and of synaptic delay in the cross-inhibitory pathway.

For intermediate rates where the interval between pulses is commensurate with the self-inhibitory time constants, firing alternates between the two units. This is made possible either by an innate circuit asymmetry (since precise equivalence of threshold is practically impossible), or by any noise fluctuation which permits one unit to become momentarily dominant. In the steady state, a given excitatory impulse finds the unit that has just fired still relatively refractory (that is, the self-inhibitory time course has not yet run out). But the opposing unit, well recovered from self-inhibition two input periods back, is now dominant because of lower threshold, and it fires. Thus, firing activity in the pair alternates.

The alternating activity described so far depends only on self-inhibition —that is, refractoriness—and not on reciprocal suppression. However, at high stimulus rates, where the interval between pulses is commensurate with the time constants for reciprocal inhibition, the dominant unit becomes more effective in suppressing the opposing unit because of accumulated cross-inhibition. In the limit, at sufficiently high rates, complete and sustained dominance is possible.

A rather surprising result is obtained if the frequency of the stimulus is decreased. Consider Fig. 3*a*. Let us assume operation at some point between f_{LO} and f_{HI}, producing pattern P_1 (in this case 1/1). As was seen earlier, this pattern will persist with increasing stimulus frequency until f_{H1} is reached, at which time there will be a discontinuous jump to a new pattern P_2. Now, if the frequency of the stimulus is decreased, the original path is not retraced. Instead, the new pattern P_2 persists, even though the stimulus frequency lies between f_{LO} and f_{HI} (for example, the operating point indicated by P_2*), for which stimulus the pattern P_1 was previously elicited. The "captured" pattern P_2 continues as the stimulus frequency decreases until f_{LO} is reached and pattern P_1 reappears.

Hysteresis, in which the approach path to a particular stimulus uniquely determines the response, is seen for all patterns shown in Fig. 2. Moreover, a number of radically different hysteresis loops can be produced by modifying the circuit's temporal parameters. For example, the loops of Fig. 3, *b*, *c*, and *d*, were obtained by changing both of the time constants for mutual inhibition by factors ranging from 0.5 to 4.0. The arrangement of the ordinate response patterns follows the natural ordering with increasing stimulus frequency (as in Fig. 2). The classes of patterns change somewhat with different circuit constants.

One may speculate that if such hysteretic switching action were used by real nervous systems then a similarly simple, economical control of pattern states might be expected. For example, may only a transient shift of stimulus frequency be required in order to go from one state to another—that is, can a change in pattern be obtained merely by injecting an extra pulse into the stimulus train? Such indeed is the case for the model. The hysteresis loop shown in Fig. 3*a* is readily traversed by single-pulse control; for a fixed stimulus frequency between f_{LO} and f_{HI}, a single intercalated spike causes P_1 to change to P_2, while a single deleted impulse (or an injected inhibitory spike) triggers the converse change.

Neither hysteretic action nor its control (as described) has yet been demonstrated physiologically, but a seemingly similar effect is found in some crustacean nerve-muscle preparations (*12*). In those experiments, a given muscular tension produced by a background stimulus of constant frequency applied to a single motor fiber can be triggered into a state of greatly increased tension simply by intercalating a single extra shock. Further, Katz (*13*) suggests that prompt relaxation without reduction of background activity might be obtainable by injecting a few inhibitory impulses. However, the available evidence does not suggest, nor does it seem very likely, that these results depend on effects like those described herein. Clearly, though, physiological latching mechanisms exist which do not depend on elaborate neural networks.

The ubiquity of recurrent and reciprocal inhibition makes flip-flop action in nervous systems at least plausible. It may well be that Renshaw cells, for instance, produce effects similar to those described here, but the brief antidromic volleys commonly used as probing stimuli are inappropriate for disclosing such effects. Furthermore, stimulus frequency is not often used as an experimental variable, while at least for the class of experiments reported here it is a revealing parameter. If hysteresis actually occurs in nature then appropriate neurophysiological experiments may disclose entirely new modes of information-processing at the single-cell level.

LEON D. HARMON
Bell Telephone Laboratories, Inc., Murray Hill, New Jersey

References and Notes

1. D. M. Wilson, *J. Exptl. Biol.* **41**, 191 (1964).
2. ———, in *Neural Theory and Modeling*, R. F. Reiss, Ed. (Stanford Univ. Press, Palo Alto, Calif., 1964), pp. 331–345.
3. L. D. Harmon, *Kybernetik* **1** (3), 89 (1961).
4. W. McDougall, *Brain* **26**, 153 (1903).
5. C. S. Sherrington, *Integrative Action of the Nervous System* (Yale Univ. Press, New Haven, Conn., 1906).
6. H. K. Hartline, F. Ratliff, W. H. Miller, in *Nervous Inhibition*, E. Florey, Ed. (Pergamon, New York, 1961), pp. 241–284; K. Kirschfeld and W. Reichardt, *Kybernetik* **2** (2), 43 (1964); G. G. Furman and L. S. Frishkopf, *J. Acoust. Soc. Amer.*, in press.
7. B. Renshaw, *J. Neurophys.* **4**, 167 (1941); R. M. Eccles, A. Iggo, M. Ito, *J. Physiol.* **153**, 49P (1960); R. Granit, in *Brain Mechanisms*, G. Moruzzi, A. Fessard, H. H. Jasper, Eds. (Elsevier, New York, 1963), pp. 23–37.
8. E. Retzlaff, *J. Comp. Neurol.* **107**, 209 (1957); ——— and J. Fontaine, *Science* **131**, 104 (1960).
9. R. F. Reiss, in *Proceedings of the Joint Computer Conference, Spring 1962* (National Press, Palo Alto, Calif., 1962), pp. 171–194.
10. L. D. Harmon, in *Information Processing in the Nervous System*, R. W. Gerard, Ed. (Excerpta Medica Foundation, Amsterdam, 1964), pp. 117–124.
11. Excitatory and inhibitory time courses, described by time constants of charge τ_c and of discharge τ_d, are as follows: excitation, τ_c = 0.25 msec, τ_d = 9 msec; mutual inhibition, τ_c = .07 msec, τ_d = 3 msec; self-inhibition, τ_c = 60 msec, τ_d = 5 msec.
12. H. Blaschko, McK. Cattell, J. L. Kahn, *J. Physiol.* **73**, 25 (1931); C. F. A. Pantin, *J. Exptl. Biol.* **13**, 159 (1936); C. A. G. Wiersma and A. van Harreveld, *ibid.* **15**, 18 (1938); C. A. G. Wiersma and R. T. Adams, *Physiol. Comp. Oecol.* **2**, 20 (1949).
13. B. Katz, *Biol. Rev.* **24**, 1 (1949).
14. The technical assistance of E. J. Sitar is gratefully acknowledged.

16 October 1964

Electroencephalographic Correlates of Binocular Rivalry in Man

Abstract. *Under conditions of ocular rivalry, changes in the rhythmic brain response to flicker stimulation of one eye correspond closely to the subject's report of changes in the perceptual dominance of that eye.*

When the fields of view for the two eyes are similar they are combined by a central fusion process, forming a single unified perception of the visual field. If the stimuli presented to corresponding parts of the two retinas differ markedly, however, a binocular rivalry occurs in which the visual image of one eye alternates with or suppresses that of the other (*1*). The degree of suppression and rate of alternation de-

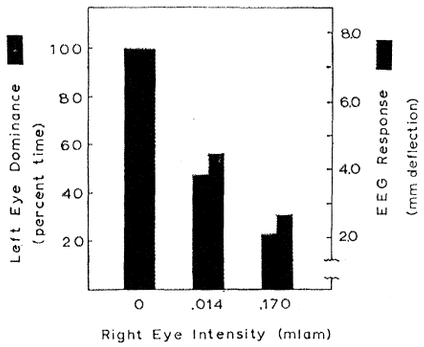

Fig. 1. Percentage of time the flickered left eye was perceptually dominant, and the amplitude of the EEG response to the flicker, as the intensity of the stimulus field to the right eye was increased. Data are averages for eight subjects.

pend largely on differences in color, pattern, intensity, and attention value of the retinal stimuli (*2*). Rivalry probably occurs frequently under natural viewing conditions, working coordinately with fusional mechanisms to maintain singleness of vision. Although perceptual fusion and rivalry have been classical problems in the experimental investigation of binocular vision in man, the physiological processes underlying these phenomena are still not known. In the work reported here I have attempted to relate electrophysiological and perceptual measures of ocular interaction in human subjects.

The visual input to one eye was physiologically labeled by presenting flickering light at a flash rate which produced a rhythmic response of the same frequency in the electroencephalogram. The effect of rival stimuli to the other eye on the cerebral response and perception could then be studied. The discrepant visual fields were presented stereoscopically: the bright flickering light to the left eye, and a steady red light with diagonal stripes to the right eye. These fields, each with a visual angle of 50°, were superimposed as the subject fixated on a small center point, and produced good binocular rivalry. Two display units (*3*) illuminated the separate eye fields of the stereoscope. A Grass S-4 stimulator controlled the left eye display unit, and delivered pulses of white light of 30 msec duration, 500 mlam intensity, at a flash rate of 6 to 8 per second. The right eye display unit, presenting the steady red field, was controlled by a Heath regulated power supply; intensity varied from 0 to 16.8 mlam according to the conditions of the experiment. As the subject viewed the stimulus fields he indicated with two keys whether the left or right eye field was perceptually dominant. Simultaneous recordings of stimulus signals, the subject's key responses, and brain potentials were obtained with a Grass model 5 polygraph. Bipolar EEG's were recorded from midline occipital-parietal scalp electrodes placed 1 cm and 9 cm above the inion. In addition to the primary tracing, a narrowly tuned filter (*4*), set at the flash frequency of the flickering field, was used to selectively record the cerebral response to the left eye stimulus. The filter write-out, recorded on a separate channel of the polygraph, was measured with a planimeter (*5*) to determine changes in amplitude of the photic response.

The flickering stimulus to the left eye remained the same throughout the experiment, while variations in the intensity of the red stimulus to the right eye were used to manipulate perceptual dominance and examine corresponding changes in the EEG. Eight subjects were studied under three conditions of stimulation: (i) with increasing intensities of the stimulus to the right eye; (ii) with the onset and offset of a stimulus of high intensity to the right eye; and (iii) with a stimulus of moderate intensity to the right eye, selected to produce "spontaneous" alternation of perceptual dominance from one eye to the other.

Under all three conditions, perceptual dominance of the eye subjected to flicker corresponded closely to the amplitude of the rhythmic EEG response to stimulation of that eye. Under the first condition, the stimulus to the right eye was presented at intensities of 0, 0.014, and 0.17 mlam for 20-second periods while the left eye was being

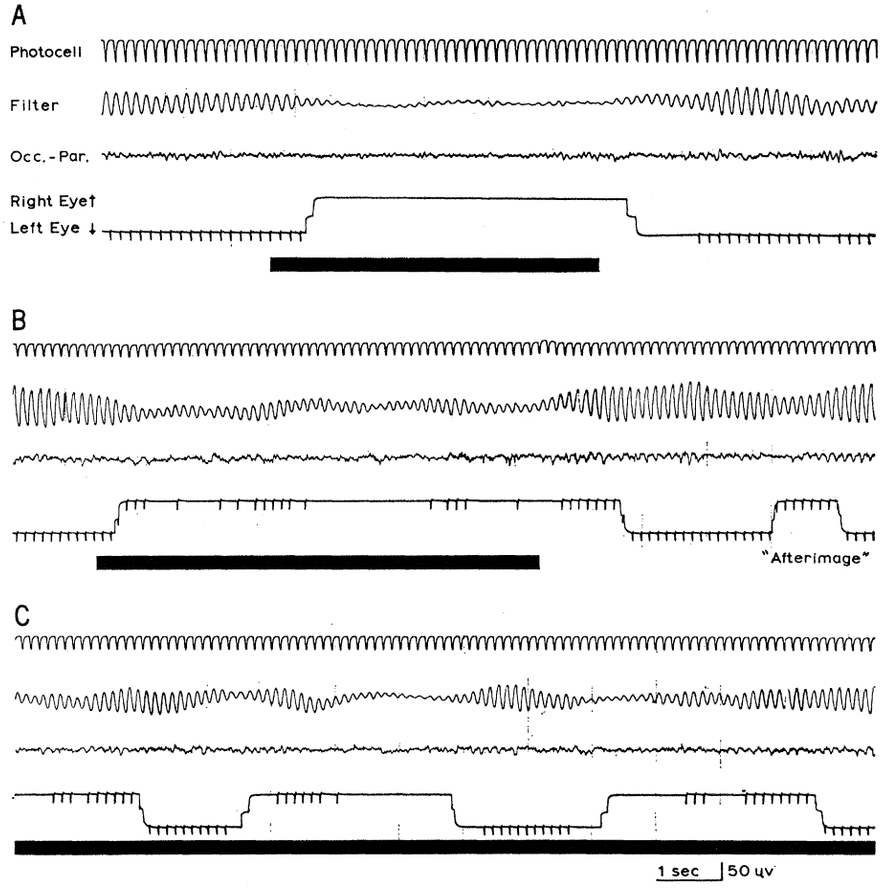

Fig. 2. *(A)* Typical effect of the onset and offset of a red patterned stimulus to the right eye (wide solid line) on perceptual dominance and EEG response to left eye flicker. *(B)* Same as *(A)* for a subject who reported brief negative after-images following the offset of the right eye stimulus. *(C)* Spontaneous changes in EEG and perceptual response during continuous stimulation of the right eye. Channel 1, photocell monitoring flicker stimuli to the left eye; channel 2, filtered occipital-parietal EEG response; channel 3, occipital-parietal EEG; channel 4, subject's responses indicating right eye ↑ or left eye ↓ perceptual dominance ("pips" on this channel are signalling EEG filter responses above an arbitrary amplitude).

stimulated with the flickering light. The percentage of time the left eye was judged to be dominant and the amplitude of the EEG response were measured for the last 15 seconds of each stimulus period. Figure 1 shows that as the intensity of the right eye stimulus increased there was a decrease in perceptual dominance of the left eye accompanied by a reduction of EEG photic response. The effects of intensity on both perceptual dominance and EEG were statistically significant ($p < .01$) when tested by Friedman's Chi-square test for ranks. Subjects varied widely in the degree of suppression shown, particularly at the lower intensity (0.014 mlam), suggesting individual differences in the threshold for rivalry effects. This variability may be related to the fact that the rival stimulus was delivered to the right eye of all subjects regardless of ocular differences in dominance or acuity. The great sensitivity of the rivalry mechanism is shown by the fact that a red patterned stimulus to one eye of only 0.014 mlam could so effectively reduce the response to a stimulus of 30,000 times greater intensity to the other eye.

In the second experimental condition, the effects of onset and offset of stimuli to the right eye were studied. The flickering light was presented continuously to the left eye for 1 minute while the red striped stimulus to the right eye (0.66 to 16.8 mlam) was alternately turned on for 5 to 10 seconds and off for 5 to 10 seconds. In all subjects this procedure produced complete reversals in perceptual dominance from the right to left eye with corresponding decreases and increases in EEG response. These changes were quite apparent in the recordings (Fig. 2, *A* and *B*) and were so repeatable that the experimenter could shift the responses at will. Occasionally (Fig. 2*B*), the offset of the right eye stimulus was followed by positive and negative afterimages which appeared to coincide with momentary perceptual and EEG reversals (*6*). The EEG photic response averaged 6.2 mm (filter pen deflection) during the offset period and 1.1 during onset, an 82 percent change. The EEG and perceptual shifts corresponded closely in time but, because of the slow paper speed and the time lag in the filter response, no latency measures were obtained.

Under the third condition, those intensities of the stimulus to the right eye were selected (0.014 to 0.53 mlam) which produced "spontaneous" alternations in left and right eye dominance. The EEG response to left eye flicker, measured for six consecutive alternations, paralleled the spontaneous shifts in perceptual dominance (Fig. 2*C*). The photic response amplitude averaged 6.8 during left eye dominance and 5.1 during right eye dominance, a difference (26 percent) considerably smaller than that found for the onset and offset condition (82 percent). This smaller difference may be related to the subject's report that "spontaneous" shifts were more difficult to judge, and the dominance of one eye field over the other was not as great. The precise time relations between the EEG and perceptual responses were not considered meaningful because subjects frequently said that they watched for a second or two after a change had occurred before deciding to respond.

In spite of the consistency with which EEG responses and perceptual judgments of rivalry were related, occasionally, for brief recording epochs, there was a lack of congruity between the two. The subjects were untrained and were limited to an either/or choice of eye dominance, therefore the perceptual response may have been a less sensitive and reliable measure of the degree of rivalry than the EEG recording.

The physiological basis for the EEG changes observed under conditions of rivalry is not known. Since the photically driven waves are probably projected diffusely over multisynaptic pathways to the occipital association areas (*7*), their suppression could have occurred at a number of points along the visual pathways or at later stages in their cortical elaboration. Peripheral oculomotor influences may be ruled out since the suppression occurs even when the two eye fields are well fixated, with no eye movements recorded, and when artificial pupils are used. General EEG desynchronization, resulting from an increase in attention when the red stimulus field was dominant, might explain the reduction of cerebral response to the flickered eye. Other evidence, however, indicates that simply increasing the level of attention to visual stimuli should enhance the photically driven potentials (*8*). If attentional processes contributed to the results of this study, they must have been peculiarly linked to the special conditions of discrepant retinal stimulation.

Evoked potential and single unit recordings in animals show that the centrally converging influences from the two eyes may be antagonistic as well as summative (*9*). Although Grüsser-Cornehls and Grüsser (*10*) suggest that such inhibitory effects recorded in the cat's visual cortex may be the basis for ocular rivalry, it is difficult to extend these findings directly to human perception. The results of the present investigation suggest that combining EEG recordings of evoked potentials and psychological measures may be fruitful in the study of binocular processes in man.

ROBERT W. LANSING
Department of Psychology
University of Arizona, Tucson

References and Notes

1. H. von Helmholtz, *Physiological Optics*, J. P. C. Southall, Ed. (Dover, New York, rev. ed., 1962), vol. 3, pp. 493–528; K. N. Ogle, *Researches in Binocular Vision* (Saunders, Philadelphia, 1950), pp. 59–68; R. S. Woodworth and H. Schlosberg, *Experimental Psychology* (Holt, New York, rev. ed., 1954), pp. 397–402.
2. B. B. Breese, *Psychol. Monogr.* **3**, No. 1 (1899); L. T. Alexander, *J. Exptl. Psychol.* **41**, 376 (1951); H. Wallach and P. A. Adams, *Am. J. Psychol.* **67**, 513 (1954); E. Engle, *ibid.* **69**, 87 (1956); L. Kaufman, *Vision Res.* **3**, 401 (1963).
3. Industrial Electronics Series 120,000 In-line Readouts, with No. 327 bulbs, were used for the display units.
4. The filter, described by H. Becker, W. A. Mickle, R. G. Heath, *Electroencephalog. Clin. Neurophysiol.* **10**, 731 (1958), was set at a Q value of 28.5.
5. This method of determining average wave amplitude is described by M. A. Bruck, *Electroencephalog. Clin. Neurophysiol.* **12**, 528 (1960). In the present study, the amplitude of the flicker response on the EEG was measured as the increased filter output above the control level prior to stimulation. The filter write-out was calibrated so that 1-mm pen excursion was produced by a 1.5-μv sine wave signal at the frequency to which the filter was tuned. An immediate monitor of changes in EEG response was provided by a trigger circuit which produced a "pip" on the signal channel each time a filtered wave exceeded an arbitrary amplitude (see Fig. 2).
6. Perceptual rivalry between afterimages from the two eyes was reported some time ago by B. B. Breese, *Psychol. Monogr.* **3**, No. 1 (1899), and by A. De Vries and M. F. Washburn, *Am. J. Psychol.* **20**, 131 (1909).
7. R. Cohn, *Electroencephalog. Clin. Neurophysiol.* **4**, 297 (1952); W. G. Walter, in *Brain Mechanisms and Consciousness*, J. F. Delafresnaye, Ed. (Blackwell, Oxford, 1954), pp. 345–369; P. Buser, in *Les Grandes Activités du Lobe Occipital*, P. Alajouanine, Ed. (Masson, Paris, 1960), pp. 53–57; R. W. Lansing, *Electroencephalog. Clin. Neurophysiol.* **16**, 290 (1964).
8. N. N. Zislina, *J. Higher Nerv. Function USSR* **5**, 677 (1955); K. A. Kooi and R. S. Boswell, in *Recent Advances in Biological Psychiatry*, J. Wortis, Ed. (Grune and Stratton, New York, 1960), pp. 172–182; H. Thomas, thesis, Univ. of Arizona (1962).
9. S. A. Talbot and W. H. Marshall, *Am. J. Physiol.* **133**, 476 (1941); B. D. Burns, W. Heron, B. Grafstein, *ibid.* **198**, 200 (1960); S. D. Erulkar and M. Fillenz, *J. Physiol.* **154**, 206 (1960); D. H. Hubel and T. N. Wiesel, *ibid.* **160**, 106 (1960); O.-J. Grüsser and U. Grüsser-Cornehls, *Arch. Ges. Physiol.* **272**, 51 (1960).
10. U. Grüsser-Cornehls and O.-J. Grüsser, in *The Visual System: Neurophysiology and Psychophysics*, R. Jung and H. Kornhuber, Eds. (Springer, Berlin, 1961), pp. 275–286.

22 October 1964