

## ROLE OF THE INFEROTEMPORAL CORTEX IN VISUAL SELECTIVE ATTENTION<sup>1</sup>

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In the past 25 years it has become clear that the processing of visual input involves brain systems beyond the primary visual projection (striate) cortex. Thus the peristriate (prestriate) cortex has been shown to be important to the perception of size constancy (Ungerleider et al. 1977), and the inferotemporal cortex has proved integral to visual choice (see reviews by Pribram 1954, 1958, 1974; Gross 1971; Mishkin 1973). Hence we have undertaken a series of studies to determine the relationship between electrical activity recorded from visually active cortex in a variety of visual situations.

Though one attempt using this approach was uninformative (Gerstein et al. 1968), the studies of Rothblat and Pribram (1972) and Pribram et al. (1976) proved rewarding. These latter studies succeeded, in part because it became apparent that the wave forms evoked in the performance of the task were related to the *response* as well as to the stimulus as recorded through a technique first reported by Pribram et al. (1967).

The following study is an attempt to replicate and extend these findings. Specifically, interest centers on the locations from which the electrical brain response, related to the various aspects of a visual task, can be

recorded. Additionally, stimuli matched for luminance and contour were used to rule out the possibility that the wave form relationship reported in the earlier studies occurred as an artifact of the particular stimuli employed. Finally we hoped to determine which part of the electrical brain activity evoked in the task indicates perceptual processing and which part reflects the decision mechanisms that lead to an overt behavioral choice.

### Method

#### *Subjects*

Subjects were 7 preadolescent rhesus monkeys all naive to visual discrimination tasks.

#### *Apparatus*

For pretraining an automated discrimination apparatus for discrete trial analysis, DADTA III (see Pribram 1969), was employed. Training and testing during the main portion of the experiment then proceeded in an apparatus described by Pribram et al. (1967). Briefly, during training sessions monkeys were seated in a restraining chair and placed in the test apparatus which consisted of a computer-controlled display back-projected onto a transparent panel, split vertically so that each half of the panel could be depressed independently (see also Rothblat and Pribram 1972). A lever pulled by the monkey initiated each trial and caused the computer to activate a modified carousel projector. The stimuli were projected onto

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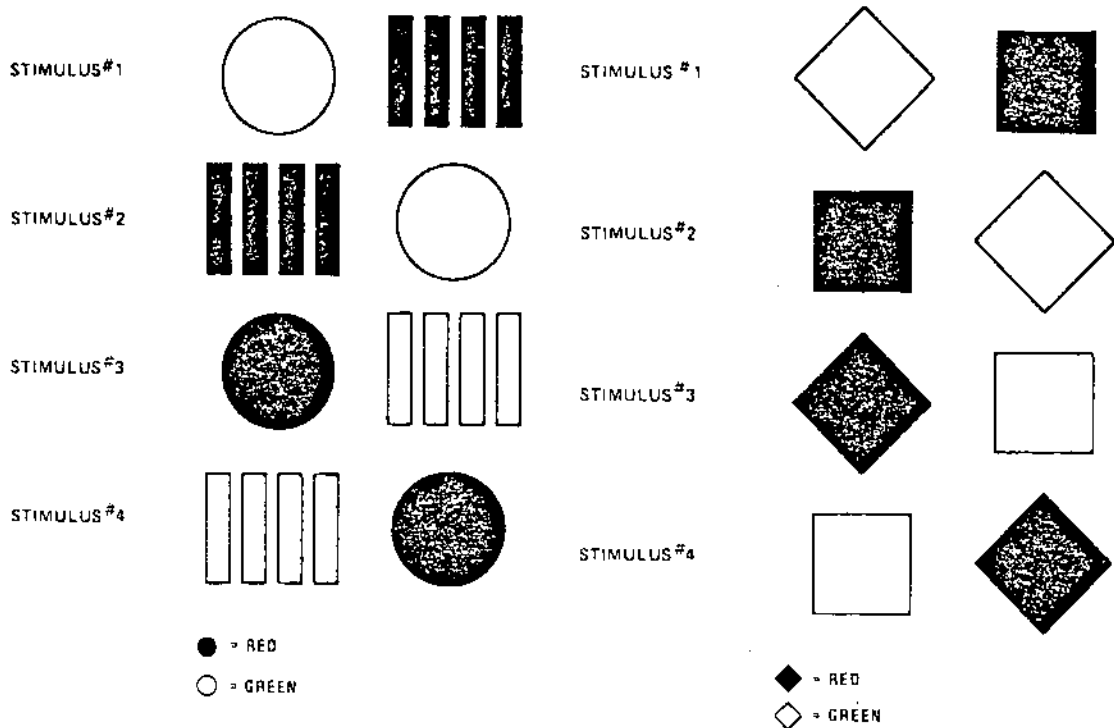


Fig. 1. The 2 display sets of 4 pairs each of stimuli used in this experiment. Area and luminance were equated as was contour in the square-diamond set.

the transparent panel using a Grass PLT-2 lamp, and luminance at the display was 7 ft. Lamberts. A correct response (pressing one or the other half of the split panel) was rewarded by the delivery of a 190 mg food pellet in a food well directly beneath the display. Response location and time were relayed by a microswitch to a PDP-8 computer.

#### Stimuli

Two different sets of colored stimulus patterns were displayed. One display set consisted of red and green stripes and circles, and the other was composed of red and green diamonds and squares (see Fig. 1). The 4 possible arrangements of each display pair were distributed in the carousel tray pseudorandomly across 60 trials, using a modified Gellerman series. Both display sets were equated for area and luminance, and

the diamond-square patterns were equal in contour. The circle and stripes (4 in number) subtended  $14^\circ$ , and the diamond and square subtended  $11^\circ$  of visual angle. Of the 7 monkeys in this study, 4 were run on the diamond-square condition and 4 on the circle-stripes condition; one animal was tested in both conditions.

#### Procedure

*Pretraining sessions.* The monkeys were pretrained in DADTA III to discriminate either a numeral 0 or 1, or between blue and yellow. They were then gradually accustomed to sitting in a restraining chair and testing was begun in the experimental apparatus.

*Training sessions.* The chaired subjects were placed in front of and within easy reach of the translucent split panel. During the shaping procedure the stimuli were displayed by

repeated flashes until the monkey pressed one or the other half of the panel. (Simultaneous pressing of both panels failed to activate the reinforcement.) The duration of exposure was quickly shortened to one flash lasting 10  $\mu$ sec. Following an exposure there was a time-out procedure of 500 msec to assure adequate separation of wave forms related to the stimulus from those related to the response. If the monkey pressed during this period the trial would abort and produce a repeat of that same trial. Two seconds were allowed for panel press after the time-out period. Reinforcement was initiated immediately after a correct response. If the animal failed to press either panel during this 2 sec period, the trial was terminated and discarded. In either case, a 3 sec intertrial interval ensued, the slide tray of the projector was advanced to the next position, and the computer would wait for the next lever pull. In this manner, 60 trials were run sequentially, 7 days per week for each animal. Records were taken during 3 consecutive sets of 60 trials at times when the animal was behaving at 30%, 50%, 75% and 90% criterion.

After the monkey had achieved the first criterion (e.g., responded to red in the color tasks) to 90% proficiency (90% on 3 successive sets of 60 trials), the reinforcement contingencies were reversed, i.e., the monkey now had to respond to green in order to receive a reward. After two reversals, the other task dimension (e.g., respond to square in the pattern task) became the rewarded one. On attaining criterion on the initial cue of this dimension, the reinforcing contingencies were again reversed (i.e., response to diamond became rewarded). A typical sequence of tasks was green, then red, green again, then diamond, square, and diamond again. In addition, certain animals were overtrained on the tasks. Overtraining was defined as 1000 trials beyond initial 90% criterion. Note that during all these variations the *stimuli* (the 4 possible display sets) randomly presented to the retina remained *identical*; only the reinforcement contingencies were altered.

#### *Electrophysiological recording and data collection*

Before or during shaping, each monkey had, under general anesthesia, chronically implanted 12 small bipolar nichrome electrodes (300  $\mu$ m; see Pribram et al. 1967). The separation of the electrodes tips was about 1.5–2.0 mm and the electrodes were placed in such a way that the shallow tip would be at the surface and the deep electrode at the junction of cortex with white matter. Locations were ascertained using a stereotaxic apparatus and later checked using standard histological techniques. Electrodes were kept in place using dental acrylic and connected to an allicrodate 25-pin plug. Fig. 2 shows the placement of the electrodes in the 7 monkeys. The figure includes the 58 cortical electrodes from which records were taken. (Twenty-four additional electrodes were eliminated from the figure and the analysis due to poor signal to noise ratios.) All cortical electrodes were implanted on the left side.

Electrical activity was recorded from 5 electrodes simultaneously, usually 10 electrodes in all at each performance level. All records were of a transient electrical response and were amplified, filtered (with a highpass 80% attenuation at 0.2 Hz and lowpass at 50 Hz), then digitalized with an 8 bit resolution. A subsequent computerized ramp filter (100% pass at 0 Hz and linearly decreasing to zero pass at 60 Hz) was used to attenuate residual high frequency noise. Digitalization used time bins of 2 msec which gave 250 discrete numbers reflecting the moment-to-moment amplitude of the evoked electrical activity within each 500 msec recording. Records from the 5 electrodes taken during the 500 msec after the stimulus (stimulus-synchronized or *stimulus-evoked* activity) and the 250 msec before and 250 msec following the response (response-synchronized or *response-evoked* activity) were stored separately on 0.75 in. digital (DEC) magnetic tape. Also stored for each trial was information regarding which of the 4 possible stimuli had been presented on the trial; whether a

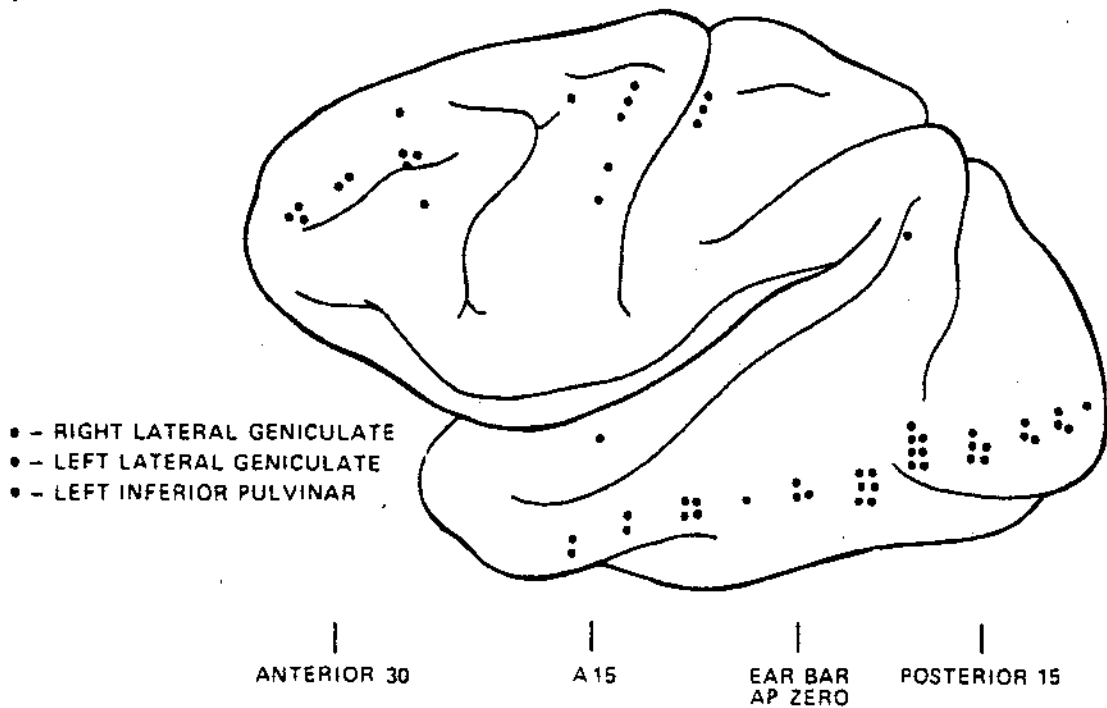


Fig. 2. Locations of electrode placements. Each dot represents an implanted electrode. All cortical electrodes were in the subjects' left hemisphere.

correct, incorrect or no response was made; and the stimulus-response latency.

#### Data analysis

Data analysis was initiated by separating the wave forms from a single electrode into two color categories. Although there were 45 trials in the 3 day sample, only the correct trials (usually about 40) were used to calculate averaged wave forms for each color. At criterion performance there were an insufficient number of incorrect trials to utilize those wave forms recorded when errors occurred. Thus comparisons were always made between wave forms recorded for correct trials.

Next, slopes of these averaged wave forms were computed. Slopes were chosen because they proved to be the most reliable indicators of wave form differences. Onset latencies are often difficult to identify (especially by computer), peak latencies vary as a function of

wave form amplitude, and amplitude is sensitive to changes in an animal's state which may alter from day to day. Slopes of wave forms, though not completely immune to these difficulties, are more reliable measures in the awake, freely behaving organism.

Slopes were computed by subtracting each time bin from the previous bin. For each day of testing, the wave forms recorded on trials 'red-left/green-right' were calculated and the 3 day total for these trials was obtained. This total was then compared to a similar total calculated for the 'red-right/green-left' trials. A *t*-test comparison was made on partially averaged data using blocks (4) and days (3) yielding 12 data points (*df* 10) for the millivolt differences along the slope for each of the corresponding 10 msec bins of recording.

Next, the same procedure was repeated for the pattern categories. Slopes of wave forms obtained on trials 'square-right/diamond-left'

were compared with those obtained on 'square-left/diamond-right'.

In this manner, color-sensitive and pattern-sensitive differences were determined from recordings of each of the 58 electrodes at each of the levels of behavioral proficiency (30%, 50%, 75%, 90%) for each task. When an electrode recorded wave forms which showed consistently color-sensitive differences (or showed consistently pattern-sensitive differences), irrespective of what was being reinforced, then that electrode was labeled as showing 'slide-related' differences. When the wave form showed color-sensitive (or pattern-sensitive) differences during color (or pattern)

reinforced performances then that electrode was labeled as showing 'task-related' differences.

Finally, the wave forms were separated into right-panel press and left-panel press categories independent of color or pattern arrangement on the slides, and independent of the reinforcing contingencies. Thus these right-panel press and left-panel press categories depended only on the position of the response and their wave forms were labeled 'panel-related' when they showed such differences.

These 'slide-related', 'task-related' and 'panel-related' differences were determined separately for each of the 'stimulus-evoked' and 'response-evoked' data epochs. Thus, 6 separate sets of values were investigated for each electrode placement.

Some of these values are illustrated in Fig. 3. Four wave forms are depicted. Each is the average of about 40 individual traces recorded on correct trials over 3 successive days (at 15 total trials on each day). The figure shows the averaged wave forms for 90%

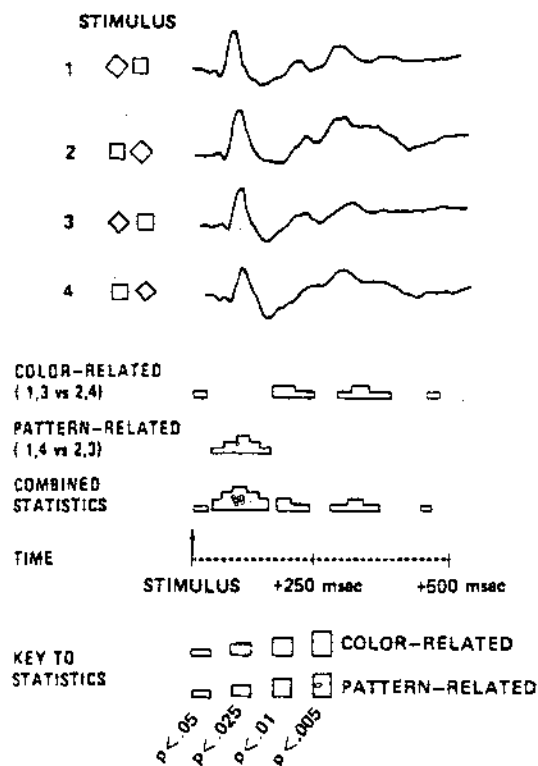


Fig. 3. Demonstration of how differences in wave form are identified. Four wave forms are shown here as averages of approximately 40 correct trials across 3 successive days of testing. The key to statistical probability levels is presented below the figure and shows that reliable differences can be assessed even when wave forms differ only subtly as in this illustration.

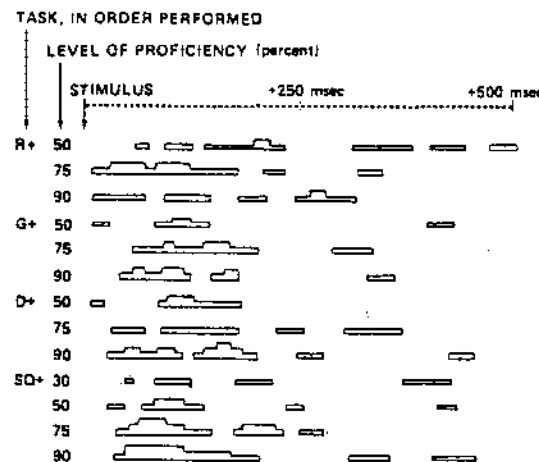


Fig. 4. An illustration of the time-locked analysis of wave forms for the stimulus-evoked epoch. Statistically significant color-related (white bars) and pattern-related (dark bars) differences are shown. This example is taken from an electrode implanted in the striate cortex. It demonstrates 'slide-related' variations since the differences found in the shapes of the wave form (especially at  $\pm 125$  msec) are consistently correlated over trials with the color arrangement on the slide-pair.

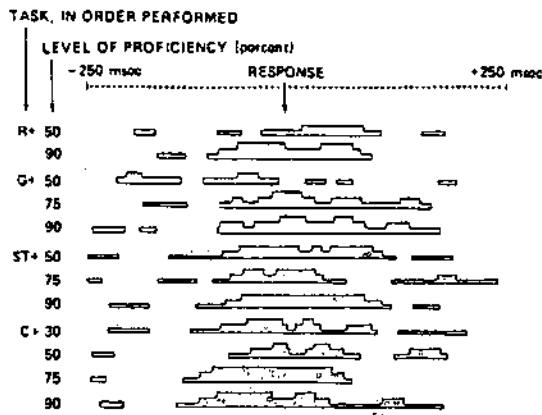


Fig. 5. An illustration of the time-locked analysis of wave forms for the *response-evoked* epoch. Statistically significant color-related (white bars) or pattern-related (dark bars) differences are shown. This example is taken from an electrode implanted into the inferior temporal cortex. It shows 'task-related' variations since there are consistently color-related (white bars) differences during color-reinforced tasks, and only pattern-related (dark bars) differences during pattern-reinforced tasks. Compare and contrast this to Fig. 4.

criterion performance on a square-positive (square-reinforced) task. The bars below the wave forms indicate the portion of the wave form in which the slopes were significantly different according to the *t*-test statistical procedure described. Each set of bars was calculated for the conditions noted: color-related and pattern-related (i.e., color-sensitive and pattern-sensitive).

Figs. 4 and 5 illustrate collections of such bars showing typical differences: Fig. 4 shows a 'slide-related' color-sensitive recording during the 'stimulus-evoked' epoch. Note that the statistically reliable differences (white bars) extend across all tasks. Fig. 5 shows a 'task-related' color and pattern sensitive recording during a 'response-evoked' epoch. Note that the color related differences in wave forms (white bars) are found primarily during color-reinforced tasks, and pattern-related differences in wave forms (dark bars) are found primarily during pattern-reinforced tasks.

## Results

### (1) Stimulus-evoked epoch

The main results obtained during the stimulus-evoked epoch are summarized in Table I. These results, and those for the response-evoked epoch described below, were all obtained while the monkeys were performing at 90% proficiency.

**Striate cortex.** Eight out of 10 electrodes (80%) showed slide-related wave forms, mainly dependent on the arrangement of the colors on the slides. One electrode (10%) also showed pattern-related activity in the middle of its color-related activity, creating for that one electrode 3 distinct temporal events during each trial: (1) color-related activity (50–100 msec post-stimulus), (2) pattern-related (125–200 msec), and (3) color-related again (200–300 msec). There were no task-related or position-related wave forms recorded from the striate cortex.

**Prestriate cortex.** The findings recorded from the prestriate cortex were for the most part similar to those recorded from striate cortex. Five of the 6 electrodes (83%) recorded slide-related wave forms around 50–250 msec post-stimulus, again primarily dependent on the color arrangement on the slides. However, in contrast to the results obtained from the striate cortex, the sixth electrode (17%) recorded task-related wave forms. Position-related wave forms were not seen.

**Inferotemporal cortex.** In contrast to the preponderance of slide-related wave forms recorded from the striate and prestriate cortex, task-related wave forms were recorded from 6 of the 16 inferotemporal cortical electrodes (37%) most frequently from the anterior inferotemporal region. Five of the remaining electrodes (31%) recorded slide-related wave forms, and these electrodes were all located in the more posterior parts of the inferotemporal cortex. Position-related wave forms did not appear in the records.

**Other regions.** There were no consistent relationships seen in recordings from frontal,

TABLE I

Stimulus epoch. Number of electrodes in various cerebral locations which showed *statistically reliable differences* (at  $P < 0.05$  or less) in the shapes of wave forms during the stimulus epoch. Column 1 lists the number of electrodes showing differences related to the slides presented as *stimuli* differing in the arrangement of their colors and patterns. Column 2 lists the number of electrodes showing differences related to the task required of the subject differing by virtue of their reinforcing contingencies. Column 3 lists the number of electrodes showing differences related to the position of the panel actually pressed by the monkey irrespective of which slide had been displayed or of the reinforcing contingencies operative in the task.

	Slide-related	Task-related	Panel-related	None	Total no. of electrodes
Striate	8			2	10
Prestriate	5	1			6
Posterior inferior temporal	2	2		2	6
Anterior + middle inferior temporal	3	4		3	10
Anterior frontal	1			5	6
Motor	1			2	3
Other	2			5	7

central, parietal, superior temporal or sub-cortical placements during the stimulus-evoked epoch.

In summary, recordings of stimulus-evoked brain electrical activity from the posterior end (striate cortex) of visually active cortical areas showed slide-related wave forms (usually color-dependent) at 50–250 msec post-stimulus presentation. More anteriorly (inferotemporal cortex) task-related waves became more common, although just as many of those anteriorly placed electrodes showed no stimulus-evoked relationships at all. Outside the visual systems, no consistent stimulus-evoked brain electrical activity occurred.

#### (2) Response-evoked epoch

*Striate, prestriate and inferotemporal cortex.* Slide-related wave forms were seen in 6 of the 33 electrodes (18%) in these regions during the response-evoked epoch. However, task-related differences were much more common, appearing in 3 out of 11 (27%) of striate leads, 3 out of 6 (50%) of prestriate leads, and 11 out of 16 (69%) of infero-

temporal cortex leads. These results and those for other regions are summarized in Table II. Position-related wave forms were not observed in these recordings.

The findings in the inferotemporal recordings showed that the task-related differences were present in both the 250 msec preceding and the 250 msec following the response. The average duration over which the differences occurred was longer for inferotemporal than for striate and prestriate leads ( $\chi^2 = 7.6$ ,  $df = 16$ ,  $P < 0.05$ ).

*Parietal lobe, motor cortex, and frontal lobe.* In recordings made from parietal cortex only 1 of 3 electrodes (33%) showed any response-evoked differences. That electrode was near the hand representation of the post-central gyrus, and showed only position-related differences between 20 msec pre-response and 50 msec post-response. Recordings from 2 of the 3 motor cortex (66%) and 3 of the 6 anterior frontal leads (50%) also showed only position-related differences, but these occurred across the whole 500 msec period. Only one other electrode (middle inferior temporal) showed such a long dura-

TABLE II

Response epoch. Number of electrodes in various cerebral locations which showed *statistically reliable differences* (at  $P < 0.05$  or less) in the shapes of wave forms during the response epoch. Column 1 lists the number of electrodes showing differences related to the slides presented as *stimuli* differing in the arrangement of their colors and patterns. Column 2 lists the number of electrodes showing differences related to the task required of the subject differing by virtue of their reinforcing contingencies. Column 3 lists the number of electrodes showing differences related to the position of the panel actually pressed by the monkey irrespective of which slide had been displayed or of the reinforcing contingencies operative in the task.

	Slide-related	Task-related	Panel-related	None	Total no. of electrodes
Striate	1	3		7	11
Prestriate	1	3		2	6
Posterior inferior temporal	2	4			6
Anterior + middle inferior temporal	2	7		1	10
Anterior frontal	2	1	2	1	6
Motor	1		2	0	3
Other	2		1	4	7

tion of relevant activity. The averaged duration in non-frontal leads was usually about 160 msec.

Some of the anterior frontal electrode recordings showed differences which were intermediate between the position-related differences seen primarily in the motor cortex and the task-related differences seen primarily in the inferotemporal cortex.

*Subcortically*, there were no consistent patterns of slide, task, or position specific activity recorded from the lateral geniculate nuclei or other loci in which electrodes had been implanted.

*In summary*, during the response-evoked epoch, task-related rather than slide- or position-related differences in wave forms were the general rule for recordings made from the inferotemporal cortex. By contrast, response-evoked activity observed in the recordings made from motor cortex reflected solely the position of the panel pressed.

### (3) Effects of acquisition

The slide-related and task-related differences reported in the previous two sections

were most evident when the subjects performed at the 90% proficiency in the required tasks. Data were also obtained to provide information on the changes which take place during learning of those tasks. Two types of changes were assessed. One is the change that occurs during learning and overtraining within a cue dimension. The second is the change that occurs when the reinforcing contingencies are shifted so that, e.g., a response to color must be changed to a response to a pattern.

*Within tasks*. Although recordings from the majority of electrodes did not show any relationship to change in performance over trials, 3 electrodes did show such changes during stimulus-evoked activity and 8 during the response-evoked activity epoch. Records taken at the 90% criterion showed higher statistical significance in the relationship between wave form and behavior than at the 75% level of performance. These differences were in turn significant at  $P < 0.05$  ( $\chi^2$ ). Surprisingly, however, when monkeys were overtrained, the recordings from these same leads showed a *decline* in the magnitude of



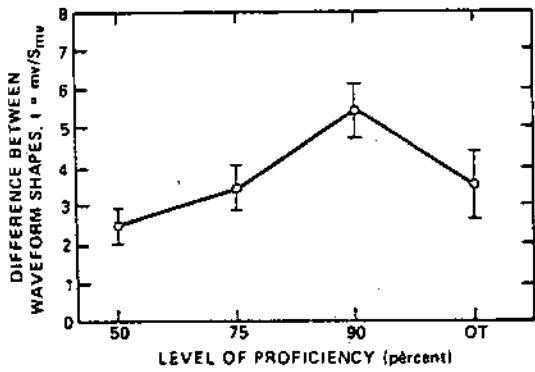


Fig. 6. Discrimination reversal learning changes. Example of peak of significance of differences occurring at 90% proficiency for one inferior temporal electrode. Horizontal axis shows the various proficiency levels achieved; OT = overtrained. Vertical axis shows the averaged (over-all tasks performed) amount of color-related (or form-related) differences found at that proficiency level, expressed as  $t$ -values ( $df = 10$ ) of the millivolt (mV) slope differences recorded. Such peaking of electrical differences around 90% proficiency was most often seen among task-related differences recorded from inferior temporal cortex during the response epoch.

significance ( $P < 0.05$ ), so that the 90% records show the greatest correlation between brain wave and performance. This effect is illustrated in Fig. 6, for those electrode placements which were sensitive to learning effects. The data are collapsed over leads and conditions. All records showing this effect were made from electrodes implanted in the inferotemporal cortex except one which recorded from the anterior frontal region.

*Between tasks.* At the onset of the initial change in reinforcement, the most noticeable effect was a *delay* in the disappearance of the wave forms related to the already learned task. This delay was observed for up to 2 reversals in the new dimension and the phenomenon is seen in all 4 of the task-related middle inferotemporal recordings. Fig. 7 illustrates this effect, showing that the color to pattern wave shift does not match the behavioral shift until the second change in reinforcing contingencies.

DELAY BETWEEN BEHAVIORAL AND ELECTRICAL SHIFTS FROM COLOR TO PATTERN

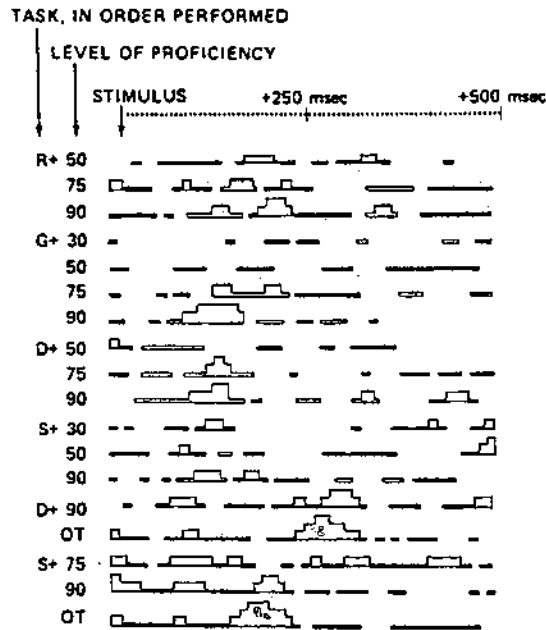


Fig. 7. Dimensional shift changes. This figure shows data taken during the stimulus-evoked epoch from one electrode implanted in the middle inferior temporal cortex. Of special interest are the data plotted between 50 and 200 msec post-stimulus. When the reinforcement contingencies were changed from a color dimension to a pattern dimension, after the seventh line on the graph, note that the wave form differences recorded still showed color-related difference (open bars) despite the fact that behaviorally the monkey was performing at a 90% criterion on the pattern problem. It was not until the second reversal of the pattern task that the recorded wave differences switched to being pattern-related (filled bars). R+, G+, D+, S+ are red-positive, green-positive, diamond-positive, and square-positive tasks.

Discussion

The general findings are clear. In the *stimulus-evoked* epoch the majority of sites produced either slide-related brain potential changes (especially to the color arrangement on the slides) or no relationship between the wave form of the brain potentials and the stimulus array. Such slide-related relationships

occurred in approximately 80% of the striate and prestriate leads but decreased to about 30% in the anterior regions of the inferotemporal cortex. By contrast, recordings from the electrodes implanted in the inferotemporal cortex (and one in the prestriate cortex) and only these showed wave form relationships to appropriate task-related parameters.

Analysis of the event-related potentials obtained during the *response-evoked* epoch even more often show that recordings from inferotemporal leads are overwhelmingly related to task, i.e. to the reinforced stimulus parameters in the situation. Recordings from only 5 of the 16 inferotemporal electrodes showed no such task-related electrical activity. Thus 60% of these electrodes showed task-related wave form differences. By contrast, only 27% of the occipital leads and half of prestriate leads showed a relationship to the task. Finally, when response-related effects were recorded from parietal, motor and anterior frontal leads, they reflected solely the position of the panel pressed and thus differed markedly from the inferotemporal and other visual system recordings.

The timing of the task-related activity also proved of interest. First, task-related differences in the wave forms recorded from the inferotemporal and other visually related cortex during stimulus-evoked epochs occurred well before such task-related differences appear in response-evoked activity and in the absence of any similar stimulus-evoked electrical response from motor and frontal sites. This suggests that the selection process begins well before a response is initiated. However, the task-related wave forms recorded from inferotemporal and other visually related cortex did not begin to develop until approximately 125 msec had elapsed since stimulus presentation, suggesting this as the latency of onset for the process.

Further evidence as to how the selection process operates in monkeys performing these tasks comes from the data obtained in the within-tasks and between-tasks experiment. Recordings from 11 leads, 10 from infero-

temporal cortex and 1 from anterior frontal cortex, were found to show an increased correlation with achieving criterion but a subsequent decrease with overtraining. This finding supports earlier observations made on monkeys with inferotemporal resections. These studies reported that if a task is highly overtrained before surgery significant savings are observed postoperatively (Chow and Orbach 1957). According to these data, the inferotemporal cortex is more critically involved when a particular selection is being learned than when it is already established. This observation is dramatically supported by the evidence that a dimensional shift can be accomplished behaviorally while the electrocortical activity continues to reflect earlier selections. Perhaps the simplest explanation of this dissociation is that the monkey is still 'thinking' color while responding behaviorally to pattern, much as an American may 'think' to himself that looking to the left is an inappropriate response in crossing a street in England before he overtly looks right and starts the crossing. The possibility thus exists that the current experiments have employed a technique by which covert information processing by the brain can be usefully assayed. Dewey (1916) defined 'thinking' as 'active uncertainty' while Shannon and Weaver (1949) defined 'information' in terms of a selection that reduces uncertainty. Experiments are planned to pursue the intriguing possibility that information processing in the Dewey and Shannon-Weaver sense can, by electrical recording of event-related brain recordings, be directly related to thought processes in animals and man.

### Summary

Electrocortical recordings were made from monkeys performing in a multidimensional visual task. Wave forms dependent on the stimulus presented (irrespective of task required) were recorded immediately follow-

ing the stimulus primarily from electrodes implanted in the striate and prestriate cortex. Wave forms dependent on the *panel* pressed (irrespective of the stimulus or of the task) were recorded especially from motor and post-central cortex, and to a lesser extent in anterior frontal cortex, always just prior to or following the time of the response. Wave forms dependent on the *task* as determined by the reinforcing contingencies (but independent of the particular stimulus presented or the particular panel pressed) were recorded primarily from the inferior temporal cortex, and rarely from prestriate and anterior frontal cortex. While task-related wave forms began to appear shortly after stimulus presentation, they became especially apparent around the time of the response. This response-linking increased in prominence as the subject achieved 90% proficiency in each task, only to drop off with overtraining. Further, the task-related wave form does not change as rapidly as does overt behavior when the reinforcement contingency is shifted from one stimulus dimension to another. The relevance of these results to an understanding of the process of selective attention is discussed.

### Résumé

#### *Rôle du cortex temporal inférieur dans l'attention visuelle sélective*

Des enregistrements électrocorticaux ont été réalisés chez des singes au cours de la réalisation d'une tâche visuelle multidimensionnelle. Des ondes dépendant de la stimulation présentée (quelle que soit la tâche demandée), sont enregistrées immédiatement après le stimulus, et d'abord au niveau d'électrodes implantées dans le cortex strié et pré-strié. Des ondes dépendant du clavier pressé (quelle que soit la stimulation ou la tâche) sont enregistrées tout particulièrement au niveau du cortex moteur et post-central et à un moindre degré dans le cortex frontal

antérieur, toujours juste avant ou juste après le moment de la réponse. Des ondes dépendant de la tâche, déterminée par les contingences de renforcement (mais indépendantes de la stimulation particulière présentée ou du clavier particulier pressé) sont enregistrées tout d'abord au niveau du cortex temporal inférieur et rarement au niveau du cortex pré-strié et du cortex frontal antérieur. Alors que les ondes liées à la tâche commencent à apparaître peu après la présentation du stimulus, elles deviennent spécialement apparentes au moment approximatif de la réponse. Cette liaison à la réponse augmente au fur et à mesure que le sujet parvient à une performance de 90% pour chaque tâche, pour diminuer ensuite avec le surapprentissage. De plus, l'onde liée à la tâche ne change pas aussi rapidement que ne le fait le comportement apparent quand la contingence de renforcement varie d'une dimension de stimulation à une autre. Les auteurs discutent les apports de ces résultats à la compréhension du processus d'attention sélective.

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