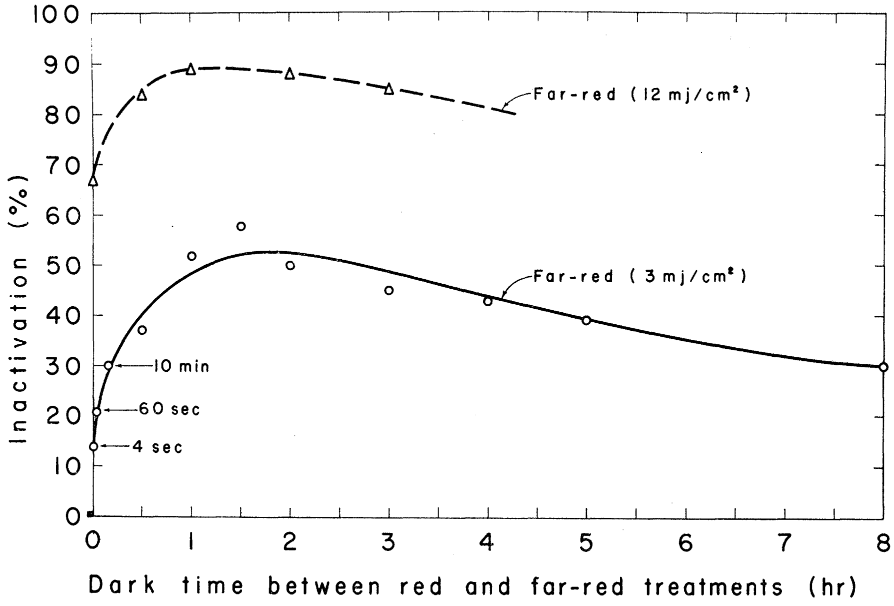

Fig. 1. Time course of far-red inactivation of red-induced morphogenesis in the hypocotyl hook of the bean seedling. Curves are shown for energy levels of 3 and 12 mj/cm^2, applied at 1000 μw/cm^2 for 3 and 12 seconds, respectively.

lecular collision in either direction and that both photoreactions follow first-order kinetics.

If such a simple reversal obtains, with no intervening collision step, it seems logical to assume that the system would be immediately reversible at the maximum rate, and that the time course would show a constant value of reversibility, to the point where the consequences of the red induction result in irreversible growth reactions.

In view of these considerations, it was decided to determine the time course for photoinactivation of red-induced photomorphogenesis in the bean seedling (7). A high-intensity carbon arc, in combination with interference filters, was used as the source. The irradiation periods were as short as could be obtained with this system, and were a matter of seconds. The bioassay was the rate of opening of the hypocotyl hook of bean, the technique of which has been described by Klein *et al.* (8). In this system, the induction response has a peak of activity in the red at 660 mμ, and photoinactivation peaks at 710 and 730 mμ (3). The angle of hook opening is proportional to the logarithm of the incident red energy over an irradiance range of at least 1 million for short periods of photoinduction, and the inactivating effect of the far-red is directly proportional to irradiance. A total energy of 10 mj/cm^2 of far-red energy distributed over a 30-minute period produces about maximal photoinactivation, the percentage of inactivation rising linearly with energy to approximately 85 percent and then leveling off rapidly thereafter.

The hypocotyl hooks were excised from 6-day old Black Valentine bean seedlings and arranged in a circle on moist filter paper in a 150-mm petri dish. The excised hooks were exposed to red energy at 25° with a carbon arc for 3 minutes at an irradiance of approximately 1500 μw/cm^2, which yielded a total energy of 250 mj/cm^2 at 660 mμ. The hooks were then kept in the dark until time for the far-red exposure, which was given at approximately 1000 μw/cm^2 at 730 mμ for 3 and 12 seconds for total energies of 3 and 12 mj/cm^2, respectively. The two filter systems were mounted in a sliding panel so arranged that the shortest dark time was 4 seconds.

The results are given in Fig. 1 as time-course curves. It will be noted that the capacity for photoinactivation by the far-red increases rapidly with time, reaching a maximum at between 1 and 2 hours and then decreasing gradually. The decrease is consistent with the hypothesis that irreversible growth reactions have occurred. For the shortest periods of time, the percentage inactivation is approximately proportional to the far-red energy. Data are available (9) which show that the far-red is incapable of producing significant inactivation at proportionately low energy levels in the presence of the red. Therefore, it is probable that the curve falls back to zero, either at zero time or slightly prior to the end of the red-induction period.

These results suggest that a thermochemical step intervenes between the absorption of red photons and maximum capacity for inactivation by the far-red. There are several possibilities about the nature of this step. It may involve the direct modification of the pigment itself to a far-red absorbing form so that inactivation cannot proceed until thermal conversion occurs. On the other hand, it may be concerned with synthesis of a reactant essential to the completion of the inactivation step, the concentration of which limits the far-red reversal process. The complete system is being studied with a complex of variables of incident energy, time, and temperature, with the view of determining the nature of the intervening step.

W. H. KLEIN, R. B. WITHROW,
A. P. WITHROW, V. ELSTAD
Division of Radiation and Organisms,
Smithsonian Institution,
Washington, D.C.

References and Notes

1. L. H. Flint and E. D. McAlister, *Smithsonian Inst. Publs. Misc. Collections* 94, 1 (1935).
2. H. A. Borthwick *et al., Proc. Natl. Acad. Sci. U.S.* 38, 662 (1952).
3. R. B. Withrow, W. H. Klein, V. Elstad, *Plant Physiol.*, in press; W. H. Klein, R. B. Withrow, V. Elstad, *ibid.* 31, 13 (1956).
4. R. J. Downs, *ibid.* 30, 468 (1955).
5. H. A. Borthwick, S. B. Hendricks, M. W. Parker, *Proc. Natl. Acad. Sci. U.S.* 38, 929 (1952).
6. S. B. Hendricks, H. A. Borthwick, R. J. Downs, *ibid.* 42, 19 (1956).
7. This paper is published with the approval of the secretary of the Smithsonian Institution.
8. W. H. Klein, R. B. Withrow, V. Elstad, *Plant Physiol.* 31, 289 (1956).
9. A communication describing these data is in preparation.

13 March 1957

Some Characteristics of Cortical Recruiting Responses in Unanesthetized Cats

In 1941, Morison and Dempsey (1) demonstrated that trains of 8- to 12-per-second stimuli delivered to the intralaminar thalamic nuclei of the anesthetized cat evoked long-latency, surface-negative potentials which were widely distributed over the cerebral cortex. Because the first stimulus of the train evoked little or no cortical response, and because the responses to each successive stimulus showed a progressive increase in amplitude to a maximum, these potentials were termed "recruiting responses." Subsequent investigations have further defined the thalamocortical pathways and the character of the synaptic connections which mediate recruiting responses (2–4). It was shown that pentobarbital lowered the threshold for recruiting responses (5), and, since stimulation of the brain-stem reticular formation prevented their occurrence (6), it was assumed that recruiting responses could not be obtained in the waking animal.

The study described in this report employed the technique of chronic implantation of electrodes, which was developed by Sheatz (7), to explore this

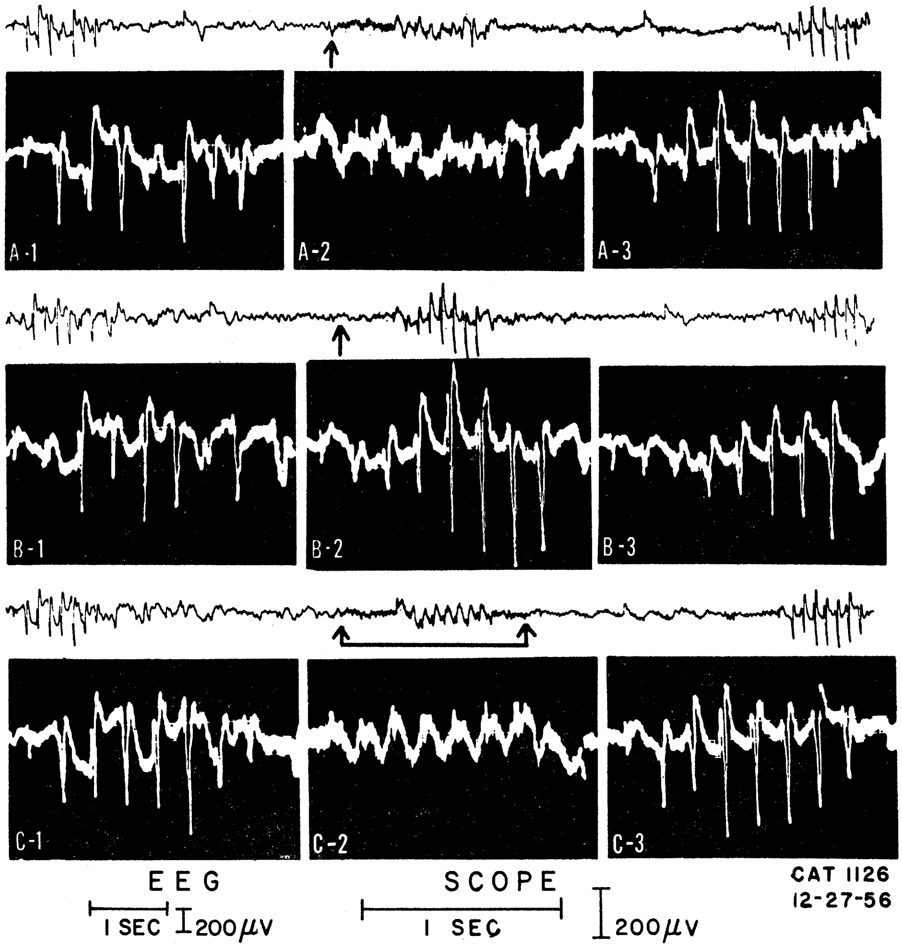

Fig. 1. Recruiting responses in unanesthetized cats. Electroencephalographic records (above) and corresponding oscillographic traces (below) show the recruiting responses recorded from the anterior suprasylvian gyrus following 6-per-second submaximal stimulation of the ipsilateral center median nucleus. *A*-1 and *A*-2, responses recorded before (*A*-1) and after (*A*-2) a noise, which occurred at the arrow. The rapid return of recruiting responses to normal amplitude following the noise is shown in *A*-3. *B*-2, failure of the noise (at arrow) to reduce recruiting responses following repeated presentation of this stimulus. (Bottom row) Recruiting responses before (*C*-1), during (*C*-2), and after (*C*-3) 100-per-second stimulation of the brain stem for 2.5 seconds. The period of brain-stem stimulation is indicated by the solid line between the two arrows (positive is up).

matter further. It was found that stimulation of the intralaminar nuclei may evoke well-developed recruiting responses in the normally waking animal. Figure 1 shows such responses evoked in the anterior suprasylvian gyrus by submaximal 6-per-second stimulation of the ipsilateral center median nucleus. At the time when these responses were recorded, the cat was sitting up in its cage with an alert appearance, occasionally looking about. No detectable behavioral alterations were associated with the recruiting responses. With more intense stimuli, a variety of behavioral alterations resulted, some of which were similar to those described by Hunter and Jasper (*8*). When a loud noise was made, there was a marked decrease in the amplitude of the recruiting responses (Fig. 1, *A*-2). Within 5 seconds of this auditory stimulus, however, responses had returned to original amplitude (Fig. 1, *A*-3). Repeated exposure of the animal to the originally effective auditory stimulus was associated with a gradual disappearance of its blocking effect, as had been previously shown by Jasper *et al.* (*3*). Figure 1, *B*-2, shows this failure of the same auditory stimulus to cause reduction of recruiting responses following habituation. Figure 1, *C*-2, demonstrates the reduction in the amplitude of recruiting responses which results from stimulation of the brain-stem reticular formation. Unlike the effects of the auditory stimulus, the effects of the brain-stem stimulus did not become attenuated with repeated presentation of the stimulus. The effects of brain-stem stimulation were, however, abolished by anesthetic doses of pentobarbital.

Contrary to the expectations based on previous work, therefore, it has been found that the presence of a "desynchronized" electroencephalogram and of behavior indicative of an alert waking state is not incompatible with the induction of recruiting responses. Under such circumstances, these responses can be reduced or prevented by novel, peripheral afferent stimuli or by stimulation of the brain-stem reticular formation. The behavioral changes which were associated with reduction of recruiting responses appeared to range from a shift or attraction of attention (either "spontaneous" or as a result of an afferent stimulus), through brief startle, to more enduring and pronounced excitement. The prevention of evoked recruiting responses in the waking animal may thus be analogous to the blocking of the alpha rhythm in the human electroencephalogram. In man, alpha activity is not prevented by the waking state and may similarly be blocked by a shift or focus of attention as well as by more marked arousal.

More generally, these observations emphasize the undesirability of drawing inferences concerning behavior from electrophysiological observations in the anesthetized or immobilized animal which is incapable of any behavioral display. This is true not only in the case of the recruiting responses but is equally relevant for the response to stimulation of the brain-stem reticular formation. The effects of brain-stem stimulation have customarily been given blanket equation with awakening (*4*), but depending on the state of the animal and the parameters and location of stimulation, such stimulation would appear to be capable of leading to a wide spectrum of behavioral changes that range from awakening to the evocation of attention, to startle, or to the arousal of generalized excitement. Now that appropriate techniques are available, it is to be hoped that such inferences may give way completely to observations of behavior.

EDWARD V. EVARTS

Laboratory of Clinical Science,
National Institute of Mental Health,
Bethesda, Maryland

HORACE W. MAGOUN*

University of California, Los Angeles

References

1. R. S. Morison and E. W. Dempsey, *Am. J. Physiol.* 135, 281 (1942).
2. H. Jasper, in *Brain Mechanisms and Consciousness* (Thomas, Springfield, Ill., 1954); M. H. Clare and G. H. Bishop, *Electroencephalog. and Clin. Neurophysiol.* 8, 583 (1956); T. E. Starzl and H. W. Magoun, *J. Neurophysiol.* 14, 133 (1951); M. Verzeano, D. B. Lindsley, H. W. Magoun, *J. Neurophysiol.* 16, 183 (1953); H. H. Jasper and C. Ajmone-Marsan, *Research Publs. Assoc. Research Nervous Mental Disease* 30, 493 (1950).
3. H. Jasper, R. Naquet, E. E. King, *Electroencephalog. and Clin. Neurophysiol.* 7, 99 (1955).
4. H. W. Magoun, in *Brain Mechanisms and Consciousness* (Thomas, Springfield, Ill., 1954).
5. E. E. King, *Federation Proc.* 13, 375 (1954).
6. G. Moruzzi and H. W. Magoun, *Electroencephalog. and Clin. Neurophysiol.* 1, 455 (1949).
7. G. Sheatz, in *Electrical Stimulation of the Brain* (Univ. of Texas Press, Austin, 1957).
8. J. Hunter and H. H. Jasper, *Electroencephalog. and Clin. Neurophysiol.* 1, 305 (1949).

* Visiting scientist at the National Institute of Mental Health.

25 March 1957