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SELECTIVE ATTENTION: INPUT FILTER OR RESPONSE SELECTION? AN ELECTROPHYSIOLOGICAL ANALYSIS

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INTRODUCTION

Organisms are constantly confronted with a variety of complex situations in which they are required to discriminate and respond to but a limited number of attributes. While several behavioral approaches to this process of *selective* attention have been assayed, neurophysiological interest has, for the most part, focussed on the more general intensive manifestations of attention such as vigilance and orienting^{1,3,7,11,12}. One exception to this disparity of interests has been the study of the role in visual attention of the cortex of the inferior part of the temporal lobe of monkeys^{2,5,8,10,17,21}. Further analysis of the contribution of this part of the brain to the attentional mechanism thus affords an opportunity to bring together the behavioral and neurophysiological research and theoretical contributions to the problem of selective attention.

Two classes of behavioral theories of selective attention can be characterized: those suggesting that a sensory filter becomes imposed on input⁴ and those stating that all stimulus attributes are first fully analyzed by central brain mechanisms and that selection is made subsequently on the output of these analyzers to determine remembering and responding^{6,14,15}. Behaviorally it has been difficult to distinguish between the input filter and response selection interpretations although the ingenious use of dichotic presentations of auditory stimuli has given results that favor the filter formulation²⁰. Our hope in the present experiment was that by recording directly from brain structures shown to be involved in selective attention, a more definitive resolution of the problem posed by the theories could be attained.

METHOD

The experimental paradigm used was to record the transient electrical brain activity evoked in 3 monkeys by brief (0.01 msec) self-initiated (pulling a lever) presentation of visual stimuli that had to be discriminated by a differential panel press. The brain recordings could thus be analyzed by grouping (summarizing) according to the stimulus presented, the responses made or the reinforcement obtained.

Behavioral procedures

The procedure was modified from those reported in detail on earlier occasions^{18,19}. Specifically 3 preadolescent monkeys were pretrained in an automated, computer controlled, discrimination apparatus (DADTA) to select one of two simultaneously presented cues (the numerals 1 and 0). The placement of zeros and ones was pseudorandomized according to a modified Gellerman series. Once the subjects had reached criterion (90% on 100 consecutive trials) they were placed in a monkey chair and training was resumed until they again reached criterion. Next the monkeys, in the chair, were transferred to the apparatus to be used in the electrophysiological experiment. In this setting the monkey worked in a darkened box; two translucent panels considerably larger than in DADTA faced him and the cues were projected onto them by a modified Kodak Carousel projector. In order to perform the task the monkey had to pull a lever attached to the chair; this activated the Carousel. The monkey in order to receive reinforcement (a 190 mg banana pellet delivered by a Davis pellet dispenser through a tube to a small receptacle just below the panels) had to respond within 1 sec after the stimulus flashed on; except for this limitation, the monkey determined his own pace.

For the present experiment the stimulus display consisted of colored patterns. The monkeys were first trained to respond differentially to one of two colors (red or green) and then to one of two patterns (circle or vertical stripes). Initially the displays were flashed onto the panels at the rate of 30/sec until the monkey responds. As training proceeded the display was progressively shortened until only one 0.01 msec flash is presented per trial. Correction technique was 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.

As soon as the monkey became proficient at responding to the single flash, electrodes were implanted, a 2-week postoperative period was allowed to elapse, and then the body of the experiment was begun.

For this main part of the experiment the contingencies of reinforcement were programmed by a small general purpose computer (PDP-8) which was also used to record the time of the stimulus flash, the moment of response, its position and whether it was correct or incorrect. In addition, the computer was used on line to digitize the electrical record obtained from the monkey's brain during a trial, to record the digitized record on spools of magnetic tape and later to collate the behavioral and electrophysiological data.

Since colored patterns were used, 4 combinations of stimulus pairs occurred: green circle right vs. red stripes left; green stripes right vs. red circle left; red stripes right vs. green circle left; and red circle right vs. green stripes left. These combinations were distributed pseudorandomly across trials for 60 trials a day so that each combination occurred 15 times per day. Initially reward was made contingent on response to the panel where one of the color cues (*e.g.*, red) was displayed. (Which was correct, red or green, was different for different monkeys.) Training was continued until a criterion of 90% correct was reached on 3 successive days.

Following the initial color discrimination, a discrimination reversal problem was programmed. If the monkey had initially been rewarded for pressing the panel which displayed the red pattern he was now rewarded for pressing the panel on which the green pattern was displayed. Again the 90% criterion for 3 successive days had to be met. And then another reversal was instituted, leaving the monkey with the discrimination he had originally learned. These procedures were run in order to firmly establish a stable baseline which would ascertain the reliability needed for making comparisons of the brain electrical records.

Finally, the reinforcing contingencies were shifted so that the pattern dimension had to be discriminated. Now reward was obtained when the monkey pressed the panel which displayed one of the patterns (e.g., the circle; again, which was correct differed for the differing monkeys). Criterion (90% correct on 3 successive days) had to be met on this task and then two reversals of the pattern rewarded had to be mastered each to criterion performance. Note that in all of these color and pattern discriminations and reversals the stimulus pairs displayed were always the same 4 combinations listed earlier. Only the reinforcing contingencies varied. Therefore the monkeys' retinal image was invariant across tasks. The question is, therefore, where does the discriminative response mechanism become differentiated?

Electrophysiological procedures

To help answer this question each of 3 monkeys had, under general anesthesia (intravenous Diabutal), 12 small bipolar nichrome electrodes (300 μ m) chronically implanted in the posterior parts of the cerebral cortex. The separation of the electrode 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 and the long tip between the cortex and the white matter. Electrodes were kept in place with dental acrylic and connected to allicrodat 25-pin plug. Eight of the bipolar electrodes were placed in the visual cortex of the monkey, 4 to each hemisphere and the remaining 4 were bilaterally placed in the inferior parts of the occipital and temporal lobes. From all of these electrodes 5 were chosen that gave consistently the best electrical recordings since our digitizing system could handle only 6 channels (the sixth was used to record the onset of the stimulus display and the response of the monkey). Throughout the body of the experiment 3 electrodes in the striate (primary visual), one in the prestriate and one in the inferior temporal cortex were monitored in each monkey. Electrical activity was recorded on every trial for 500 msec following the stimulus flash (*stimulus locked brain activity*); and also, 250 msec before the response and 250 msec after the response had occurred (*response locked brain activity*) — this was done by initially recording throughout the trial, then storing only the data following the stimulus and surrounding the response. The data were put in bins so that they could be statistically evaluated by the *t*-test*.

* Analyses of stimulus locked data were computed on the amplitude of major positive and negative deflections adjusted for comparison by subtracting the initial 10 msec of baseline record. For the response locked data the analyses were performed on the 50 msec segment preceding the responses. The preceding 20 msec were used for baseline as above.

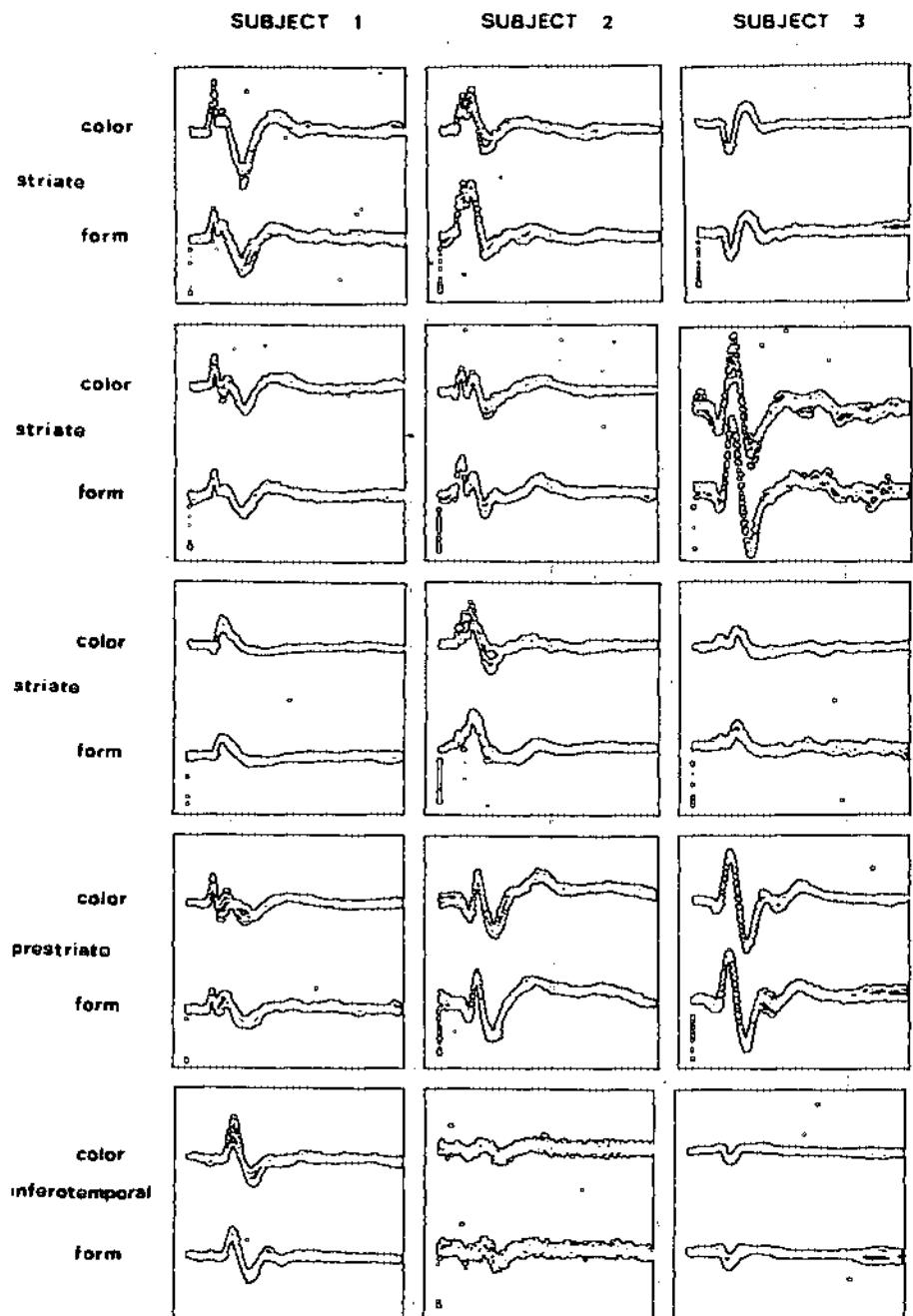


Fig. 1. Stimulus locked activity (500 msec) recorded from each of the 15 electrodes. In each panel: color—6 averaged waveforms (54–40 responses each) obtained during criterion performance on the first and second color reversals; form—6 averaged waveforms obtained during criterion performance on the first form discrimination (form shift) and first form reversal.

RESULTS

Stimulus locked brain activity

Fig. 1 shows the results of the analysis of the stimulus locked electrical brain activity for all 15 electrodes. Only the data from correct trials of criterion sessions were used and we report here only the results obtained during the two color reversals, and the first two form problems. The top traces in each panel are averages of the electrical activity recorded when the animals were responding on the basis of color; the traces below were obtained when the animals were responding to form. Note the absence of stimulus locked differences in the shape of the electrical activity under the two conditions. In none of the electrodes were there reliable changes in stimulus locked activity due to the changed reinforcement contingencies.

To show that the electrical recordings differ with the different stimulus displays, Fig. 2 was constructed. Here averages were obtained for specific stimulus pairs: e.g., where red was displayed on the left (top and bottom trace in each record), the record is appreciably different from that obtained when red was displayed on the right (middle two traces on each record). In both the color and form relevant conditions these differences are most pronounced in the recordings made from the striate cortex ($df = 5, P < 0.05$, in both conditions), much less marked in the prestriate and totally absent in the recordings from inferior temporal cortex. It is again apparent in this analysis that stimulus locked activity remains constant regardless of the dimension to which the animal attends.

Response locked brain activity

The situation is entirely different when response locked electrical activity is examined. Analysis made on the basis of the occurrence of a differential response shows, as reported in earlier studies¹⁹, a difference between records made from the striate cortex when monkeys press the right panel and those in which they press the left panel. Of more immediate interest, however, is the lack of difference obtained in striate and prestriate recordings when the analyses are made either according to the 4 possible stimulus pairs or according to stimulus dimensions (color vs. form). By contrast, as shown in Fig. 3, recordings made from the inferior temporal cortex are markedly sensitive to these categorizations. The response locked electrical activity of the inferior temporal cortex reflects the dimension attended and anticipates by approximately 50 msec the cue selected for response. Thus, during the first color reversal (upper panel, Fig. 3) when the monkey was responding to red regardless of shape, the recordings made when red was displayed on the right differed from those when red was displayed on the left panel ($t = 5.54, df = 2, P < 0.05$). That this does not reflect mere sensitivity of the record to position is made evident in the record obtained in the next reversal (second panel, Fig. 3): when the monkey is responding to green, the relationship between categories is the same as when he is responding to red,

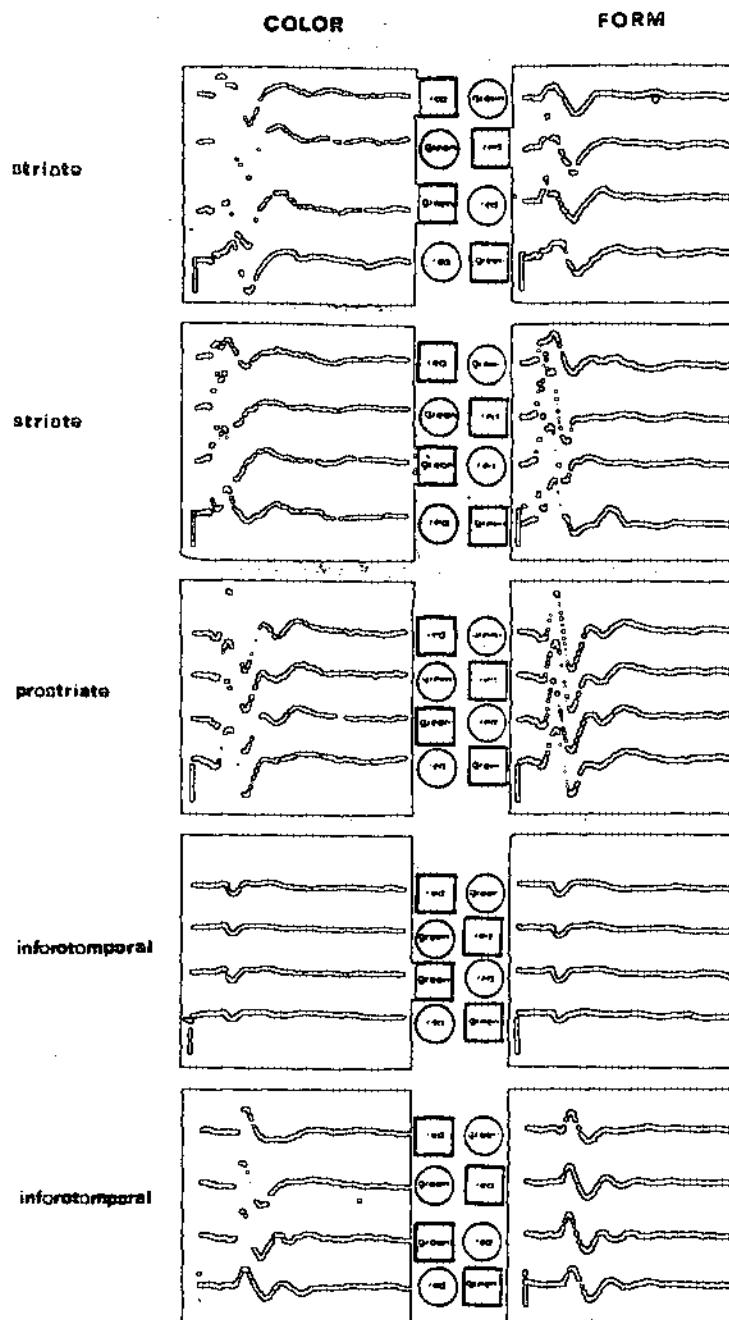


Fig. 2. Stimulus locked activity (500 msec) evoked by the stimulus display (vertical stripes represented by square) at the side of each trace. The left column shows averaged waveforms (recorded from 5 electrodes) obtained on criterion sessions of the first and second color reversals; the right column shows averaged waveforms obtained on criterion performance of the form shift and first form reversal. Each trace represents up to 90 responses (approximately 15 from each criterion session).

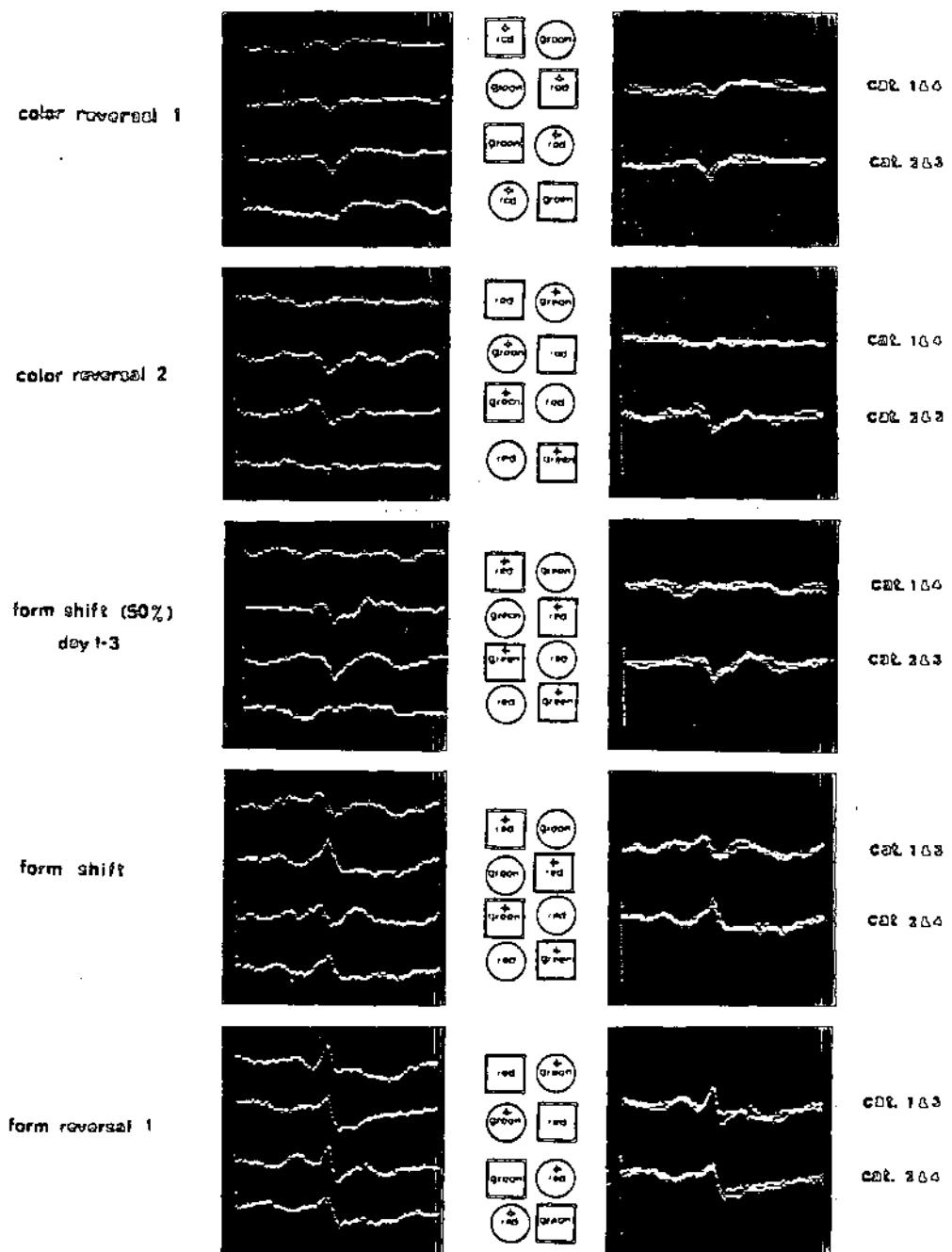


Fig. 3. Response locked activity (500 msec) generated by the stimulus display shown at the right (correct cue indicated with a +) and recorded from the inferior temporal cortex. Response in each case is occurring at 250 msec. Each averaged waveform contains approximately 45 responses. Records obtained during criterion performance on color (upper two panels) and form (lower two panels) problems. The center row shows electrical activity collected during the first 3 days of the form shift while performance was at chance. The right column shows the traces superimposed as marked (e.g., traces 1 and 4).

even though his responses are now to the opposite panel for each stimulus pair ($t = 5.23, df = 2, P < 0.05$).

When recordings are analyzed from criterion sessions on initial learning of the shape discrimination (form shift) (fourth panel, Fig. 3), the relationships change. Here the upper and third trace (reflecting stripes on left; circle on right) become similar as do the second and lower (reflecting stripes on right; circle on left) and each pair of traces is reliably different from the other ($t = 4.71, df = 2, P < 0.05$). A similar trend can be seen on the form reversal, although in this case, the differences only approached a statistically reliable level. The middle panel of Fig. 3 demonstrates that these changes in the electrical brain record are not simply due to the changed environmental contingencies — these recordings were made when the contingencies were already programmed to reinforce the form dimension but the monkey was still performing at chance level.

DISCUSSION

The results obtained in the present study thus confirm and extend those found previously. Physical differences in the stimulus display are reflected in stimulus locked analyses of electrical recordings made from the striate cortex¹⁸, but such differences are not reflected in the electrical recordings made from the inferior temporal cortex⁹. By contrast, response locked analyses are considerably richer in content. As previously reported, when taken from the striate cortex such records show whether a learned response is to the right or the left and whether it is correct or incorrect¹⁹. When (as in the current study) a particular stimulus dimension (such as color or form) must be attended and selected from others, response locked analyses show the electrical activity of the inferior temporal cortex to be involved in the process. Initially these dimensionally related differences are not found in recordings made from the striate cortex. However, with subsequent overtraining (another two reversals of the color and form tasks) both prestriate and striate recordings come to reflect these dimensional changes¹³.

These results help clarify the issues posed by the input filter and response theories of selective attention: the selecting process is response, not stimulus locked. Initially the inferior temporal, not the striate cortex, is involved. However, the striate cortex does become involved in the selection process once overlearning has taken place. Thus both the response and the input filter theories are supported: during learning, selection occurs subsequent to analysis of stimulus attributes in the striate cortex but then becomes encoded (by overlearning) in the input mechanism where it can act as a filter.

These data also suggest ways in which the response linked mechanism of selective attention may work. Deutsch and Deutsch⁶ suggested that the arousal level is adjusted during the selective process to take in stimulus attributes of greater or lesser significance to the organism. The results of the current experiment suggest rather that selection is attained through responding which produces differential consequences

(reinforcement). Attention is thus truly *selective* of stimulus dimensions not just levels of significance.

SUMMARY

Electrical brain activity was recorded from the occipital and temporal cortex of monkeys while they were performing a task which demanded selecting either the color or the form dimension of a complex stimulus display. Results show (1) that stimulus selection occurs at the time of response, not stimulus presentation, and (2) that initially, though not with overtraining, the inferior temporal cortex rather than the occipital cortex is involved in the selection process. Thus both the simple response and filter theories of selective attention need to be modified.

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