THE INTERACTION OF VISUAL ATTENTION AND TEMPORAL CORTEX STIMULATION ON ELECTRICAL ACTIVITY EVOKED IN THE STRIATE CORTEX

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As one looks at either single cell firing patterns (Polyanskii 1967) or at potentials measured by macro-electrodes (Evarts et al. 1960), it becomes clear that all cells do not react equally to excitation all the time. Rather, an "excitability cycle" characterizes responsiveness. For example, a second flash of a pair does not evoke a response that is as large as the first one until they are separated by approximately 100 msec or more. Subsequent periods of augmentation and depression can often be seen (Bartley and Bishop 1933; Chang 1950).

Because the excitability cycle affects redundancy in neural channels, it has been regarded as theoretically important for the assessment of information processing characteristics (Harter 1967). The demonstration that stimulation of the infero-temporal (IT) cortex of monkeys slowed considerably the time needed for the recovery of potentials evoked to a second flash (Spinelli and Pribram 1966) could therefore be of importance to an understanding of the role of this structure in visual information processing (e.g., Wilson and Kaufman 1968).

The present study began initially as an attempt to replicate the Spinelli and Pribram finding so that it could be extended to show how ablation of the IT cortex affects the recovery cycle to double flashes. The first experiment reports a failure to find the original effects. The results of this failure could be understood, however, if it were assumed that the state of the monkeys being tested was a crucial variable which could prevent the occurrence of the effects observed by Spinelli and Pribram. The second experiment reports the utilization of a measure of this state to show that it is sensitive to environmental variables inducing attention. In the third experiment, variations in this measure are used to judge the state of the striate cortex. Flash recovery cycles occurring when the measure indicates a low state of visual attention are separated from those occurring during a high state of attention. The recovery cycles obtained under the condition of high attention are shown to be similar to those obtained in the Spinelli-Pribram experiment. Finally, in the fourth experiment, it is shown that stimulation of the IT cortex produces the same effects on the state of the striate cortex as those utilized in the second experiment to induce attention.

EXPERIMENT 1

Methods

Subjects. Four adolescent rhesus monkeys anesthetized with Nembutal, 35 mg/kg, received 24 bipolar, nichrome wire (300 μ) electrodes for electrophysiological recording. Each electrode tip was uninsulated for 1 mm, and the tips were vertically separated by approximately 2 mm. Electrodes were placed in the IT cortex (2 or 3 pairs bilaterally), parietal cortex (1 pair bilaterally), striate cortex (6 pairs bilaterally), lateral geniculate body (1 pair bilaterally) and the optic nerve (1 or 2 pairs) of each monkey. Cortical and optic nerve electrodes were placed by visual guidance, whereas the geniculate...
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Electrodes were placed stereotaxically. The monkeys were used in an experiment on the habituation of evoked potentials to tone and to light before use in the present experiment.

**Apparatus.** Two AEL stimulators and isolation transformers were used to generate biphasic electrical pulses for IT cortical stimulation or to trigger double flashes from a Grass PS-2 photo-stimulator (intensity 4). The pulses delivered across each electrode pair were monitored to insure 1 mA of current (at offset) bilaterally at the IT cortex for 1 msec, at the rate of 10 c/sec. The electrodes usually required from 5 to 15 V to achieve this current. The photoflash strobe unit was placed in front of a translucent screen on the door of the shielded test chamber in which the monkey sat. The strobe light was placed at head level, and the translucent screen was approximately 9 in. in front of the monkey.

Each monkey was placed in a restraining chair in the shielded experimental box, and two Microdot cables were attached to each 25-pin Microdot connector set in dental acrylic on the monkey's head. The electrodes were connected to Tektronix 122 pre-amplifiers and Philbrick P65 amplifiers via the Microdot cables, and the brain activity was amplified 15,000 times. Usually two channels of amplified activity were then analyzed on line by a Mnemotron CAT 400A computer.

**Procedures.** Typically a monkey was placed in the restraining chair for 30 min, and in the shielded experimental box with electrode cables attached for 15 min before data acquisition; 50 flash pairs were then delivered for each experimental condition. IT stimulation and no-stimulation conditions were run. The order of intervals between flash pairs was 30, 60, 90, 120, 180 and 240 msec. Each flash pair was presented at a rate of 1 pair each 2 sec. Approximately 1 min elapsed in the interval between each sum of 50 pairs, during which Polaroid photographs of the results were taken and marked for identification. IT cortex stimulation was turned on for 5 sec before each series of 50 paired flashes and was turned off immediately after this series. This procedure was repeated on 4 separate days for each monkey.

**Results and discussion**

The results obtained in this experiment may be seen in Fig. 1. Clearly stimulation of the IT cortex did not affect the rate of recovery of the second flash of each pair. The means and ranges for the conditions with and without IT stimu-
lateral geniculate body (LGB) with 0.25-2 mA, 0.05-0.10 msec, once each 2 sec.

Procedures. In this experiment the effects of a visual attention condition were observed when the amount of current used to stimulate the LGB was varied. Visual attending was produced by allowing the monkey to see out of the front of its shielded box. This condition is called open box. The closed box condition differed from the open box condition not only by the behavioral attending that was observed but by the 1.5, compared to the 10, foot-candles of illumination measured by a Weston illuminometer at the position of the monkey's head. The open and closed box conditions were counterbalanced with respect to the 0.25, 0.50, 0.75, 1.00, 1.25 and 1.50 mA of current levels of LGB stimulation. Six striate cortex electrodes were tested in each monkey, each with three replications. Recording of 50 responses by the CAT was performed as in Experiment 1.

Results and discussion
In three of the four monkeys tested (S28, S29, S332) the later components of the averaged potentials evoked in the striate cortex by LGB stimulation were increased considerably by allowing the animal to look out of the front of the experimental box. A greater than 40 % increase was found in 3 out of 6, 2 out of 6, 1 out of 6 and 0 out of 6 of the electrodes tested.

If a change of state (e.g., attention) that slows recovery time is to be invoked as an explanation for the discrepant findings, it is necessary to find a sensitive monitor of this state in the visual pathway. In the following experiment, therefore, potentials evoked in the striate cortex by lateral geniculate stimulation are compared in situations producing differences in visual attending.

Methods
Subjects. Two of the monkeys used in Experiment 1 were also used here. In addition, two rhesus monkeys received chronically implanted electrodes similar to those of the previous animals but without optic nerve implants and with 2 extra pairs of lateral geniculate electrodes. These last two monkeys were experimentally naive.

Apparatus. The same stimulators, amplifiers and computer were used as in Experiment 1. One AEL stimulator was used for the 1 mA, 1 msec, 10 c/sec IT stimulation, and the other to stimulate the lateral geniculate body (LGB) with 0.25-2 mA, 0.05-0.10 msec, once each 2 sec.
in monkeys S332, S29, S28 and S331, respectively. As can be seen in Fig. 2, although the open box effect always enhanced the averaged potential, the effect is greatest beyond 0.5 mA of LGB stimulation current and reaches its maximum between 0.75 and 1.25 mA of current on the three monkeys showing the greatest difference between the open and closed box conditions. In all monkeys the effects were greatest at the surface negative wave which occurs at 4–12 msec onset latency. Indication that illumination per se is not the sole variable responsible for these differences can be seen in Fig. 3. In this figure, both records were taken during the open box condition, but in one case the monkey was staring blankly out the front of the box, whereas in the other it was looking at novel junk objects shown to it approximately each 10 sec. The open box condition initially increased the late negative wave by only 25% unless the monkey was repeatedly shown junk objects, in which case the surface negative component could be increased by another 58%. Eliminating pupillary changes with Neosynephrine (10%) did not reduce these differences. In the two remaining monkeys showing large amplitude increases in the open box condition, spontaneous visual sampling was frequent. The one monkey showing only 29% facilitation in the open box condition (S331) avoided looking out the front of the box when it was open. These results confirm those of Doty et al. (1964) who had also found that geniculo-striate potentials in monkeys were increased in amplitude by variables leading to enhanced attention.

A simple interpretation of these effects in terms of the non-specific or reticular arousal is not warranted; using the blocking of augmenting responses as an indicator of non-specific or reticular arousal (Gauthier et al. 1956), we found that in the three monkeys showing the most pronounced effects, augmenting responses produced by an 8 or 10 c/sec stimulation of the LGB were unaffected or increased by the open box condition. An example of this effect is shown in Fig. 4. Augmenting was blocked in the open box condition only in the monkey showing the smallest effect from opening the box (S331). Second, in one monkey reliably smaller geniculo-striate responses (and a concurrent fast, desynchronous, low voltage EEG) were produced when noises occurred outside the box while the monkey was in the closed box condition. This effect occurred in the same monkey and the same electrodes (S332) where in the open box condition the geniculo-striate potentials were increased when junk objects were shown.

**EXPERIMENT 3**

The results of Experiment 2 demonstrate that the state of visual attention is associated with larger geniculo-striate potentials and that changes in the size of these potentials might be used as a probe of changes of state during a flash recovery experiment. If visual attentiveness is responsible for the ceiling reached in recovery to flashes in Experiment I, then large geniculo-striate potentials should be associated with slower rates of flash recovery than would occur while small geniculo-striate potentials are moni-

tored. Also, small geniculo-striate potentials should occur very infrequently during the flash recovery test if the monkeys in Experiment 1 are predominantly visually attentive. This experiment examines these relationships.

Methods

Subjects. The same monkeys used in Experiment 2 were used again in this study.

Apparatus. The same stimulators and amplifiers used in the previous experiments were used here. In this experiment, however, the AEL stimulator that was used to deliver pulses (0.1 msec) once each 2 sec to the LGB (the same current level was used for an animal in all sessions), was also used to trigger the second AEL stimulator after a delay of either 50 or 100 msec. The current level that was used to stimulate the LGB in each animal was that level which produced the largest difference between open and closed box conditions in Experiment 2. The second AEL stimulator was used in turn to trigger double flashes from a Grass PS-2 Photoflash unit as in Experiment 1. Synchronizing pulses and brain activity were recorded with an Ampex SR-300 FM tape recorder. The recorded activity was then written out electrographically, using a Brush recorder at 25 mm/sec, and each geniculo-striate probe potential in an 'IT sensitive' electrode (cf. Experiment 4) was classified according to relative size at first major peak-to-peak amplitude as either small or large. The minimal large probe response was chosen to be twice the size of the maximal small probe response. The cut-off for size of the maximal small response was determined from cyclical changes that occurred over an entire recording session. When a reliable run of relatively large evoked potentials was followed within 2-5 transitional potentials by a run of 5 or more potentials of small appearance, this run was bracketed. The modal largest potential over all the bracketed runs was used as the size of the maximal small response. The recorded activity was then digitized and the pre-selected small and large classifications were each averaged on a PDP-8 general purpose computer.

Procedures. As in the first experiment, each monkey was placed in the restraining chair for approximately 30 min and in the shielded experimental box with electrode cables attached for approximately 15 min before data acquisition. The FM tape recorder was turned on for the duration of the experiment. From 100 to 120 triplets of LGB stimulation-flash 1-flash 2 were then run in the order 30, 60, 90, 120, 180 and 240 msec. Approximately 30 sec were allowed between each inter-flash interval. These tests were run in the closed box condition, and the room lights were extinguished so that background light leakage into the experimental box was reduced to approximately 1.5 foot-candles.

Results and discussion

In the previous experiment, the geniculo-striate responses were shown to be related to changes in visual attending. In the present experiment the size of the geniculo-striate probe proved to be an indicator of the sensitivity of the visual system to recovery. These results are graphed for all monkeys in Fig. 5; in Fig. 6 a sample (S29) is shown of the actual averaged responses to the LGB stimulation-flash-flash triplet at four inter-flash intervals. As can be seen, the time needed for flash recovery was generally greater when a large geniculo-striate probe response was present. The distribution in size of these responses was highly skewed toward large responses. In fact, the large probe responses usually occurred 2-4 times as often as small probe responses. These results indicate

In four monkeys the flash recovery functions are plotted for probe stimulation of the LGB which results in small (dashed line) or large (solid line) responses in the striate cortex. See text for details.

Fig. 6
A record of flash recovery, after either small or large responses in the striate cortex produced by the LGB probe stimulation, is shown at 4 inter-flash intervals (60, 90, 120 and 180 msec) in S29. Marks on the time axis below each pair of wave forms indicate the onset of the response to each flash. The amplitude calibration mark represents a 100 \( \mu \)V deflection.

Fig. 7
Comparison of flash recovery functions obtained when the probe stimulation of the LGB results in small (solid line) or large (dotted line) striate cortex response. Control without probe stimulation is indicated by dashed line.

that a predominately high state of attention will result in slowed flash recovery rates.

Another possible interpretation of these results is that the geniculo-striate probe activity is itself creating a recovery cycle that will fully account for slowed recovery with preceding large geniculo-striate probes and faster recovery with preceding small geniculo-striate probes. Since a period of depression usually follows LGB stimulation of up to 100 msec (Schoolman and Evarts 1959; Doty et al. 1964) it would seem that the order of events that should occur would be extreme attenuation of the first flash response amplitude after LGB stimulation, with less attenuation of second flash amplitude. In other words, faster recovery should be associated with larger geniculo-striate probes. In this experiment, the results are generally opposed to such an effect in the IT sensitive electrodes; slower flash recovery is associated with larger probes. Also, changes in flash recovery are associated with changes in second rather than first flash potentials (cf. Fig. 6). Some comment might be made as well on this hypothesis by comparing flash recovery cycles taken without concurrent LGB stimulation to those recovery cycles taken with the LGB probe. Fig. 7 shows such a comparison. Here nearly identical results are obtained when the preceding geniculo-striate potential is large (and not small) and when no LGB stimulation precedes the double flashes. If these recovery cycle differences are merely an artifact of following LGB stimulation by two flashes, then a most unusual set of recovery events would have to be postulated. The smaller the preceding geniculo-striate response, the larger the effect that will be observed only on the second subsequent flash.

It seems more reasonable to assume that these changes in flash recovery rates are associated with an underlying state that is monitored by the geniculo-striate response. If the geniculo-striate potential is artifactually altering the appearance of flash recovery in any usual fashion, the effects must be small in comparison to the effects associated with the changes in state monitored by the geniculo-striate probe.

A second possible interpretation of these data would be that they are secondary to changes in EEG arousal. Lindsey (1958) has shown that EEG arousal is associated with faster rates of flash recovery. This hypothesis does not explain most of the data obtained with the monkeys in this study. In S29, slow, synchronous, high voltage waves in cortical EEG were associated with smaller geniculo-striate probes. However, faster and not slower rates of recovery occurred.
during these phases. Moreover, in S28, recovery cycles were selected on the basis of EEG synchrony or desynchrony rather than geniculo-striate probe response size. Using this procedure, slightly greater geniculo-striate probes were associated with slow, synchronous waves at all of the inter-flash intervals. Either no relationship (Gauthier et al. 1956) or depression of geniculo-striate responses is usually reported (Bremer and Stoupel 1959) during slow, synchronous EEG activity. This inconsistent association between synchronous, slow wave activity and large geniculo-striate probes was observed in another monkey as well (S332). Using EEG synchrony or desynchrony as a basis for selection, changes in recovery in either direction were not found consistently. Over-all, the ideal case for changes in recovery owing to reticular arousal would seem to be fast, low voltage EEG and large geniculo-striate probe responses, with associated fast recovery. This combination was never found here.

EXPERIMENT 4

The fact that the “inattentive” state in Experiment 3 induced recovery cycles similar to the ones shown by Spinelli and Pribram (1966) in their condition of IT stimulation suggested to us that our monkeys in Experiment 1 failed to show the IT effect because they were too attentive, hence slowed in recovery. If this were the correct explanation, we should find in the striate cortex evidence of convergence of attention and IT stimulation. The following experiment was therefore undertaken.

Methods

The same monkeys, apparatus and procedures were used as in Experiment 2. In addition, however, the IT cortex was stimulated, and the monkeys were tested in both the open and closed box conditions.

Results and discussion

The results obtained during IT stimulation with and without visual attention (open and closed box, respectively) are shown in Fig. 8. Note that IT stimulation during the closed box condition enhances the size of the cortical responses (surface positive to negative peak starting at approximately 12 msec latency) in three monkeys. In two monkeys (S29, S332), the ranges of response during IT stimulation in the closed box condition do not overlap with the corresponding unstimulated condition; in the third (S28), a correlated t test (t = 4.2; P<0.02) shows the overlapping difference also to be significant. The monkey who had previously shown the smallest increases in response in the open box condition (S331) gave virtually overlapping responses when the IT stimulation and non-stimulation conditions were compared. Only 1 of the 6 electrodes found to show enhancement in the open box condition failed to show enhancement with IT stimulation.

None of the monkeys, however, showed any effects of IT stimulation during the open box condition. This failure to obtain effects of IT stimulation while the monkeys are attentive also supports the suggestion that visual attention and IT stimulation share common neural elements.

CONCLUSIONS

The finding by Spinelli and Pribram (1966) that the time needed for second flash recovery
was greater during stimulation of the IT cortex, was significant in two respects. First it demonstrated the importance of efferent control of the IT cortex upon the visual pathways. Second, by virtue of the theoretical relation of recovery cycles to information processing, it suggested one possible role that the IT cortex may have in information processing.

The conclusion that the IT cortex can have efferent control over the primary visual system is corroborated in Experiment 4 of the present series. Although effects of IT stimulation were not observed on flash recovery cycles in Experiment 1, effects were observed on potentials in the striate cortex which were evoked by lateral geniculate body stimulation. Together with the anatomical findings of Whitlock and Nauta (1956), who showed efferent projections from the IT cortex to the superior colliculus, these findings are in direct support for the notion of an efferent function of the IT cortex on the visual system.

The role of these efferent connections was called into question, however, by the inconsistency of the effects of IT stimulation on recovery cycles in our own laboratory, an extreme example of which is reported here in Experiment 1. The failure to obtain effects on flash recovery cycles with IT stimulation in this experiment was attributed to the much slower rate of recovery observed in both IT stimulated and control conditions in this experiment, compared to the control condition in the Spinelli and Pribram experiment.

It was postulated that the monkeys in Experiment 1 were already too visually alert for IT stimulation to have had an additional effect on recovery time. Experiment 2 showed that size of geniculo-striate response was associated with the state of attention. Experiment 3 investigated whether greater attentiveness was in fact associated with slower recovery by using as a criterion for visual attention the relative size of geniculo-striate probe responses. In the monkeys tested in Experiment 3, large probe responses indicative of visual attention occurred at 2-4 times the frequency of the small geniculo-striate probe responses. Furthermore, large probe responses were associated with slower rates of flash recovery. This finding is consistent with the idea that visual attentiveness was high in the monkeys used in this series of experiments and that attentiveness and IT stimulation may share common neural elements.

This interpretation was further supported by the demonstration in Experiment 4 of a ceiling effect where IT stimulation influenced striate responses evoked by geniculate stimulation. During visual attending, IT stimulation had no effect on these geniculo-striate responses, whereas when the monkeys were not allowed to look out of the experimental chamber, a large incremental effect was produced by IT stimulation. As a result of these experiments, therefore, the qualification must be added that IT stimulation effects are demonstrable if, and only if, the animal is visually not attending. When the state of the visual system is not monitored, failures to obtain IT effects in recovery cycle experiments, either from stimulation as in Experiment 1 or from ablation (Schwartzkroin et al. 1969), are thus not a surprising outcome.

Another consideration must be made concerning any failure to find recovery changes owing to IT stimulation or ablation. All striate cortex electrodes are not sensitive to attentional variables; only 5 out of 24 electrodes in Experiments 2 and 3 showed the effects of attention and IT stimulation. There is, however, a high correlation between those locations that are sensitive to attention and to IT stimulation. Thus the slowed recovery during high attentiveness could be seen in all of the electrodes showing significant reactivity to IT stimulation in Experiment 4. Since in the study by Schwartzkroin et al. (1969) results are reported for only one electrode in each of three monkeys, it is not surprising that they failed to find effects of IT ablation on flash recovery. We found IT stimulation effects in only 20% of our electrodes. Generalizing from our results, there is an 80% chance that removal of the IT cortex will not affect responses evoked in a given striate cortex electrode.

The importance of the efferent influence on the IT cortex can be evaluated in two ways. Schwartzkroin et al. (1969) have suggested that the theoretical importance of IT efferent control is proportional to the generality of the evidence for it. They imply that negative instances
decrease the theoretical importance of these known anatomical connections. A different evaluation can be made as in this study. Here the generality of observed effects was shown to depend on the sensitivity of electrodes to the attentive functions that control the remainder of the animal's brain. The negative instances were thus used to theoretical advantage by allowing a more precise specification of the variables involved in the recovery phenomenon.

SUMMARY

Four experiments were directed at finding an index of the activity of the infero-temporal (IT) cortex on the visual system. In the first experiment, electrical stimulation of the IT cortex failed to alter recovery functions in the striate cortex of four monkeys. This result was different from that reported in an earlier experiment, but comparison of the initial recovery functions obtained in the two experiments allowed us to attribute the discrepancy to differences in the attentional state of the monkeys. This suggestion was tested by developing, in the second experiment, a reliable measure of state in the visual system, a measure responsive to environmental variables inducing attention. This measure was used in the third experiment to select and classify recovery cycles on the basis of the state of the visual system. Only when the attentive state was present were the recovery cycles similar to those recorded in the first experiment. Finally, the measure, a potential evoked in the striate cortex by geniculate stimulation, was shown to be sensitive to IT stimulation only when monkeys were in an inattentive state.

REFERENCES

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