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Research Reports

NEURAL CORRELATES OF STIMULUS RESPONSE AND REINFORCEMENT

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INTRODUCTION

In previous reports we detailed experiments in which it was shown that wave shape of electrical recordings made from visual cortex could be correlated with the stimulus¹⁶, response and reinforcement variables¹² which guided the discriminative behavior of the monkey from whom the records were obtained. The present report as the previous ones, combines behavioral and electrophysiological techniques^{4-6,15,17} and deals with two studies aimed at discovering something of the neural mechanism by which such differential responses can become established. The first study focussed on the origin of the response related wave form. Electrodes were implanted in the precentral motor cortex to ascertain whether such response related activity could also be recorded from this locus and what, if any, resemblance it bore to that recorded from the visual cortex.

In the second study we chose to gauge the effect of resections of the inferior temporal cortex on the differential electrical records since such resections have been repeatedly shown to impair visual discrimination behavior⁹⁻¹¹. Is the effect of such resections primarily on the processing of the stimulus, the response or the reinforcement related aspects of the discrimination?

METHOD

Behavioral procedures

Four preadolescent rhesus monkeys were used in the experiment. The method of training was modified from that previously described¹². The monkeys were pre-trained in an automated, computer controlled, discrimination apparatus (DADTA) to press the right of two simultaneously presented numeral zeros and the left of two simultaneously presented numeral ones. The order of presentation of zeros and ones

was pseudo-randomized according to a modified Gellerman series. Once the subjects had reached criterion (90% on 100 continuous trials) on this successive discrimination they were placed in a monkey chair and training was resumed until the monkeys again reached criterion. Next the monkeys, in the chair, were shifted to the apparatus previously used. In this setting the monkey works in a darkened box; two translucent panels considerably larger than in DADTA face him and the cues are projected onto them by a modified Kodak Carousel projector. Initially the displays are flashed onto the panels at a rate of 30/sec until the monkey responds. As training proceeds the display is progressively shortened until only one 0.01 msec flash is presented per trial. In the present experiment two circles or two sets of vertical stripes, equated for brightness and area were presented simultaneously, one cue displayed on each panel. Again a pseudo-random sequence of presentation was given. However, in this setting, the correction technique had to be used. Thus an error was followed by repetition of the trial until a correct response was made. Correction was manually controlled. One hundred trials were given per day.

In order to perform the task the monkey has to: (1) pull a lever attached to the monkey chair; this activates the Carousel which displays one of the two patterns onto the panels; (2) when the circle is presented the monkey must press the right panel to receive a peanut. When the vertical stripes are presented, the monkey must press the left panel to receive a peanut. The monkey had to respond within 5 sec after the stimulus flashed on; except for this limitation the monkey determined his own pace.

Electrophysiological procedures

Under general anesthesia, 12 bipolar electrodes were implanted in the monkeys. The separation of the two tips was about 1.5–2 mm and the electrodes were located in such a way that the short tip would be at the surface of the cortex and the long tip between the cortex and the white matter. The electrodes were made from insulated nicrome wire 300 μm in diameter. They were kept in place with dental acrylic and connected to a Microdot 25-pin plug. Ten of the bipolar electrodes were placed in the visual cortex of the monkey, 5 to each hemisphere. The remaining 2 were placed in the motor cortex of each hemisphere in that area which corresponds to the cortical representation of the hand.

Electrical stimulation was used to optimize the position of the electrodes. Under deep surgical anesthesia motor responses are not always easily obtained. Nonetheless, 1 of the 4 monkeys stimulated produced flexion of the thumb and of the first finger of the contralateral hand for each hemisphere. Another one of the monkeys produced movement localized in the proximal musculature of the forelimbs, namely, in the region of the shoulders and shoulder blades. The motor cortex for the two hands could not be electrically identified in the other 2 monkeys, even after extensive searching with the stimulating electrodes; the electrodes were implanted, nevertheless, on the basis of anatomical criteria.

Following surgery at least 2 weeks were allowed to elapse. Then records were taken on 3 contiguous days on magnetic tape and while the monkey was still per-

forming at chance level. On one channel of the magnetic tape all stimulus, response and reinforcing events were also recorded for subsequent processing. Three more days of records were taken when the monkeys were performing at about 75% correct and a final set of records, also on 3 contiguous days, was done after the monkeys reached a stable criterion of over 90% correct.

Processing of the brain electrical activity was done as follows: stimulus presentation and response were used as time markers to initiate averaging processes. Averaging of trials was done only within a day. Thus there are 3 averages for the responses evoked by the vertical stripes: one when the stimulus is followed by the correct response, one when it is followed by the incorrect response and one when there is no response at all. Similarly, averages are obtained for the presentation of the circles. In the same fashion pressing the left panel can be a correct or a wrong response for vertical stripes. Thus there are 14 average records per electrode.

After the animals were fully trained and preoperative recordings had been made, the inferior temporal cortex of both hemispheres was resected under sterile surgical conditions. About 2 weeks were allowed for postoperative recovery, after which the monkeys were again tested and on contiguous days 3 more sets of electrical brain records taken.

RESULTS

Stimulus, response and reinforcement related electrical activity in the striate cortex

The findings of these experiments closely resemble the ones obtained in the previous series¹². Before surgery the responses evoked to stimuli showed stimulus specificity at some electrode sites in the visual cortex. At some electrode locations a different electrical response was evoked by the stripes than by the circle. The components¹⁶ of this response did not change from before or after learning and there were no observed differences between electrical responses evoked by stripes and followed by a correct behavioral response as compared to those which were followed by an incorrect behavioral response or even by no response at all. On the other hand, activity correlated with the response was absent before learning, and began to appear only when the animal showed signs that he was mastering the recognition task. Response correlated activity preceding the responses was tied as in the previous experiment to the panel that the monkey intended to press irrespective of what pattern had been recognized, of the correctness or wrongness of the behavioral response. Response correlated activity following the response was tied as in the previous series of experiments to the obtaining of reinforcement: a 20-30/sec wave form followed error. (In the previous experiment this wave form was reported as being in the 30-40 c/sec range. Review of the earlier data shows them to be somewhat slower than this.)

These findings apply to electrodes which were located in the primary visual cortex, in or very near the region to which the fovea projects, and were true for all the monkeys that reached criterion. As in the previous experiment, however, activity correlated with the behavior could be recorded at some electrode sites better than at some other: out of a total of 40 electrodes 12 showed clear-cut differences correlated

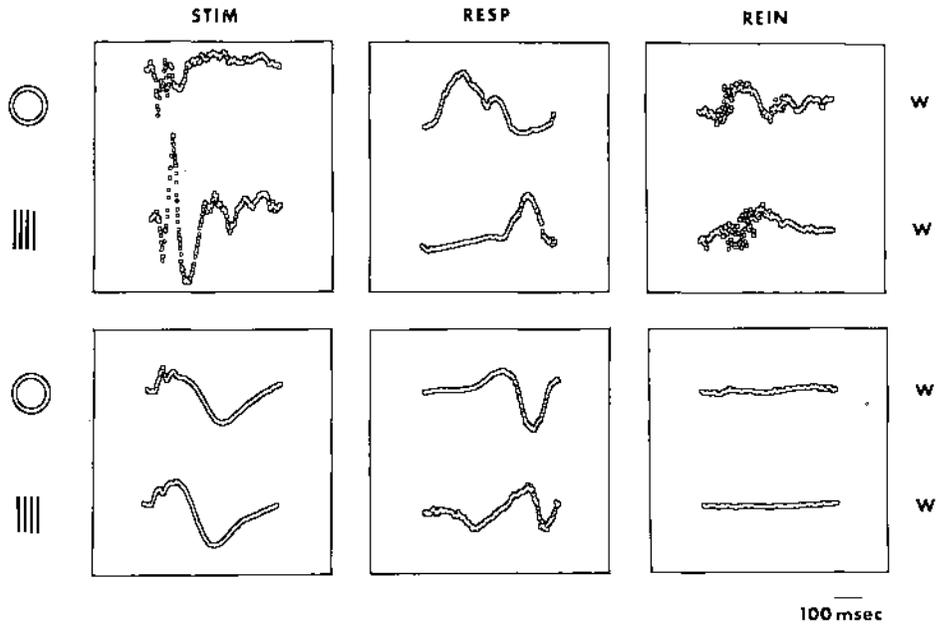


Fig. 1. This figure shows representative averages of wave forms recorded from visual cortex during visual discriminative behavior, monkey at criterion. In the top row under STIM: averaged responses evoked by the circle and by the stripes. Notice that the response evoked by the stripes is considerably different from the one evoked by the circles, but notice also that the primary components of the two wave forms are practically identical and the difference is in the second and third component. Under RESP: backward averages for left panel pressing (top) and right panel pressing (bottom). Under REIN: forward averages from the panel pressing. Notice the burst of activity which appears in the average for a wrong press (W), regardless of the stimulus presented or of the panel pressed. In the bottom row, responses are recorded to the same conditions as above but after inferotemporal cortex ablation. Among the most striking effects of the ablation were changes in the shape of the evoked response to the stimuli, the STIM column, in the sense that regions from which differential activity to the two stimuli was recorded before surgery, generated very similar waves to the two stimuli after surgery. Moreover, there was a disappearance or dedifferentiation of the activity preceding the response (RESP column) and disappearance of the activity following the response (REIN column).

to the two visual patterns, to the panel to be pressed, or with successful recognition. Fig. 1 shows some representative examples of these responses.

Response correlated activity recorded from the motor cortex

Two motor cortex electrodes gave evidence not previously reported. Two of these electrodes (the one from which movements were obtained at the time of implantation) showed a long lasting depolarization which began some 20 msec after the pattern had been flashed on the translucent screen, and continued after climbing steeply to a plateau, until almost the end of the 500 msec analysis time. At this point the negativity decays rather abruptly back to the baseline and sometimes overshoots it. It is at this time that the monkey presses the panel. This depolarization was present

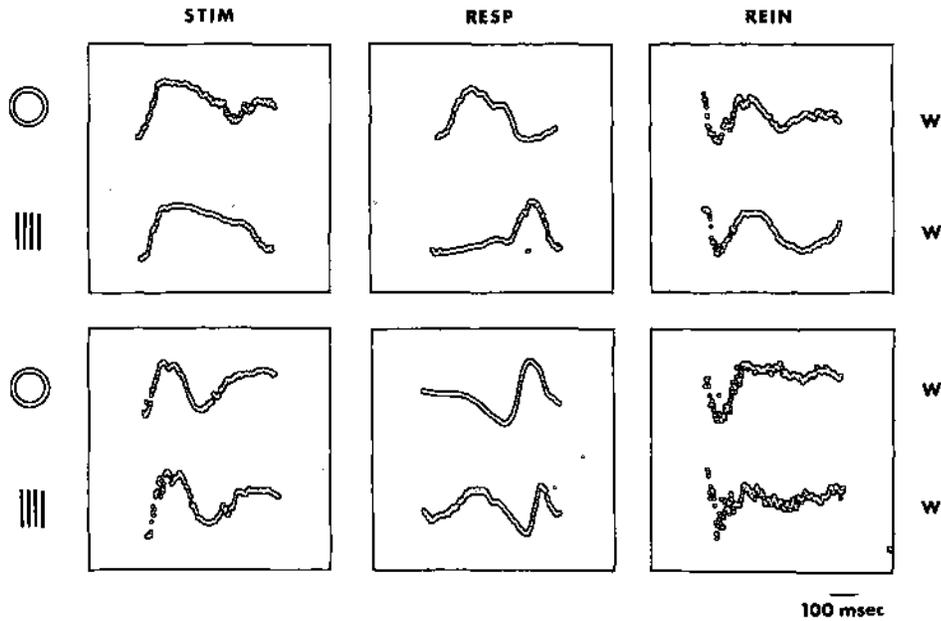


Fig. 2. This figure shows representative averages of wave forms recorded from motor cortex during visual discriminative behavior. The top row records were taken with the monkey at criterion; the bottom row records after surgery. In the top row, under STIM, it can be seen that both stimuli evoke long lasting depolarization with no stimulus specificity. The activity preceding the response, under RESP, is of special interest because of the considerable similarity it bears to the activity preceding the response recorded by one of the visual cortex electrodes (Fig. 1, top row, under RESP). Under REIN, activity following the response is shown. After surgery, in the bottom row, it can be seen, under STIM, that the stimuli evoke a shorter lasting depolarization with no stimulus specificity. There has been a dedifferentiation of the activity preceding the response, under RESP, which was panel specific. Very little or no change was produced by the ablation in the activity following the response (REIN).

before the animal learned the discrimination and remained essentially unchanged afterward. The negative variation precedes any difference in the electrical variation which can be attributed to the pressing of the right or left panels. Only toward the end of the 500 msec period is there a difference in the activity correlated with going right or left.

Averaging backward from the response, *i.e.*, looking at activity which is correlated with the response and precedes it, also shows that activity is recorded at the motor cortex before any learning of the discrimination has taken place. This activity is initially neither stimulus nor response specific (*i.e.*, it is not tied to either the stimulus pattern nor to the press of the right or left panel); but as learning progresses the wave form undergoes a progressive differentiation of shape so that by the time the monkey is performing at the 75% level it has become a clear indicator of which panel will be pressed. At no time does it become *stimulus* specific. This progressive differentiation of electrical response of the motor cortex leads and of their shape is identical with that which precedes the electrical response obtained from one of the visual cortex electrodes (Fig. 2).

The effect of inferotemporal cortex ablation on the electrical activity of the striate cortex

The effect of inferotemporal cortex ablation was that the test behavior of all the animals but one fell promptly to chance on the 1st postoperative day and remained there despite efforts to retrain (100 trials were given in the same manner preoperatively). One of the monkeys, however, (one from which motor cortex recording had proved of interest) performed practically normally for the first half of the 1st day of testing. By the end of the session, however, and subsequently, performance fell to chance levels and the state of affairs did not improve on following days despite attempts at intensive retraining. No animal recovered the ability to distinguish the circle from the stripes in 1000 trials.

The electrical recordings obtained from the visual cortex of those monkeys which performed at chance level showed immediate and dramatic changes in the shape of the response evoked by the cues. These monkeys also showed a complete disappearance of the differentiated electrical activity correlated with the response. Further, all records showed a loss of the high frequency components; the records appeared somewhat smoother, less complex.

The monkey which performed well on the first part of the 1st day of testing, on the other hand, showed no immediate change in electrical activity correlated with either stimulus or with the response during this period. This finding held both for the motor and the visual cortex leads. However, as testing progressed and behavioral deterioration set in, it was accompanied by a parallel loss of differentiation of the electrical activity recorded from both visual and motor cortex leads. Despite this, some response correlated activity recorded from visual cortex sites remained distinguishable.

DISCUSSION

The results of these studies are threefold. First, they confirm the earlier report of electrical activity recorded from the visual cortex of monkeys to be differentially related to the stimulus, response and reinforcement variables of a discrimination task. Second, the response related electrical activity can be recorded from the precentral motor as well as from the visual cortex. Third, resection of the inferotemporal cortex drastically alters the recorded electrical activity at the same time that discrimination behavior deteriorates.

The response related electrical activity recorded from the motor cortex is comparable to that obtained from the visual cortex during the final (criterion) stages of discrimination. Before this, no reliable record of response related activity is obtained from the visual cortex. However, response related activity is recorded during these earlier stages of performance from the motor cortex. It consists of a negative variation of considerable (500 msec) duration ended by a sharp positive deflection of the record coincident to or just preceding panel pressing. As training proceeds, the wave form of this negative deflection differentiates according to whether

the right or left panel is pressed. Once discrimination behavior has been established, response (go right-go left) related wave forms can continue to be recorded from both the visual and motor cortex despite the deterioration of the discriminative (circle vs. stripes) performance.

The results obtained in the other experiment fell somewhat short of expectations. It had been hoped that resections of the inferotemporal cortex would selectively affect the stimulus, response or reinforcement related electrical activity which can be recorded from the primary projection (striate) cortex while the subject is making visual discriminations. This did not happen; with one exception, behavioral deterioration in the discrimination task covaried with dedifferentiation of the previously selective electrical responses. The one exception came in a monkey whose discriminative behavioral and electrical responses were maintained intact during the first part of the first postoperative testing session. In this animal the response correlated electrical activity was differentially maintained during the subsequent period of chance discriminative performance.

The maintenance of a discrimination habit as observed in this experiment, following surgery of the inferior temporal cortex, is not a unique occurrence in our experiment. Difficulty of task and overtraining^{1,2,7,8} and successive cortical resections¹³ are known to influence the effect of inferotemporal lesions on discrimination behavior. We have also noted that occasional monkeys will perform well for the first 5-10 trials postoperatively, but could never be sure that this was not attributable to chance. An extended period of above-chance discrimination followed by chance performance, as observed in the one monkey in the present experiment, has not been reported to our knowledge.

The fact that in most monkeys all task related aspects of the electrical record became dedifferentiated when behavioral discrimination failed after inferotemporal surgery might have been due to movement of the electrodes during surgery. This appears unlikely in view of the continuing differential records obtained in the monkey who maintained his discriminative behavior after surgery, a result which was also observed in another monkey who maintained performance for about 10 trials (too short a period for any quantitative analysis to be performed).

How then do we interpret our findings? All that can be said at this time is that whatever the function of the inferotemporal cortex in vision, it is related as much to the stimulus as to reinforcement variables of the task. The fact that in one monkey the response related wave forms remained intact despite the deteriorated behavioral performance suggests that at least this variable is not directly related to the functions of the inferior temporal cortex. Perhaps ablations restricted to the anterior or posterior parts of the inferior temporal gyrus, as suggested by the studies of Iwai and Mishkin³ will prove to tease apart the effect on the stimulus from that on the reinforcement related electrical activity of the striate cortex since selective removals influence different aspects of discrimination behavior, and the connections of these two parts of the inferior surface of the brain have been found to be to some extent different¹⁴.

SUMMARY

The electrical activity of visual and motor cortex of monkeys making a visual differential discrimination was recorded from bipolar, chronically implanted electrodes. Averaging was then performed from the stimulus forward in time and from the response of the monkey backward and forward in time with the purpose of identifying differential activity induced by the stimuli and preceding and following the response. In some visual cortex locations wave forms showing stimulus specificity can be recorded; moreover wave forms indicating which panel the monkey is about to press and whether the response was rewarded or not are present. Inferotemporal cortex ablation eliminates or greatly reduces specificity of wave forms to the stimuli, and intention and reinforcement related wave forms in visual cortex.

In motor cortex, before surgery, a long lasting depolarization follows the stimuli without specificity. The activity which precedes the response, in turn, is related to which panel the monkey will press, and shows striking similarities with that which is recorded from one of the visual cortex electrodes, possibly indicating that at the time of response a functional connection is effected between visual and motor cortex. After inferotemporal cortex ablation the stimulus induced depolarization is much reduced; furthermore the panel specificity of the preresponse wave and its similarities to its visual cortex counterpart disappear.

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