covery was found facilitated at the shorter click-pair intervals without exception during all periods of selective REM sleep deprivation for both animals. This facilitation was reversible as shown by the return to base-line levels during periods of undisturbed sleep and, moreover, it was not seen during control periods which sought to evaluate the effects of (i) stress and (ii) total sleep loss upon the auditory recovery function. In all three cats (after six periods of REM deprivation) the percentage of REM on the first recovery day (8 hours) ranged from 48.4 (after 4 days) to 67.7 (after 30 days).

Table 1 shows the near-perfection of control arousal periods. For cat EP-1, the mean daily sleep times and number of arousals for the first 13 days of REM deprivation were identical to mean values obtained for the 13day control period. Daily REM time during the control period was somewhat reduced below the base-line level, but in cat EP-3 the reduction was less than 10 percent. Since the control period occurred first in EP-3, the number of arousals was estimated and in this case proved to be higher than the number required during the subsequent deprivation period, although total sleep times were again equal. However, the higher number of control arousals was additional evidence that the awakenings per se were not implicated, and during the second period of REM deprivation the number of arousals was more nearly equal to that of the control period.

Many studies of REM deprivation have been conducted by placing the animal in a situation in which REM sleep cannot occur throughout the entire 24-hour day. Under these circumstances, animals will show a marked rebound in REM sleep when allowed to sleep normally, but a basic drawback in interpreting this result is that there is no adequate control for the stress placed upon the test animal. We feel that the only method that allows adequate control of the stress variable is the one that we have used (the reason it is not used more commonly is that continually watching the emerging EEG and EMG tracings for the onset of a REM period places an inordinate demand upon the experimenters). Since awakenings during REM sleep deprivation mount into the hundreds during an 8-hour session and since the deprivation extends for many consecutive days, it is little wonder that the present method enjoys no popularity. Nonetheless,

if an effect is to be attributed specifically to the loss of REM sleep, such loss should be the only significant experimental variable.

In this study, then, a sensitive measure of central nervous system function was followed through periods of selective REM deprivation in cats. All measurements were taken during the waking state and showed no change during base-line periods or periods of control arousals. Although the precise significance of the alterations that occurred is uncertain, it is possible to conclude that a change in centralneural function is assessable during the waking state as a result of loss of REM sleep. The particular change noted in this study could be due to changes in auditory processing as far peripherally as the cochlea (10). It is certainly possible that a subtle effect upon auditory perception had occurred in these animals, but such a premise will require additional experiments to substantiate (11).

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#### **References and Notes**

- 1. W. Dement, in New Directions in Psychology, W. Denent, in New Directions in Psychology,
   T. Newcomb, Ed. (Holt, Rinchart & Winston,
   New York, 1965), pp. 137–257; G. Moruzzi,
   Harvey Lectures Ser. 58, 233 (1963); F.
   Snyder, Amer. J. Psychiat. 122, 377 (1965).
   W. Dement, Science 131, 1705 (1960);
- 2. W. Dement, Science 131, , in Aspects Anatomo-Fonctionnels de la Physiologie du Sommeil, M. Jouvet, Ed.
- la Physiologie du Sommeil, M. Jouvet, Ed. (Centre National de la Recherche Scientifique, Paris, 1965), pp. 571-611.
  N. Khazan and C. Sawyer, Proc. Soc. Exp. Biol. Med. 114, 536 (1963).
  P. Vimont-Vicary, D. Jouvet-Mounier, F. DeLorme, Electroenceph. Clin. Neurophysiol. 20, 439 (1966).
- R. Berger and G. Meier, Psychophysiology 2, 354 (1966).

- 354 (1966).
   B. Morden, G. Mitchell, J. Ferguson, A. Rechtschaffen, W. Dement, paper presented at 6th annual meeting of Association for Psychophysiological Study of Sleep, March 1966, Gainesville, Florida.
   M. Rosensweig and W. Rosenblith, Psych. Monogr. 67, 1 (1953); J. Dewson, III, K. Nobel, K. Pribram, Brain Res. 2, 151 (1966).
   W. Dement, P. Henry, H. Cohen, J. Ferguson, in Sleep and Altered States of Consciousness, S. Kety, E. Evarts, H. Williams, Eds. (Grune and Stratton, New York, in press). press).
- 9. J. Ferguson and W. Dement, Electroenceph.
- J. Ferguson and W. Dement, Electroenceph. Clin. Neurophysiol. 22, 2 (1967).
   J. Dewson, III, W. Dement, F. Simmons, Exp. Neurol. 12, 1 (1955); J. Dewson, III, J. Neurophysiol., in press.
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- Study of Sleep, Washington, D.C., March
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# Perceived Number and Evoked **Cortical Potentials**

Abstract. Evoked cortical potentials and the number of flashes perceived were compared when subjects were presented with short trains of flashes under conditions where each presented flash could not be counted individually, but the train of flashes appeared to be flickering (1 to 14 flashes at 33.3 flashes per second). The rate at which each successive perceived flash was added appeared to correspond with the rate at which the successive components of the evoked response pattern were added. The temporal nature of this pattern was similar for both single flashes and trains of flashes. The results suggest that the onset of stimulation triggers a process which has a marked effect on both the cortical and perceptual response to subsequent stimulation.

The perceived number of flashes has been compared to the actual number of flashes presented (1-4). In these studies, short trains of flashes (0 to 1000 msec) were presented at a rapid rate (20 to 50 flash/sec) under conditions where the flashes appeared to be flickering but where each presented flash could not be counted individually. The flashes were somehow grouped into perceptual units of approximately 100 msec, the perceived number of flashes being much less than the actual number of flashes presented. For example, when 14 flashes were presented at 30 flash/sec (a flash-train duration of 430 msec) subjects most frequently reported seeing four flashes, a perceived flash being added for approximately each 100 msec of stimulation (1, 2).

In working with averaged cortical potentials evoked by stimulus conditions similar to those used in the above experiments, we noted (i) that the temporal nature of visually evoked cortical potentials appeared to be related to the number of flashes perceived, and the occurrence of each successive perceived flash appeared to correspond with the occurrence of the successive components of the evoked response pattern, and (ii) that the temporal characteristics of cortical responses evoked by trains of flashes appeared to be similar to those evoked by single flashes. These observations suggest that "the onset of stimulation in some way initiates a process (or processes) which can have a marked influence on the perceptual response to any succeeding

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Fig. 1. Evoked cortical potentials elicited by flash-trains containing 1, 4, 8, and 12 flashes. Flashes were presented at 33.3 flash/sec. Background illumination 602.6 mlam and fixation point directly on flash source. Each of the three superimposed evoked cortical potential traces represents the summation of responses to 100 flash-trains. Negativity downward. Subject is C.W. stimulation" (3). We investigated the relation between the temporal nature of evoked cortical potentials initiated by single flashes and trains of flashes and the number of flashes that were perceived.

Four subjects were presented trains of flashes containing from 1 to 14 flashes. Longer trains were not used because the variability in judgment becomes too great for our present purposes. The flashes were presented at 33.3 flash/sec (there was an interval of 30 msec between flashes) and, therefore, the flash-train duration varied from 0 to 390 msec. Since the subjects did not always report the same perceived number of flashes to a given number of flashes presented, the subjects reported their perceptual response after each flash-train presentation. Each subject participated in three experimental sessions; in every session each of the 14 flash-trains was presented 50 times. A given flash-train was randomly selected and presented 25 times; then, another flash-train was randomly selected from those remaining and presented 25 times; this procedure was continued until all the flash-trains were



Fig. 2. Effects of number of flashes presented on evoked cortical potentials (*ECP*) and perceived number of flashes  $(N_s)$ . Flashes were presented at 33.3 flash/sec. Each of the three superimposed evoked cortical potential traces represents the summation of responses to all flash-trains within a single session (700 flash-trains consisting of 1 to 14 flashes). Negativity downward. Frequency of  $N_s$  reflects the number of times each flash-train was perceived as 1, 2, 3, 4, 5, or 6 flashes, each flash-train being presented 150 times. Due to conduction time-lag, flash-train onset is displaced 35 msec after trace onset.

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presented. Therefore, the three sessions, four subjects, 14 flash-trains, and 50 flash-train presentations resulted in a total of 7000 observations.

The light flashes (4 mm in diameter and 10  $\mu$ sec in duration) were viewed binocularly with the subject's eves 60 cm from the flash source. The subjects fixated a point 5 mm above the flash source. The number (1 to 14) and frequency (33.3 flash/sec) of flashes within each flash-train, as well as the time interval between flashtrains (1.5 second), were controlled with an American Electronic Laboratory model 104A laboratory stimulator which triggered a model PS-2 Grass photostimulator set on intensity 2. The flashes were approximately 2.5 log intensity units above threshold and were surrounded by a white homogeneous field (18.3 mlam). These conditions elicited a simple sinusoidal evoked cortical potential wave form and a clear perception of flicker.

Evoked cortical potentials were obtained in response to the same flashtrains used to elicit the perceptual judgments. The procedure used for recording evoked cortical potentials has been described (5). Briefly, potentials were recorded monopolarly from the occipital region of the scalp, the active electrode being placed 2.5 cm above the inion and 2.5 cm to the right of the midline. The reference electrode was attached to the right ear lobe. The potentials were amplified by an Offner type R dynograph and averaged with a Mnemotron model 400C computer of average transients. The averaged potentials were recorded on graph paper with a model 135C Moseley autograph (X-Y plotter).

The effects of the number of flashes in the flash-train on the resulting evoked cortical potential are illustrated in Fig. 1. Consistent with past findings (3), the number of flashes of this size and intensity had no apparent differential effect on the evoked potential wave form. Although Fig. 1 contains data from only one subject (C.W.) and four flash-trains (containing 1, 4, 8, and 12 flashes), these data are typical of all the flash-trains and subjects investigated. Therefore, in the remaining figure, the responses elicited by all the flash-trains are combined into a single average potential for each subject and each session.

The relation between evoked potential wave form and the number of flashes perceived is illustrated in Fig. 2. The solid lines show the oscillations in the averaged evoked cortical potential wave form and the dotted lines show the frequency that each perceived number of flashes  $(N_s)$  was reported. For example, subject C.W. most frequently reported seeing one flash when one to four flashes were presented, two flashes when four to seven flashes were presented, three flashes when seven to ten flashes were presented, and so forth.

The results indicate that there was an initial fusion period, after the onset of stimulation, when the short flash-trains were perceived as fused (the subjects most frequently reported seeing one flash). The duration of the fusion period varied between subjects, ranging from 50 to 100 msec (flashtrains containing three to five flashes). In all cases, this period ended after the first major deflection in the evoked cortical potential wave form. Otherwise, there was no apparent relationship between the evoked potential wave form and the perception of number during this period.

After the initial fusion period, that is, when the subjects most frequently reported seeing two or more flashes, the periodicity of the averaged evoked potentials appears to reflect the rate at which the successive perceived counts were added up to 350 msec after the onset of the flash-train. This relationship did not hold for subjects M.L. and R.H. when flash-trains longer than 350 msec were presented. To compare the rates at which the successive evoked potential components and the successive perceived counts were added, the average interval between the points in time when each  $N_s$  was maximally perceived was compared to the average interval between the corresponding evoked cortical potential peaks or troughs (whichever the case may be). The respective average between count and between component intervals for each subject (in msec) were 103 and 107 (C.W.), 95 and 102 (M.L.), 97 and 90 (R.H.), and 102 and 103 (J.A.). If the similarity of these two average periods is a coincidence, it is indeed a striking one. Furthermore, the fact that both measures have 10 counts per second has considerable generality in view of the number of studies which have reported evoked potential data (3, 6) and perceptual data (1-4) similar to that reported here.

Our results may be summarized as follows: (i) the temporal nature of averaged evoked cortical activity was similar for potentials evoked by both single flashes and trains of flashes; (ii) the first large deflection in the averaged evoked cortical potential wave form appeared to reflect the minimal period of time required for the perception of two flashes, assuming a conductiontime latency of 35 msec; and (iii) after the initial fusion period, the periodicity of the averaged evoked cortical potential wave form appeared to reflect the frequency at which additional perceptual flashes were added for flash-trains up to 350 msec in duration. (Sufficient data were not collected to speculate on this relationship for longer flashtrain durations.) These and other results suggest that the onset of stimulation initiates a central process which may have a marked effect on both the cortical and perceptual response to subsequent stimulation.

In conclusion, the findings of our study possibly are related to those of other studies concerned with cortical excitability cycles in humans (7, 8). In these studies, the excitability of the cortex was shown to fluctuate rhythmically after stimulation by a brief flash of light; when a pair of flashes was presented, the amplitude of the evoked cortical potential resulting from the second flash varied as a function of the time between the two flashes. The evoked cortical potential wave form elicited by the first flash may reflect the periodicity of the excitability cycle (8). In humans, a complete excitability cycle had a duration of approximately 100 msec, which is in accord with the duration of each perceived flash and evoked potential oscillation in our experiment. Apparently the flashes presented within a single excitability cycle (possibly reflected by the periodicity of the evoked cortical potential wave form) were grouped into a single perceptual unit and were perceived as a single flash. These findings are relevant to the current theoretical interest in the concept of central intermittency in perception (2, 9).

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### **References and Notes**

- D. M. Forsyth and A. Chapanis, J. Exp. Psychol. 56, 385 (1958).
   C. T. White, Psycholog. Monogr. 77, Whole 2. C.
- 3. 632 (1967).
- 4. P. G. Cheatham and C. T. White, J. Exp.
- F. G. Cheatham and C. I. white, J. Exp. Psychol. 44, 447 (1952); C. T. White and P. G. Cheatham, *ibid.* 58, 441 (1959).
   R. G. Eason, L. R. Aiken, C. T. White, M. Lichtenstein, Perceptual Motor Skills 19, 875
- (1964). 6. R. G. Eason, D. Oden, C. T. White, *Electro*-
- encephalog. Clin. Neurophysiol., in press. 7. L. Cigánek, Ann. N.Y. Acad. Sci. 112, Art. 241 (1964).
- 8. H. Gastaut, A. Roger, J. Corriol, R. Naquet, Electroencephalog. Clin. Neurophysiol. 3, 401 (1951).
- 9. P. Bertelson, Quart. J. Exp. Psychol. 18, 153 R. Harter, *Psychol. Bull.*, B. Lindsley, *Electroencephe ophysiol.* 4, 443 (1952); J. (1966); M. R press; D. B. Psychol. Buu., Electroencephalog. (1952): J. M. press; Clin. Neurophysiol. 4, 443 (1952); J. M. Stroud, in Information Theory in Psychology, H. Quastler, Ed. (Free Press, Glencoe, Ill., 1955), p. 174; N. Wiener, *Cybernetics* (Wiley, New York, 1948), pp. 156-167.
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# Permanence of Retrograde Amnesia Produced by Electroconvulsive Shock

Abstract. The permanence of retrograde amnesia produced for a single training trial by a single electroconvulsive shock was studied. No recovery from amnesia was found with either single or repeated retention tests. Amnesic effects were found to be permanent with retention intervals as long as 1 month.

Electroconvulsive shock (ECS) can produce amnesia in animals, if applied shortly after training (1). It has generally been assumed that ECS produces amnesia by disrupting time-dependent processes which underlie memory storage (2). This interpretation has been supported by evidence that the amnesia produced by a single ECS given shortly after a single learning trial is permanent for at least 1 month (3).

This permanence of amnesia produced by ECS has been seriously questioned in recent reports (4). Zinkin and Miller have reported evidence which indicates that amnesia produced by ECS may diminish when animals are given repeated retention tests. However, their data do not permit determination of the basis for the increased response latencies used to index recovery of retention. The change in performance may have arisen from several sources: repeated exposure to the test situation, passage of time after ECS treatments, or simply, nonrein-