uniform flickering field. The stationary grating appeared to drift slowly, and the flickering component contained rapid motion. When the same test stimulus was presented to the unadapted eye, only the slow drift was seen. It is well known that the traditional MAE transfers interocularly<sup>3</sup>. The flicker MAE transfers poorly if at all.

The most interesting feature of the flicker MAE is its tuning to low spatial frequencies (below 4 cycles per deg). The traditional MAE can be obtained with much finer adapting patterns of 8 or 10 cycles per deg<sup>12,13</sup>, and the direction-selective threshold elevation is present at 15 cycles per deg<sup>14</sup>. The flicker MAE shows that the direction-selective mechanisms tuned to low spatial frequency may respond to uniform flicker. This hypothesis is supported by the finding that adaptation to uniform flicker impairs detection of moving gratings only below 4 cycles per deg<sup>15,16</sup> and moving gratings below 4 cycles per deg mask uniform flicker<sup>17</sup>. Studies<sup>18,19</sup> on threshold summation between low spatial frequency patterns in rapid flicker show that transient, low spatial frequency mechanisms have high sensitivity to uniform flicker. King-Smith and Kulikowski<sup>18</sup> suggest that such mechanisms may be primarily concerned with the detection of motion. There are presumably also motion analysers sensitive to higher spatial frequencies, as demonstrated by the traditional MAE. Various investigators have obtained psychophysical evidence for several types of motion-processing mechanisms<sup>20-23</sup>. Murray *et al.*<sup>24</sup> hypothesize that two specific classes of mechanisms detect motion: fast motion,

transient mechanisms that are sensitive to low spatial frequencies and receive Y-cell inputs and slow motion, pattern mechanisms that are sensitive to higher spatial frequencies and receive X-cell inputs.

The flicker MAE shows that the lowest spatial frequency motion mechanisms are sensitive to uniform flicker and are directionally selective. An intriguing question is whether the majority of mechanisms sensitive to uniform flicker are highly directionally selective. Directional selectivity provides rich information and thus provides an economy of neural encoding.

This work was partially supported by US Air Force Grant F49620-81-K-0016.

Received 2 February; accepted 10 May 1983.

1. Sekuler, R. & Ganz, L. *Science* **139**, 419-420 (1963).
2. Brewster, D. *Trans. Br. Ass.*, 8 (1845).
3. Wohlgenuth, A. *Br. J. Psychol. Monogr. Suppl.* 1 (1911).
4. Grindley, G. C. & Wilkinson, R. T. *Q. J. J. exp. Psychol.* **5**, 183-184 (1953).
5. Levinson, E. & Sekuler, R. *J. Physiol., Lond.* **250**, 347-366 (1975).
6. Watson, A. B., Thompson, P. G., Murphy, B. J. & Nachmias, J. *Vision Res.* **20**, 341-347 (1980).
7. Stevens, S. S. *Psychol. Rev.* **64**, 153-181 (1957).
8. Keck, M. J., Palella, T. & Pantle, A. *Vision Res.* **16**, 187-191 (1976).
9. Pantle, A. *Vision Res.* **14**, 1229-1236 (1974).
10. Taylor, M. M. *Percept. Motor Skills* **16**, 119-129 (1963).
11. Masland, R. H. *Science* **165**, 819-821 (1969).
12. Over, R., Broerse, J., Crassini, B. & Lovegrove, W. *Vision Res.* **13**, 1681-1690 (1973).
13. Keck, M. J., Montague, F. W. Jr. & Burke, T. P. *Invest. Ophthalmol. vis. Sci.* **19**, 1364-1370 (1980).
14. Stromeyer, C. F. III, Madsen, J. C., Klein, S. & Zeevi, Y. Y. *J. opt. Soc. Am.* **68**, 1002-1005 (1978).
15. Green, M. *Vision Res.* **21**, 971-983 (1981).
16. Green, M. *J. opt. Soc. Am.* **70**, 1598 (1980).
17. Green, M. & Schor, C. *Invest. Ophthalmol. vis. Sci. Suppl.* **20**, 178 (1981).
18. King-Smith, P. E. & Kulikowski, J. J. *J. Physiol., Lond.* **249**, 519-548 (1975).
19. Wilson, H. R. *Vision Res.* **20**, 443-452 (1980).
20. Favreau, O. E. *Vision Res.* **16**, 181-186 (1976).
21. Pantle, A. & Picciano, L. *Science* **193**, 500-502 (1976).
22. Bonnet, C. *Perception* **6**, 491-500 (1977).
23. Braddick, O. J. *Phil. Trans. R. Soc. B* **290**, 137-151 (1980).
24. Murray, I., MacCana, F. & Kulikowski, J. J. *Vision Res.* **23**, 151-159 (1983).

## Pioneer axons lose directed growth after selective killing of guidepost cells

David Bentley & Michael Caudy

Department of Zoology and Biophysics Group,  
University of California, Berkeley, California 94720, USA

The first nerve cells to appear in the limb buds of embryonic grasshoppers are a pair which lie at the distal tip and project axons along the length of the limb to the central nervous system (CNS)<sup>1</sup>. The stereotyped route navigated by these 'pioneer' axons is followed by other neurones and eventually becomes that of a major adult nerve trunk<sup>2</sup>. The guidance cues which delineate this route are unknown, but it has been suggested that guidance is provided by a set of nonadjacent 'guidepost' cells along which the pioneers grow (Fig. 1)<sup>1,3-6</sup>. We have now tested this suggestion by selectively destroying identified guidepost cells and observing pioneer axon trajectories in their absence. Our results support the guidepost cell hypothesis.