Proc. Natl. Acad. Sci. USA
Vol. 93, pp. 3689–3692, April 1996
Neurobiology

Temporal events in cyclopean vision

(perception/primary visual cortex/time/flicker-fusion)

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Contributed by Dale Purves, December 12, 1995

ABSTRACT The majority of neurons in the primary visual cortex of primates can be activated by stimulation of either eye; moreover, the monocular receptive fields of such neurons are located in about the same region of visual space. These well-known facts imply that binocular convergence in visual cortex can explain our cyclopean view of the world. To test the adequacy of this assumption, we examined how human subjects integrate binocular events in time. Light flashes presented synchronously to both eyes were compared to flashes presented alternately (asynchronously) to one eye and then the other. Subjects perceived very-low-frequency (2 Hz) asynchronous trains as equivalent to synchronous trains flashed at twice the frequency (the prediction based on binocular convergence). However, at higher frequencies of presentation (4–32 Hz), subjects perceived asynchronous and synchronous trains to be increasingly similar. Indeed, at the flicker-fusion frequency (≈50 Hz), the apparent difference between the two conditions was only 2%. We suggest that the explanation of these anomalous findings is that we parse visual input into sequential episodes.

The singleness of binocular vision is so self-evident that it is easy to overlook its monocular origins. Although binocular cortical neurons are generally thought to be the neural substrate of cyclopean perception (1, 2), very little is known about how monocular information is actually united. We were stimulated to consider this issue by a provocative experiment carried out by Charles Sherrington nearly a century ago (3, 4). Sherrington used the measure of critical flicker-fusion (i.e., the minimum frequency under specified conditions at which a flashing light is perceived as providing continuous illumination) to explore the nature of binocular convergence. He reasoned that if monocular information is united at a single neural locus (the sensory equivalent of the final common pathway that he had established for the mammalian motor system), then the critical flicker-fusion frequency should be reduced to about half the normal value when light flashes are presented alternately to the two eyes (see Fig. 1). (The flash rate here and subsequently refers to the rate presented to one eye).

In the event, Sherrington found only a small difference (2%) between the critical flicker-fusion frequency in the two experimental conditions. He therefore concluded that the views of the two eyes must be united "psychically" by a mechanism that lay outside the province of conventional physiology (refs. 3 and 4; see, also, refs. 5 and 6). These experiments, with minor technical differences, were repeated several decades later by investigators who found a greater (10%) reduction of the critical flicker-fusion frequency in the asynchronous (i.e., out of phase) mode of presentation (7–10). Based on this outcome, C. H. Baker (11) concluded that Sherrington's interpretation was unwarranted. More recently still, Cavonious (12) has also disputed Sherrington's conclusion (although not his data), based on his demonstration of binocular interactions in sensitivity to flicker modulation.

To reexamine this contentious issue, we constructed an apparatus that could deliver stroboscopic flashes independently to the two eyes at rates and in sequences controlled by a computer (Fig. 1). In our first set of experiments, we essentially repeated the experiments of Sherrington (3, 4) [and Baker *et al.* (7–11)] on flicker-fusion with an improved paradigm (Fig. 1). The critical flicker-fusion frequency was defined as the rate at which a 1-sec train of light flashes was perceived as continuous illumination in 50% of the trials. For the 20 adult subjects tested, the mean critical flicker-fusion frequency for synchronous presentations was 47.3 ± 1.8 Hz (mean ± SEM), whereas for asynchronous presentations it was 46.3 ± 1.9 Hz (Fig. 2). Thus each of the subjects perceived flicker-fusion in the asynchronous condition at frequencies that were about the same as those that produced flicker-fusion with synchronous presentation to the two eyes. This result is identical to that reported by Sherrington.

We next examined the perception of dichoptic stimulation at lower frequencies using a binocular matching paradigm to indicate whether or not paired trains of flashes produced the same percept (Fig. 3). As in the experiments on flicker-fusion, one member of the pair consisted of synchronous dichoptic flashes and the other of asynchronously presented flashes. Asynchronous trains at each of several frequencies (2, 4, 8, 16, and 32 Hz) were paired with a range of synchronous trains, such that the extremes gave rise to obvious differences in the perceived flicker rate (Fig. 3*A*).

Trains of light flashes presented asynchronously to the two eyes at very low frequencies (2 Hz) were usually seen as identical to synchronous presentations at twice the rate (the result expected on the basis of monocular convergence) (Fig. 3*B*). However, at only slightly higher frequencies of presentation (4 Hz) and continuing to the highest rate tested (32 Hz), asynchronous and synchronous flashes presented at the same rate were increasingly judged to be the same. Thus, with increasing flash rate, the ratio of the asynchronous to synchronous presentation rate that gave rise to the same perception diminished from two to a value very near one at flicker-fusion. Moreover, fewer and fewer asynchronous presentations were seen as identical to synchronous presentations at twice the rate. Evidently, asynchronously presented light flashes begin to be conflated when the interval between successive stimuli to the two eyes is less than several hundred milliseconds. In short, a temporal limitation in the perception of dichoptically presented flashes is apparent at frequencies far less than the critical flicker-fusion frequency.

How then should one regard Sherrington's conclusion that the two monocular views are elaborated independently and that this information is united only psychically? In light of the modern knowledge that 80% or more of neurons recorded from primate visual cortex, even under anesthesia, respond to stimulation of both eyes (1), the first part of Sherrington's interpretation is wrong in the sense that information from the two eyes is unequivocally brought together in V1. Nonetheless, the results obtained nearly a century ago on flicker-fusion, which we confirm, do present a profound puzzle. If binocular

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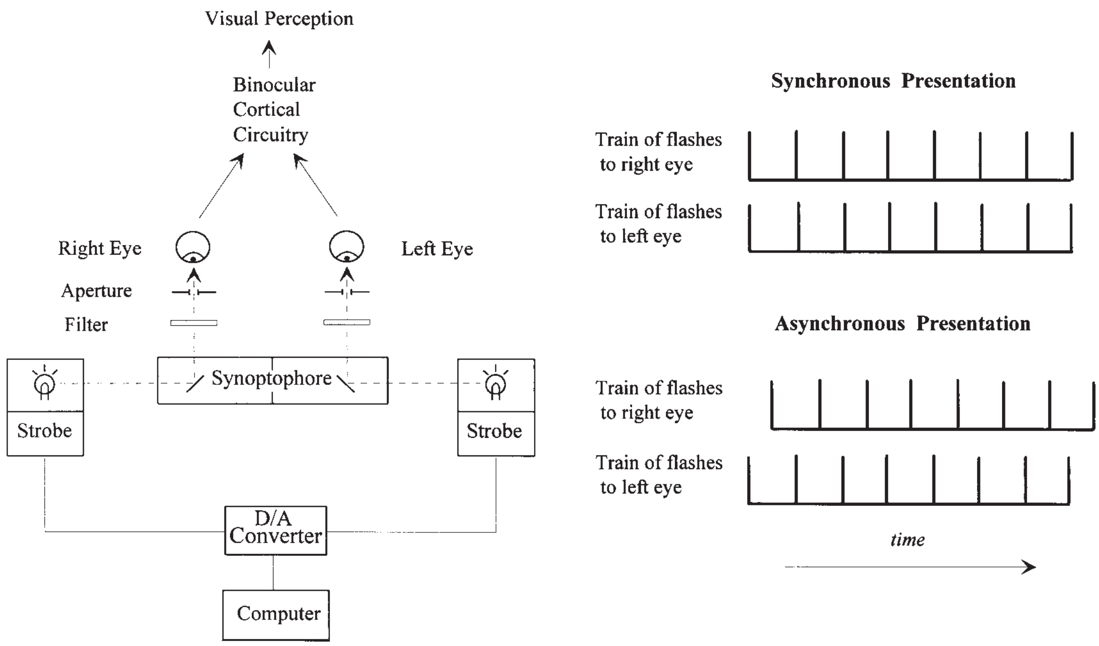

FIG. 1. Diagram of the dichoptic presentation of light flashes. (*Left*) A computer program triggered two stroboscopic light sources (30-μsec flash; 15 W; Monarch Instruments, Amherst, NH). The intensity of the light from the strobes was adjusted by neutral density filters to ensure equal photopic illumination of each eye from a modified synoptophore (Oculus type 58100, Wetzlar, Germany). Alignment of the monocular views was achieved by adjusting the arms of the synoptophore for each subject until the two images were exactly superimposed. During the trials, a low level of constant illumination allowed subjects to fixate and thereby maintain fusion of the monocular views between flashes. Thus when the two monocular images were superimposed, subjects saw a dimly illuminated circular field subtending 1.5° that was periodically the source of flashing light. (*Right*) The two types of dichoptic presentation—synchronous or asynchronous—are diagrammed. Note that the frequency of synchronous or asynchronous flash presentation refers to the rate received by one eye. D/A, digital/analog.

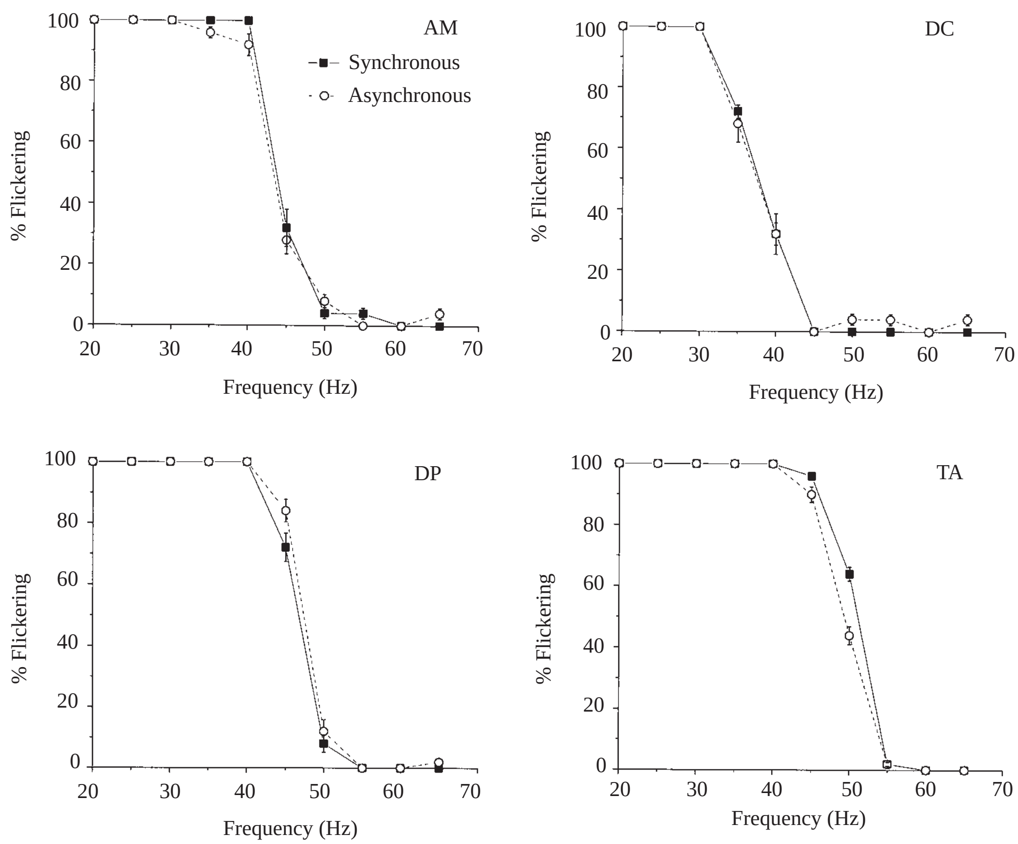

FIG. 2. The critical flicker-fusion frequency determined for synchronous and asynchronous dichoptic presentation in 4 representative subjects of the 20 tested (students, faculty, and staff with normal vision from Duke University). Each trial consisted of five synchronous and five asynchronous flash presentations lasting 1 sec at 20, 25, 30, 35, 40, 45, 50, 55, 60, and 65 Hz; the order of presentation was randomized. Subjects had to indicate whether a flashing train was perceived as flickering or fused by pressing a key pad. Each trial was repeated five times for a total of 25 synchronous and 25 asynchronous presentations at every value. All 20 subjects perceived the transition from flicker to fusion in the asynchronous condition at a frequency that was within a few percent of the value observed when the stimuli were presented synchronously to the two eyes.

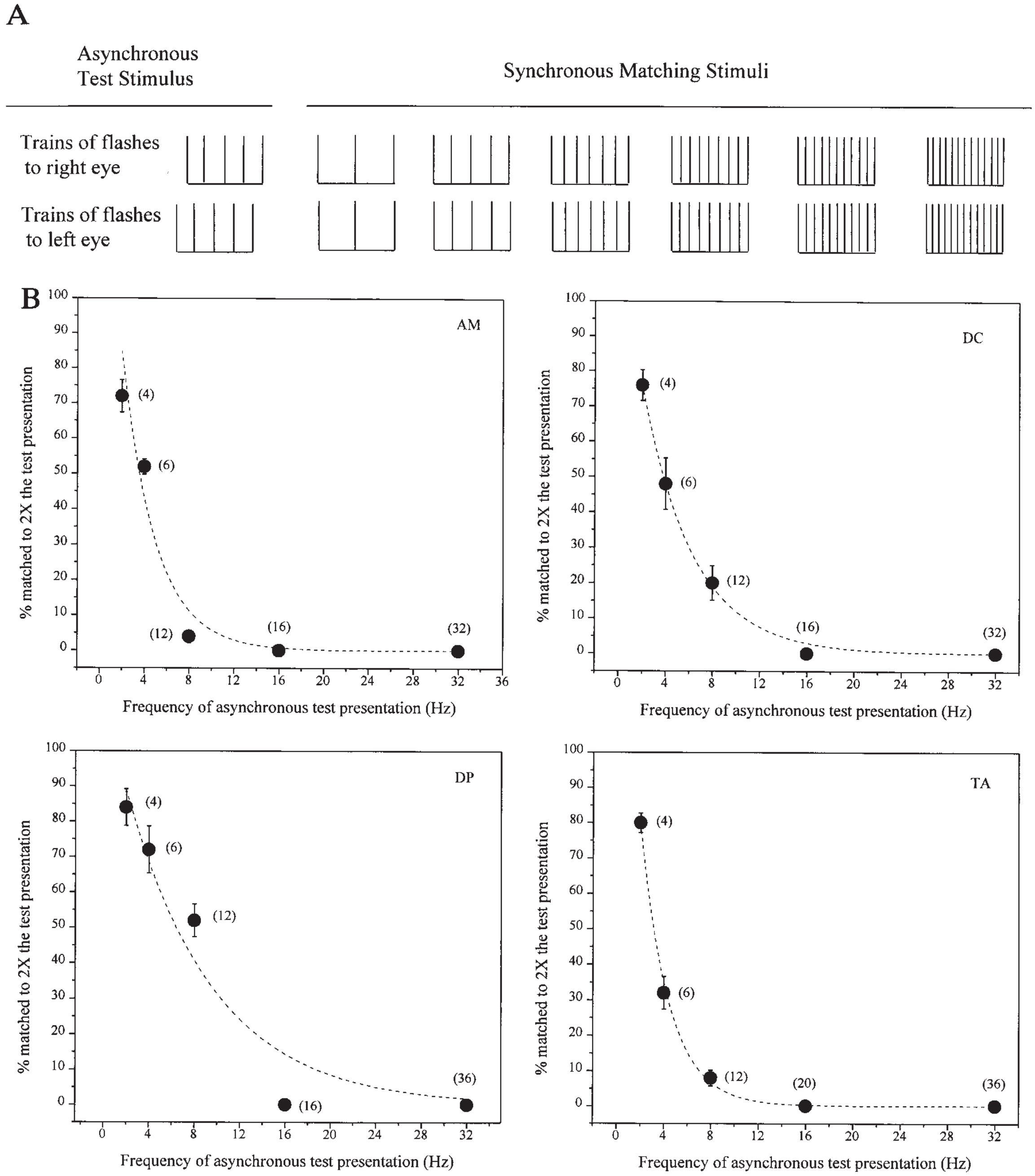

FIG. 3. Assessment of temporal integration over a wider range of frequencies. (*A*) Diagram of the binocular matching paradigm. Subjects were asked to indicate if an asynchronous train of flashes (*Left*) was identical to a synchronous train presented after a 1-sec pause. For each asynchronous test frequency, six different synchronous frequencies were evaluated (*Right*). If the signals generated by each eye were integrated at a common neural locus, dichoptic presentation of asynchronous flashes at a given frequency should be matched to a synchronous presentation at twice the rate. For example, the same subjective perception of flicker should be produced by an 8-Hz asynchronous train and a 16-Hz synchronous train. All trains were 2 sec long and were presented 1 sec apart, with a 2-sec pause between the presentation of each pair. During the trial, each pair was repeated five times for a total of 30 presentations. As a positive control for matching accuracy, an additional 30 asynchronous trains at the test frequency were also included in each trial. This entire procedure was carried out for asynchronous test frequencies of 2, 4, 8, 16, and 32 Hz; the six matching frequencies were adjusted appropriately for each test value. The order of presentation during the overall presentation of 60 pairs of flashing trains was randomized; five such trials at every test frequency were evaluated for each subject. (*B*) Results of the binocular matching experiments from the same four subjects shown in Fig. 2. At very low frequencies, each subject typically matched asynchronous trains with synchronous ones at double the test rate—the expected result based on the conventional view of monocular convergence. At higher frequencies, however, asynchronous trains were increasingly matched to synchronous trains that approached the test frequency. The numbers in parentheses indicate the frequency of the synchronous presentation that was most commonly matched to the asynchronous test presentation.

information converges in V1, why don't stimuli presented asynchronously to the two eyes elicit a lower frequency of fusion than the same stimuli presented synchronously? This question becomes even more pointed when one considers that this temporal conflation is already apparent at frequencies of just a few hertz. The answer may be that we ordinarily parse visual input into temporal episodes. If sequential flashes to alternate eyes fall into successive episodes, then our perception is of a union of the dichoptic input, as indeed occurs at very low frequencies of presentation. If, however, sequential stimuli fall within one episode, the information is conflated (Fig. 4). This process could also account for the fact that stereoscopic

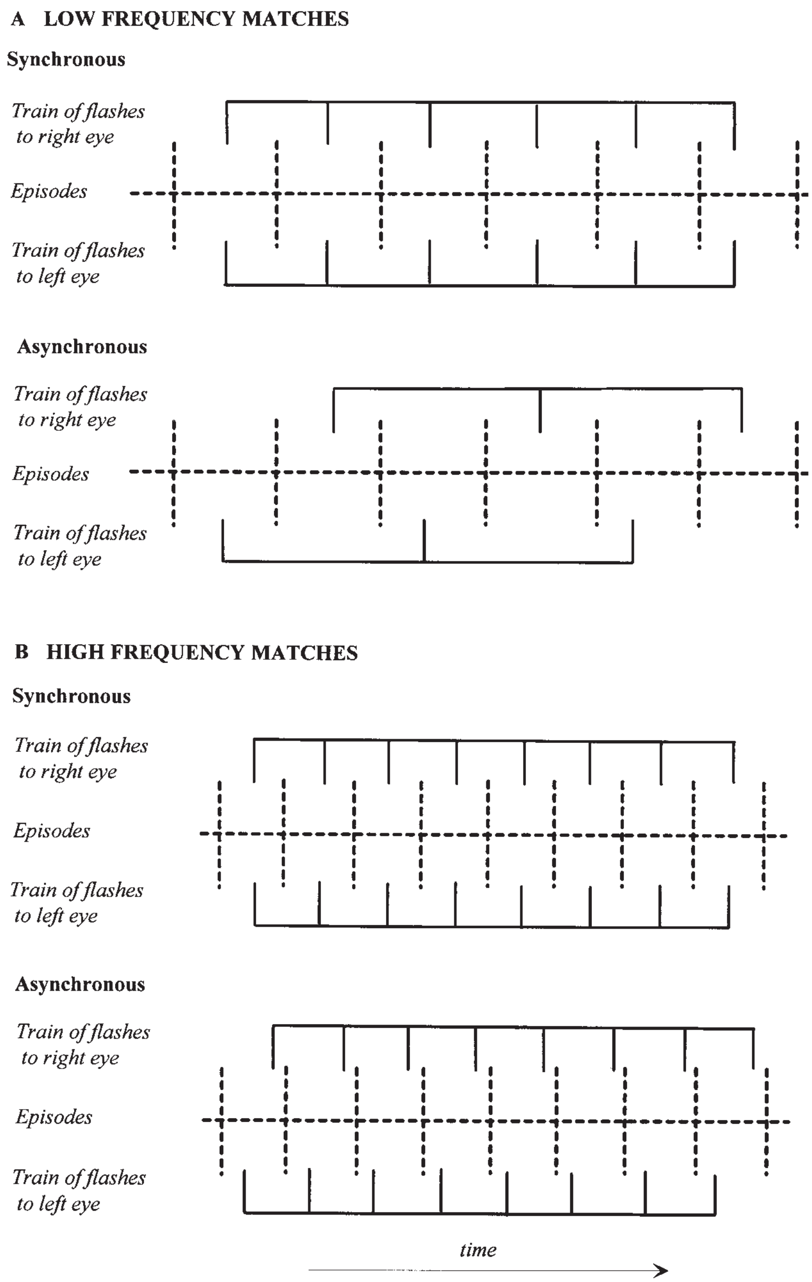

FIG. 4. Proposed explanation of the results in terms of visual episodes. (*A*) At very low frequencies of dichoptic flash presentation, the stimuli in the asynchronous train are perceived alternately by one eye and then the other. The overall perception in the asynchronous mode is, accordingly, a flash rate that is approximately the sum of the left and right eye information. (*B*) At higher rates of presentation, the dichoptic flashes begin to fall into the same episode such that sequential right and left eye flashes are increasingly conflated. As the frequency of the trains increases, therefore, the perceived rate approaches the frequency of either train of flashes alone. Note that the duration of visual episodes in this scheme decreases at higher stimulus frequencies.

depth can be perceived when information about retinal disparity is presented dichoptically at delays of up to 300 msec (13–15) and that binocular rivalry persists when incompatible stimuli are presented alternately to the two eyes over similar intervals (16). The concept of episodic visual processing has been put forward by psychologists based on a variety of evidence over the years (17–20) but has not been widely embraced. In addition to supporting the notion of visual episodes, our results also suggest that the duration of episodes varies as a function of stimulus frequency.

We are grateful to Dorothy Vaughn and John Kelley for help with programming and to David Fitzpatrick, David Coppola, Scott Halpern, Alli McCoy, and John Kelley for critical comments. This work was supported by a grant from the National Institutes of Health.

1. Hubel, D. H. & Weisel, T. N. (1977) *Proc. R. Soc. London B* **198,** 1–59.
2. Poggio, G. (1995) *Cereb. Cortex* **5,** 193–204.
3. Sherrington, C. S. (1904) *Br. J. Psychol.* **1,** 26–60.
4. Sherrington, C. S. (1906) *Integrative Action of the Nervous System* (Yale Univ. Press, New Haven, CT).
5. Helmholtz, H. L. F. (1868) *Treatise on Physiological Optics*, ed. Southall, J. P. C. (Opt. Soc. Am., Rochester, NY), 3rd (German) Ed.
6. Schrodinger, E. (1958) *What is Life?* (Cambridge Univ. Press, Cambridge, U.K.).
7. Baker, C. H. (1952a) *Can. J. Psychol.* **6,** 84–91.
8. Baker, C. H. (1952b) *Can. J. Psychol.* **6,** 123–130.
9. Baker, C. H. (1952c) *Can. J. Psychol.* **6,** 151–163.
10. Baker, C. H. & Bott, E. A. (1951) *Can. J. Psychol.* **5,** 9–17.
11. Baker, C. H. (1970) *Percept. Psychophys.* **8,** 406–410.
12. Cavonious, C. (1979) *Q. J. Exp. Psychol.* **1,** 273–280.
13. Ewald, P. (1906) *Pflügers Arch. Physiol.* **115,** 555.
14. Engel, G. R. (1970) *Am. J. Exp. Psychol.* **22,** 148–160.
15. Ross, J. & Hogben, J. H. (1974) *Vision Res.* **14,** 1195–1201.
16. O'Shea, R. P. & Crassini, B. (1984) *Percept. Psychophys.* **36,** 266–276.
17. Ansbacher, H. L. (1944) *J. Exp. Psychol.* **34,** 1–23.
18. Stroud, J. M. (1967) *Ann. N.Y. Acad. Sci.* **138,** 623–631.
19. Allport, D. A. (1968) *J. Psychol.* **59,** 395–406.
20. Sanford, A. J. (1971) in *Biological Rhythms and Human Performance*, ed. Colquhoun, W. P. (Academic, New York), pp. 179–209.