

## EFFECTS OF CORTICAL LESIONS IN MONKEYS ON CRITICAL FLICKER FREQUENCY<sup>1</sup>

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In 1947 Halstead proposed that the frontal lobes are the portion of the brain most essential to "biological intelligence." This conclusion was based on the finding of a gradient of impairment in brain damaged patients such that, over a large series of tests, patients with occipital removals obtained the highest performance scores, those with temporal and parietal removals made intermediate scores, while the lowest scores were obtained by patients with prefrontal removals.

Among the battery of tests which Halstead used to establish this gradient of impairment following brain injury was a test of critical flicker frequency (CFF), defined as that frequency of flickering light which just gives the impression of steady light. The results on this test exactly paralleled those for the battery as a whole: Occipital removals were associated with the highest CFF, temporal and parietal removals with a somewhat lower CFF, while the lowest critical flicker frequencies were found in the patients with prefrontal removals.

The results of ablation studies carried out on monkeys over the past 10 years have not conformed to this pattern of a single trans-cortical gradient for "biological intelligence." Rather, it has been found that while frontal cortex is indeed maximally important for certain types of complex behavior, others are affected maximally by posterior cortical lesions (Harlow, Davis, Settlege, & Meyer, 1952). With respect to difficult visual discriminations in particular, lesions in frontal cortex have been found repeatedly to produce

very little impairment compared with that produced by posterior lesions (Warren & Harlow, 1952; Pribram, 1954); and within posterior cortex, it has been found that temporal lesions produce less impairment than occipital lesions on visual differential thresholds (Wilson & Mishkin, 1959). Thus, unless CFF is unique among difficult visual discriminations, a test of CFF in brain-damaged monkeys would be expected to reveal a trans-cortical gradient of impairment which is just the reverse of that reported by Halstead for brain-damaged patients.

### METHOD

#### *Subjects*

Twelve experimentally naive, immature rhesus monkeys served as Ss. These were run in three replications, each consisting of an anterior frontal, an inferotemporal, a lateral occipital, and an unoperated control monkey.

#### *Lesions*

The Ss were anesthetized with 6% Nembutal (0.6 cc/kg body wt, injected intraperitoneally). Using aseptic precautions, anterior or posterior bone flaps were turned in those Ss that were to receive frontal or occipital lesions, while in those that were to receive temporal lesions the bone over the area to be excised was removed completely. One-stage, bilaterally symmetrical cortical lesions were made by aspiration with a small-gauge sucker. Wounds were closed in anatomical layers with silk sutures, the brain being protected by the replaced bone flaps, or, in those Ss that had had bone removed, by the thick temporal muscle.

The area of cortical damage in the anterofrontal Ss corresponded closely to von Bonin and Bailey's (1947) areas FD; in the inferotemporal Ss, to their areas TE and TF; and in the lateral occipital Ss, to the lateral portion of their area OC, i.e., that portion of the striate cortex which is believed to serve macular vision. (The occipital operations also indirectly involved a part of OB posterior to the lunate sulcus, due to the degeneration of this area following damage to adjacent OC.) The approximate loci of the three types of ablations are shown in Figure 1. Reconstructions have been omitted from this report since histological study of the

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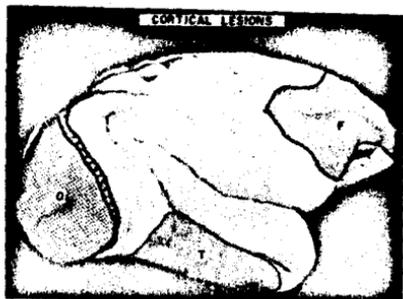


FIG. 1. Approximate loci of frontal (F), temporal (T), and occipital (O) lesions.

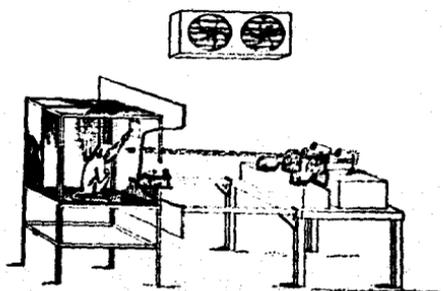


FIG. 2. Schematic drawing of discrimination apparatus.

photocell pickup of the flickering light (vertical plates). When the two signals were synchronized, i.e., when the flicker rate matched the oscillator setting, a stationary Liassjoue pattern appeared on the oscilloscope screen. The rate of flicker of the so-called "steady" light was checked periodically in a similar fashion.

#### Procedure

The variable flickering light was set initially at a rate of 30 cps, which appeared to the *Es* as an obvious flicker. The *Ss* were trained to press the panel located above the translucent disc when the disc was illuminated by this flickering light, and to refrain from pressing the panel when the disc was illuminated by the steady light. A panel press switched off the light; otherwise, the light remained on for 5 sec., after which it was switched off automatically. The correct response of pressing off the flickering light was followed immediately by the delivery of a food pellet, while the correct response of *not* pressing off the steady light was followed by delivery of a food pellet at the moment the steady light was switched off automatically. The pellets were made of lab chow and pulverized peanut (P. J. Noyes Company, Lancaster, N.H.), and were delivered by a pellet dispenser into a food dish below the panel. Food delivery was accompanied by the illumination of a 7-w. food-dish lamp for 1.5 sec., and this was followed by a 5-sec. intertrial interval during which a 40-w. overhead lamp was illuminated. An incorrect response, consisting either of pressing off the steady light or of failing to press off the flickering light, was followed by the 5-sec. interval with the overhead light and then re-presentation of the stimulus until the *S* responded to it correctly. This rerun correction technique, wherein each trial ended with a rewarded response, was used throughout the course of the experiment.

A daily session consisted of 20 "flicker-go" trials and 20 "steady-no-go" trials, presented in a balanced sequence which was varied daily. The *Ss* were trained on the preliminary discrimination, i.e., between the steady light and the light flickering at 30 cps, to a criterion of 92.5% correct in one session (37 correct responses out of 40). When this criterion was met, the rate of the flickering light was increased beyond 30 cps in 5-cps steps to 35, 40, 45, etc., each of these flicker

lesions in the present group of animals indicated that they were similar in all respects to other frontal, temporal, and occipital lesions for which reconstructions are already available (Mishkin & Pribram, 1955; Wilson & Mishkin, 1959).

#### Apparatus

The testing apparatus, shown schematically in Figure 2, was placed in a ventilated, soundproofed room, and automatic programming equipment and event counters were placed in an adjacent room. The two rooms were joined by a one-way-vision window.

Stimuli were obtained by projecting the narrowed beam of one or the other of two 20-c.p., 6-v. d.c. lamps onto a circular translucent disc,  $\frac{1}{4}$  in. in diameter, inserted in the side of the testing cage. The stimuli generated by the two separate sources had matched brightness values of 5.25 ft.-c. Each beam was interrupted by its own rotating sector disc consisting of two equally spaced, 90-degree vanes, resulting in a light-dark ratio of 1 to 1. It should be noted that while only one lamp was illuminated at a time, both sector discs revolved continuously.

One sector disc rotated at the fixed speed of 70 rps, producing a flicker rate of 140 cps when its lamp was illuminated. This disc was driven and regulated by a universal motor to which a very light governor was attached. The resulting flicker rate of 140 cps is far above the CFF for man and it is hereafter referred to as the "steady" light.

The rate of the other sector disc could be varied between 10 and 70 rps, producing flicker rates between 20 and 140 cps when its lamp was illuminated. The main driving torque for this disc was also supplied by a universal motor, the speed of which could be roughly controlled by a Variac. Precise control, however, was achieved by the use of a high-powered phonic wheel mounted on the same shaft as the motor. The phonic wheel, composed of a field coil and a two-pole rotor, was connected to the amplified output of an oscillator. By properly adjusting first the Variac and then the oscillator controls the rotating disc could be driven, and then "locked," at any desired speed. The adjustments were monitored on an oscilloscope which was connected to the oscillator (horizontal plates) and to a

rates being paired with the steady light for one daily session, until the S's correct responses on any one day fell below 75%. Since chance performance in this situation was 50% correct, CFF was defined as the interpolated 75% point, i.e., that rate of flickering light which S discriminated from the steady light one-half the time. To avoid extinguishing or disrupting the discrimination habit on which the measurement of CFF depended, the day after S's correct responses fell below 75%, the rate of the flickering light was decreased by one 5-cps step each day until the S scored 92.5% once again. From these data the flicker rate at the 75% point, and also that at the 92.5% point, were calculated both for the ascending (increasing flicker rate) and for the descending (decreasing flicker rate) runs. Data for eight pairs of ascending and descending runs, extending over approximately two months of daily testing, were gathered on each of the 12 Ss before operation.

After completing the threshold runs, each S received, in addition, two control sessions, first with a flicker rate which was one 5-cps step higher than any it had yet received, and then with an even higher flicker rate of 100 cps. In these last two preoperative sessions all Ss obtained subthreshold and near-chance scores, respectively, indicating that rate of flicker was in fact the stimulus dimension along which the Ss had been discriminating.

When each replication of four Ss completed preoperative training, three Ss were operated, each receiving a different one of the three types of lesion, and the fourth was kept as an unoperated control. The Ss in the first replication were assigned randomly to the four groups. With each of the next two replications, however, an attempt was made to so assign the Ss that the groups would be equated for final preoperative thresholds. Beginning two weeks after operation, all Ss were retrained to criterion on the discrimination of the 30-cps light vs. the steady light, tested for eight paired ascending and descending runs, and then given the two control sessions.

Finally, beginning six months after operation, the eight Ss in the first two replications were run through the entire testing series once again.

### RESULTS

Preoperatively, the 12 Ss formed the basic discrimination between the flickering light and the steady light in an average of 21 sessions. Their subsequent performance on the alternating ascending and descending threshold runs yielded the critical flicker frequencies shown on the left in Figure 3. There are two effects which may be noted in this curve: First, CFF rises steadily with training; and, secondly, the CFFs on ascending runs (increasing rates of flicker) are slightly higher than those on descending runs (decreasing rates). Every monkey showed both effects. It should be noted further that by the end of preoperative training the four experimental groups-to-be

were evenly matched, their final CFFs (averaged for the last two pairs of ascending and descending runs) falling within 1 cps of each other.

Following the operations all Ss relearned the basic discrimination between the 30-cps light and the steady light in far fewer sessions than they had required initially. Nevertheless, there was a small but consistent difference among the groups: The frontal Ss and the unoperated controls reattained the 92.5% criterion in an average of only one or two sessions, while the temporal and occipital Ss required an average of six to eight retraining sessions. There was no overlap among the Ss in these two pairs of groups.

It may be seen in Figure 3 that the same pattern of group differences, separating the frontal and control groups on the one hand from the temporal and occipital groups on the other, reappeared when their thresholds were tested. On the first two determinations after operation, all frontal and control Ss had CFFs which were equal to or higher than their final preoperative values, but the CFFs of five out of the six temporal and occipital Ss fell from their preoperative values. Using the control group's performance as a baseline, the average reduction in the CFFs of the temporal and occipital groups was 9 and 7 cps, respectively. The differences were evaluated by Dunnett's

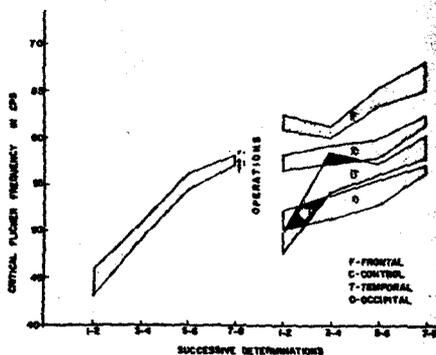


FIG. 3. Critical flicker frequencies before and after operation. The eight successive determinations at each stage are grouped into four successive pairs. The upper boundary of each shaded curve represents CFFs on ascending runs; the lower boundary, CFFs on descending runs.

(1955) multiple-comparison procedure, and both were found to be significant at the .05 level ( $F$ 's of 5.13 and 2.60, respectively). In contrast to these postoperative decreases in CFF, the CFF of the frontal group increased after operation, though the increase was not significantly greater than that of the controls.

With further testing, the discrimination performance of the occipital, and particularly, of the temporal Ss improved, so that by the last two determinations they had recovered most or all of their initial postoperative losses. Nevertheless, because the performance of the other Ss also improved, a small impairment was detectable in the Ss with posterior lesions throughout the postoperative period. This was determined from an analysis of variance of the postoperative threshold data. The first part of the analysis evaluated group differences averaged for all eight pairs of ascending and descending runs. The sum of squares for the variance among groups (with 3  $df$ ) was subdivided into three independent sums of squares (each with 1  $df$ ) according to the method for orthogonal comparisons described by Cochran and Cox (1950). The three independent comparisons were (a) frontal and control Ss vs. temporal and occipital Ss, (b) frontal Ss vs. controls, and (c) temporal vs. occipital Ss. Each comparison was tested against an error term (with 6  $df$ ) from which the variance due to replication differences had been removed. The first comparison yielded a significant  $F$  value of 7.75 ( $p < .05$ ), confirming the prediction that Ss with posterior lesions would have lower CFFs than would Ss with frontal lesions and controls. The results of the second comparison also conformed to prediction in that the CFFs of the frontal and control Ss were not significantly different from each other. The results of the third comparison, however, failed to confirm the prediction that occipital Ss would have significantly lower CFFs than temporal Ss, although the difference was in the expected direction.

The second part of the analysis involved the correlated scores. The only  $F$  ratios which attained significance were those for successive threshold determinations ( $F = 5.69$ ,  $p < .05$  with the minimum of 1 and 8  $df$ ) and for CFFs on ascending vs. descending runs ( $F = 26.68$ ,  $p < .001$  with 1 and 8  $df$ ). Thus, as in the pre-

operative tests, Ss improved with training and had higher CFFs on ascending than on descending runs. There were no differences on these measures among the groups, however, as indicated by the fact that none of the interaction terms was significant.<sup>2</sup>

One potential source of group differences which was not examined in the preceding analysis relates to the kind of errors the Ss made. Two types of errors were possible in this situation: Pressing the panel in the presence of the steady light an error of commission; and failing to press in the presence of the flickering light an error of omission. An analysis of the errors (excluding those made on re-presentations within a trial) revealed that 75% to 80% were errors of commission, and this was so for all groups, and whether the discrimination was relatively easy or difficult (i.e., above or below threshold). The distribution of the two types of errors was thus found to be related, not to the amount of confusion between the lights, but, rather, to the Ss' preferred mode of response, a preference that was unaffected by any of the cortical lesions.

One final aspect of performance which was examined for group differences was the shape of the discrimination function as it fell from nearly 100% correct responses to chance. Figure 4 presents such discrimination functions for the four groups postoperatively, as well as an average curve for all Ss preoperatively. The shape of the preoperative curve was estimated from five values selected as follows (refer to procedure):

1. Final performance on the preliminary discrimination
2. 92.5% points on the last two determinations
3. 75% points, or CFF, on the last two determinations
4. performance on the first of the two control sessions; and
5. performance on the second control session.

The same procedure was followed to obtain the postoperative curves. No differences are apparent in the slopes of the discrimination functions for the various groups. Rather, differences in thresholds among groups were reflected in roughly comparable differences

<sup>2</sup> The detailed statistical analyses of the postoperative thresholds are available on request.

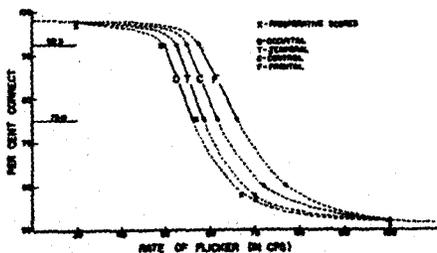


FIG. 4. Percentage of correct responses on the discrimination between flickering light and steady light as a function of the rate of flicker.

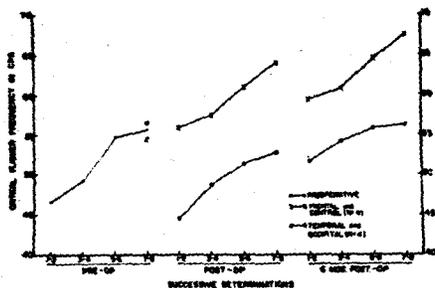


FIG. 5. Critical flicker frequencies of the eight Ss tested at all three stages of the experiment.

both above and below threshold, resulting in the horizontal displacement of the entire curve from one group to the next. Compared with the final level of preoperative performance, only the occipital Ss failed to show any postoperative improvement; and of the others, the temporal Ss improved the least.

All of the foregoing analyses were based on the first series of postoperative tests which were completed within the first three months after operation. The results of the second series of tests, covering the period from six to about nine months after operation, are plotted on the right in Figure 5. Only the 8 Ss in the first two replications were run on this second series. Successive thresholds were averaged for all 8 Ss preoperatively, and for the two pairs of groups—i.e., the frontal and control Ss vs. the temporal and occipital Ss—postoperatively. It can be seen that the impairment found in the Ss with posterior lesions immediately after operation persisted through the end of the

second testing period. There was no overlap between their thresholds and those of the frontal and control Ss.

#### DISCUSSION

Two characteristics of the CFF, the steady improvement with training and the superiority of thresholds on ascending runs, were noted in all groups of animals at all stages of the experiment. These would seem to deserve further discussion. The first effect, improvement with practice in discriminating along a single physical dimension, has been described before in the literature on sensory acuity in animals (Gibson, 1953). What is, perhaps, surprising in the present study, is that the unoperated Ss learned to make finer and finer discriminations throughout the entire course of the experiment. For any given S the experiment covered nearly one year, and the steadily accumulated improvement in CFF amounted to as much as 25 cps, with no indication that the limits of improvement had yet been reached. This is a striking demonstration of the influence of learning on the measurement of what is commonly considered to be a stable sensory function.

An influence of learning on CFF is also suggested, though less directly, by the finding that the CFF on ascending runs was consistently higher than that on descending runs. Superficially this phenomenon resembles one which often appears in human psychophysical experiments when the method of limits, or serial exploration, is used. Thus, in man, also, a gradually increasing rate of flicker yields a higher CFF than does a gradually decreasing rate (Knox, 1945). However, the similarity between the phenomena is probably only coincidental, for when man's CFF is determined by serial exploration, the rate of flicker is varied in an orderly sequence from moment to moment, whereas in the present experiment the rate of flicker was varied only from day to day. It thus seems unlikely that the present results reflect an "inertia" of the flicker experience on ascending runs, and of the fusion experience on descending runs, as has been inferred for man (Knox, 1945). It is more reasonable to suppose that when the Ss in the present study could no longer discriminate

reliably the flickering light from the steady light at the end of an ascending run, their learned observing or differential panel-pressing responses underwent partial extinction from which they did not recover until some time after the start of the descending run. According to this analysis, the CFFs even of highly overtrained normal Ss were periodically lowered due to the periodic disruption of their learned responses.

The evidence that various learning factors were important determinants of the CFF in normal Ss helps to explain the unexpected finding that a lesion outside the primary visual system was nearly as effective as a lesion within it in reducing the CFF. Previous work points to an impairment in learning as the principal source of the visual disturbance associated with inferotemporal lesions (Wilson & Mishkin, 1959). This, together with the recognition that CFF is jointly determined by sensory and learning processes, suggests that occipital and temporal damage may have produced similar effects on CFF by interfering with quite different mechanisms. Thus, inferotemporal lesions may have interfered with retention of the level of discrimination learning that the Ss had attained preoperatively; also, their learned observing and instrumental responses may have been more easily disrupted by the proposed extinction process, particularly just after operation. The impairment following occipital lesions, on the other hand, was presumably the result of direct interference with sensory processes, though the precise nature of the sensory impairment—macular field defect, amblyopia, or some quite different abnormality—remains to be determined.

In contrast with the lasting deficits displayed by the animals with posterior lesions, there was no evidence of impairment in the animals with frontal lesions at any stage of the experiment. In this respect, the results on critical flicker frequency are consistent with those ordinarily obtained on difficult visual discriminations in brain-damaged monkeys. While these results reverse the transcortical gradient of impairment in CFF originally reported for man (Halstead, 1947), it should be noted that they are in agreement with more

recent investigations in man (Battersby, Bender, & Teuber, 1951; Battersby, 1951; Medina, 1957) which have also failed to obtain evidence of a reduction in CFF following damage to the frontal lobes, but have found, instead, a significant and lasting depression in this function following damage to the occipital lobes.

## SUMMARY

The critical flicker frequencies of 12 monkeys were determined by a modified "method of limits" before and after various cortical ablations. The results confirmed the prediction, based on studies of other visual functions in monkeys, that CFF in this species would not be impaired by anterior frontal lesions, but would be impaired by both inferotemporal and lateral occipital lesions. These findings are compared with the results of investigations of CFF in brain-injured men.

Certain characteristics of the animals' performance provided evidence of the important influence of learning on the CFF. It is suggested that occipital and temporal lesions may have had deceptively similar effects on this function by interfering with sensory and learning mechanisms, respectively.

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MORTIMER MISHKIN AND LAWRENCE WEISKRANTZ

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## EFFECTS OF SPACING OF TRAINING AND GANGLIA REMOVAL ON CONDITIONING IN EARTHWORMS<sup>1</sup>

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A recent study by Ratner and Miller (1959) clearly demonstrated conditioning of a withdrawal response with earthworms as an earlier study had done with flatworms, members of a lower phylum (Thompson & McConnell, 1955). Prior research with earthworms had emphasized learning of orienting movements in such situations as a T maze, and several of these studies indicated that removing the "cerebral" ganglia did not impair the previously learned response nor did it preclude learning of the response (Yerkes, 1912; Heck, 1920). However, at the present time, no information is available about the effects of removing these ganglia on a classically conditioned response.

Those variables which have been found to affect learning with vertebrates have in general not been investigated with invertebrates. Since the previous Ratner and Miller study (1959) had found only 42% CRs at the end of conditioning using earthworms with moderately massed training, the massing variable was selected for co-investigation with the extirpation variable in this study. Specifically, the present study was designed to investigate with earthworms in a factorial design the effects of removing the pharyngeal ganglia and the spacing of trials on the conditioning of a withdrawal response and the reconditioning of this response after a rest period.

### METHOD

#### Subjects

Sixty earthworms, *Lumbricus terrestris*, varying in size from 121 to 240 segments were obtained from a plot of ground on the Michigan State University campus. The Ss were kept in sphagnum moss during the short trip from their natural habitat to the laboratory. On arrival at the laboratory, the worms were assigned

randomly to one of six groups and used immediately under their assigned conditions. The experiment was conducted during June, July, and August.

#### Apparatus

Essentially the same apparatus was used in this study as was used in the earlier study by Ratner and Miller (1959). The main part of the apparatus consisted of a clear, round Koroseal tube which was 62.5 cm. long with an inside diameter of 0.8 cm. The tube was vented on the top and sides with small holes and was set on a plywood base so that the ends of the tube met and made a circular runway in which the worms were contained. A 6-v. d.c. bell buzzer with buzzer removed was attached on the plywood base at the center of the circle formed by the Koroseal tube. One No. 2 G.E. photo flood bulb in a spun-aluminum reflector was mounted 46 cm. above the tube and constituted the source of the US. A ruby-red darkroom bulb provided general illumination.

All parts of the apparatus, for example, stop-watch holder and clock, which could have produced vibration, were padded with foam rubber. Two identical pieces of apparatus were constructed so that two Ss could be run, one during the intertrial interval of the other. The CS and US were timed and automatically presented by Time-O-Lite and Hunter Decade Interval timers. Latency of the CR was timed by an electric stop clock which was activated by the CS timer and stopped by a microswitch operated by E.

#### Procedure

The six groups of Ss, each of which contained 10 worms, were: normal, spaced-trial group (NS); normal, massed-trial group (NM); operated, spaced-trial group (OS); operated, massed-trial group (OM); operated, spaced control group (OSC); and operated, massed control group (OMC). Each S in the normal groups, that is nonoperated groups, was removed from the sphagnum moss and allowed to crawl, anterior end first, into one end of the Koroseal tube which had been moistened with 0.6 cc. of water. The ends of the tube were then fastened together with thin wire so that S had a tubular circle to traverse. A 20-min. adaptation period followed during which time the 8-c.p. ruby-red bulb was illuminated.

Following this adaptation period, Ss in Group NM were given a total of 90 conditioning trials with a 10-sec. intertrial interval except for a 20-min. rest in the apparatus between Trials 80 and 81. A conditioning trial consisted of a 6-sec. presentation of the vibratory stimulus (CS), after the first 4 sec. of which the light (US) was presented for 2 sec. Thus, the CS and US

<sup>1</sup> The experiment reported here was submitted by the second author in partial fulfillment of the requirements for the MA in psychology at Michigan State University.

<sup>2</sup> Now with Armor Human Research Unit, Fort Knox, Kentucky.