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Occipital and Inferotemporal Responses to Visual Signals in the Monkey

J. WESSON ASHFORD AND JOAQUIN M. FUSTER[1]

Department of Psychiatry and Brain Research Institute, School of Medicine, University of California, Los Angeles, California 90024

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This study analyzes cellular and field-potential responses in striate and inferotemporal cortex to visual stimuli in monkeys performing a memory task (delayed matching-to-sample). Each trial was initiated by a brief alerting diffuse flash preceding presentation of the memorandum (sample); the latter was a lighted circle (red or green, 1.5 s) to be retained by the animal during a subsequent delay for correct behavioral response (color match). The alerting flash evoked distinct excitatory cell responses and field potentials in the occipital cortex; those two orders of phenomena were broadly related to each other in temporal terms. By contrast, most cells in the inferotemporal region were inhibited by the flash, although the local evoked field potential had a configuration similar to that of the occipital potential. In each region, the sample stimuli elicited excitatory unit responses which summed to a unimodal distribution with an initial component roughly corresponding in time course to the local field potential. Although the shortest response latencies were found in occipital cortex, considerable temporal overlap of the sample-related activities in the two cortices was observed. The finding that most inferotemporal cells, unlike occipital cells, treated only the sample with excitatory response indicates that the inferotemporal cortex is selectively attuned to visual detail. However, the largely simultaneous activation of both cortical regions following the onset of the sample suggests that discriminative visual information is processed by hierarchic interactions of the two cortices through their reciprocal connections.

Abbreviation: SC, superior colliculus.

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INTRODUCTION

In the last two decades, there has been considerable interest in the capacity of the visual system to represent details of the environment. However, broader questions are now being asked regarding the neural integrative processes at the basis of visual perception. Of special concern are the mechanisms by which the organism analyses visual stimuli as a function of their behavioral relevance.

The retinal–genicular–striate pathway has long been established as the anatomically dominant visual pathway (49). Major projections of the striate cortex lead through prestriate regions to inferotemporal cortex (36, 38, 47). The anatomic evidence of successive stages of projection from the retina to the inferotemporal cortex has led to the proposition that photic signals are analyzed sequentially; at each stage progressively more complex analysis would be completed (33, 43, 44). That idea is supported by the finding of progressively longer latencies of unit and evoked-potential response to a stimulus as the hierarchy of structures within that pathway is ascended (7, 29, 46). Furthermore, lesions at any level within the sequence block transmission of impulses to subsequent stages (28). Lesions in lower stages tend to impair the sensory aspects of vision (39), whereas those in higher stages affect mainly its cognitive aspects, such as discrimination and memory (44). That is in accordance with the assumption that there is a hierarchy of sensory functions underlying perception (32).

In the primate nervous system, however, there have been numerous demonstrations that the flow of information may follow a diversity of functional pathways depending on the nature of the visual stimulus. Initial suggestion of functional dichotomies came from the demonstration that retinal ganglion cells can specialize to encode two different types of information: either large and abrupt changes in the visual field or fine details (6, 16). The retinal–genicular–striate pathway appears to convey both of them along separate channels (3, 34, 35, 40) into the prestriate areas (59, 63). The transiently responding retinal cells send a second projection to the superior colliculus (SC), presumably for detection of major environmental changes (55, 62), and the SC in turn projects through the pulvinar (4) to visual cortex (5). Furthermore, coordination of information from these two pathways may explain why inferotemporal cortex units not only respond to specific complex visual stimuli (27), but show sensitivity to task demands (41) and context (23). Thus, there may be two retinal–cortical pathways to support visual integration (11).

We identified and analyzed patterns of cortical activity related to visual events in order to ascertain the temporal aspects of visual cognitive processing in the cortex. Two types of visual information—a brief alerting signal and a prolonged color discriminandum—were presented to attentive monkeys in the behavioral context of a visual, short-term memory task. One objective

was to determine whether or not the temporal characteristics of event-related neuroelectrical responses, in striate and inferotemporal cortices, warrant the assumption of two separate and sequential stages of information processing in those two cortical regions.

METHODS

Subjects. The experiments were conducted on two male rhesus monkeys (*Macaca mulatta,* 8 and 10 kg). The monkeys had access to food *ad libitum* but water was restricted during experimental periods.

Behavioral Paradigm. The monkeys were trained to perform a delayed matching-to-sample task (8) while seated in a primate chair facing a stimulus panel (Fig. 1). The panel contained an upper rectangular section (22 × 45 cm) of translucent plastic and a lower white opaque section (38 × 45 cm) in which three translucent stimulus-response buttons (2.5-cm diameter) were placed. The three buttons formed an isosceles triangle with the vertex up, the latter at eye level and at a distance of about 18 cm from the eyes. A white flash (10 μs, 13 lx at the position of the monkey's eyes), diffusely illuminating the panel's upper section, alerted the animal and initiated each trial. Two seconds later, the top button was fully illuminated with colored light projected from the rear through Cinemoid color filters. That colored light, either green (530-nm peak wave length, 4.5 ft lamberts) or red (620 nm peak wave length, 3.0 ft lamberts) was the sample for the trial. The monkey was allowed only 1.0 s to press the lit button, though the illumination lasted 1.5 s. Ten seconds after the offset of the sample, the two lower buttons were illuminated, one red and the other green. The animal, for juice reward, was then required to press the button whose color matched the sample. Sample color and position of that color in the two choice buttons were randomized and counterbalanced across trials (25). Therefore, in order to perform the task correctly, the animal was obliged to remember the color of the sample. Throughout the experiment the monkeys performed 80% correct or better. The intertrial interval was about 30 s.

Surgical Procedure. The monkeys were surgically prepared (pentobarbital anesthesia) for electrophysiologic recording. Metallic sleeves were attached to the skull to anchor the animal's head in the primate chair. Two electrode wells were implanted over striate and inferotemporal cortex. The occipital well was positioned with its center 1.0 cm above the occipital ridge and 1.5 cm lateral to the midline. This position is approximately two degrees from the center of the cortical representation of the animal's visual field (9). The temporal well was placed in front of the ear, under stereotaxic guidance, 1.5 cm anterior to and 1.0 cm above the interaural zero position. This position is over anterior inferotemporal cortex, area TE (61). Wound margins were

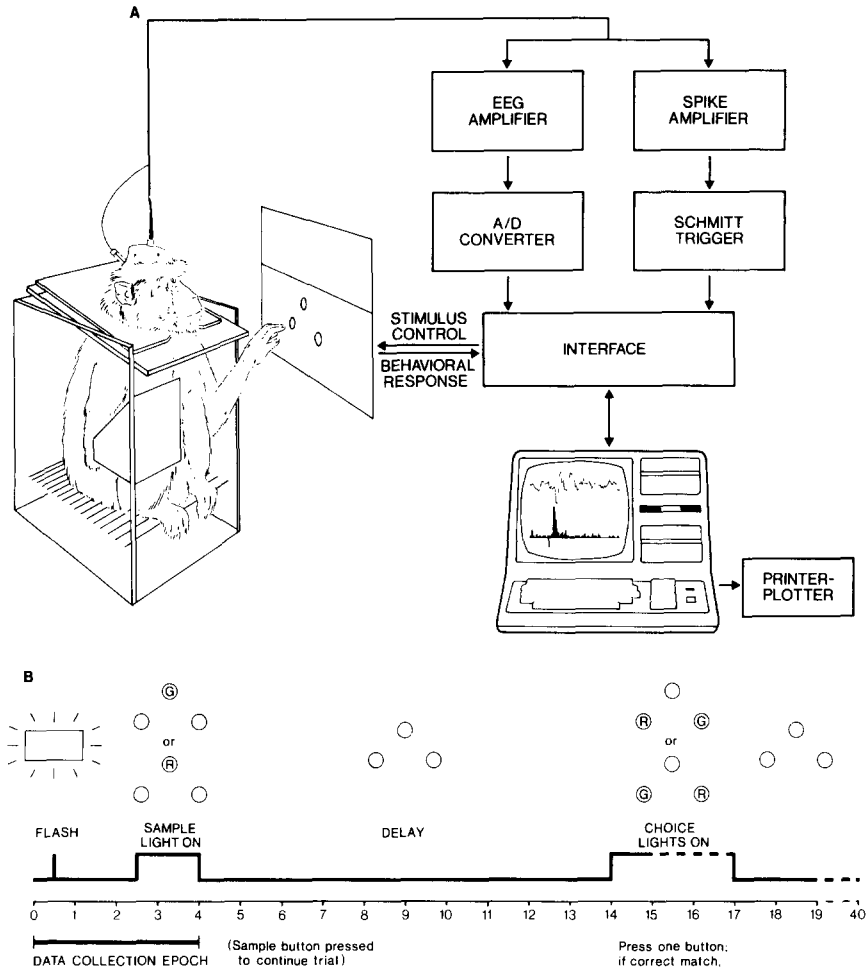


FIG. 1. A—schematic diagram of the experimental apparatus. The monkey is seated in front of the stimulus panel which has two sections: the upper section is a translucent screen on which the alerting (strobe) flash is presented; the lower section contains three translucent buttons for presentation of sample and choice colors and for manual responses. B—event sequence in an experimental trial. Note that the data for this study were collected in a 4-s epoch ending with sample-off. (G, green; R, red).

tended with hydrogen peroxide and furacin ointment. Bicillin was administered systemically at regular intervals. Several weeks elapsed before experimentation commenced.

Recording. Recordings were made predominantly with glass-coated Elgiloy microelectrodes [modified from Suzuki and Azuma (2, 57)]. Electrode

impedance was about 200 kΩ. The electrodes were of high enough conductance to record field-potential activity relatively free of artifact, and small enough to allow isolation of spikes from single cells or small groups of cells.

The steel microelectrode positioner allowed penetration of the underlying cortex around a 2.5-mm-diameter circle. The electrode was mounted on a specially designed carrier and advanced by turning a 0-80 screw [adapted from Harper and McGinty (31)]. It was advanced until neuronal discharge could be audibly and visually distinguished in the amplified signal. That position was designated "zero depth" in the cortex. In the occipital cortices of both monkeys and the inferotemporal cortex of one, where the penetrations were later proven to have been perpendicular to the surface, units could be recorded for about 1.9 mm.

The microelectrode was connected by a shielded Y-junction to two amplifiers (Grass P511). One amplifier had a high-pass filter setting (30 to 3000 Hz) for amplifying the fast-frequency voltage changes usually associated with unit activity. The signal was led to an oscilloscope for display and through a Schmitt trigger circuit to a computer (TRS-80, Model III) for analysis (Fig. 1).

The second amplifier had a low-pass filter setting (0.1 to 100 Hz). The steel electrode well, in contact with the overlying dura, was used as the reference. The low-frequency signal was led to an oscilloscope for monitoring slow-potential activity. The amplified signal was led through an analog-to-digital converter to the computer. Comparison of both channels revealed a complete separation of unit and field potential activities.

Histology. Marking lesions were made in the brain with iron-containing microelectrodes. The brain was extracted and fixed in Formalin. Coronal sections were stained by the Nissl method. In both monkeys, the electrode penetrations of the striate cortex were perpendicular to the surface (Fig. 2). The inferotemporal penetrations of one monkey were made in the cortex of the inferior temporal convexity; those of the other were made in the lower bank of the superior temporal sulcus.

Data Analysis. Only spikes from individual units or groups of units that could be clearly distinguished on the oscilloscope (50% above the background "hash") were sampled at various electrode depths. In some cases, the activity of only a single cell was evident in the record. However, most records were obtained from groups of several cells. Attempts were made to sample visually responsive units from all locations across the breadth of cortex. Slow-potential records were taken concomitantly with unit records. Unit and field potential were sampled every millisecond; however, both unit counts and field potential averages were computed in 4-ms bins. A frequency histogram of unit activity and averages of field potential activity were obtained and displayed on line.

For each unit set, the 0.5-s preflash baseline epochs were tested for stability

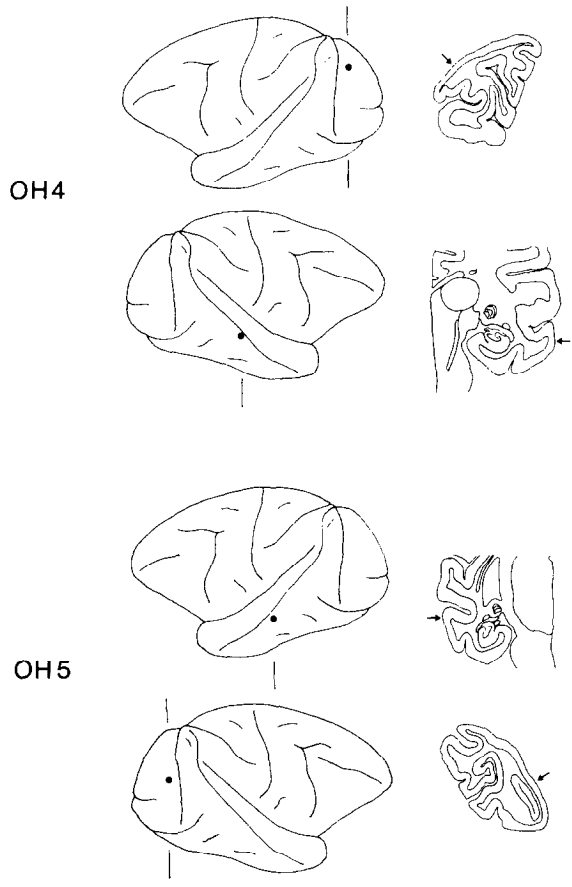


FIG. 2. Anatomic drawings showing the locations of electrode penetration in the two experimental animals (OH4 and OH5). The tracings on the right are from histologic sections, each arrow marking the center of an electrode well.

of firing. The poststimulus epochs were examined for departures from that baseline. Unit sets were defined as responsive if at least three bins in the following 3.5 s departed from that baseline by at least three standard deviations. After transformation of frequency data by a binomial smoothing function, a process that does not introduce phase distortion (1), response latencies were measured. Onset latency was defined as the time between stimulus onset and the second consecutive bin of significant deviation from baseline. Peak response latency was defined as the time to the first point at which there was a change of frequency trend following the start of response. [Low levels of interdependence of units were presumed (58).] To determine the time of maximal overall activity of the cells in a given region of cortex, the scaled unit-

frequency data from that region were summed. The onset and peak latency of the composite response were measured. A similar statistical procedure was followed for field potential analysis, except that voltages were used instead of spike counts.

RESULTS

Unit activity was recorded in the course of 54 penetrations of occipital cortex and 23 penetrations of inferotemporal cortex. Units responsive to one or more of the visual stimuli in the behavioral task were recorded from 170 positions, 111 of them in occipital cortex and 59 in inferotemporal cortex. Evoked field potentials were recorded simultaneously at all locations.

Occipital Cortex. In the occipital cortex, spontaneous baseline activity (i.e., unit discharge between task trials) was highly variable, ranging for different units roughly between 1 and 20 spikes per second. Mean spontaneous discharge was approximately 5/s. The EEG showed predominantly low-voltage, fast activity. The incidence of cells responding to the stimuli varied considerably for different penetration tracts around the perimeter of the electrode well. Along several tracts most units were responsive, whereas along others, as little as 1 mm away, very few responsive units were found. In general, responsive cells were activated by both the alerting flash and the sample stimuli, although the relative degree of responsiveness to each varied considerably.

Responses to alerting flash. Many occipital cells showed a brisk reaction to the flash stimulus. Among the responsive unit sets (Table 1), 71% exhibited reactions approximating a unimodal frequency distribution (Fig. 3); others showed the overlap of two, three, or four separate distributions (Fig. 4). Such clusters of unit activity will be referred to as "response pacquets." The overall envelope distribution of response pacquets summed vertically across a region of cortex was unimodal (Fig. 4, bottom) and had an onset latency of about 20 ms and a peak latency of about 70 ms (Table 2). The biphasic field potential response was concurrent with that overall unit response (Fig. 4), the temporal span of the first coinciding with that of the second. Thus, it appeared that the composite of unit firing was the integral of the power of the field potential. Following responses to the flash, units and field potential returned to baseline values and remained at those values until the onset of the color sample, although occasional units did show sustained increases of activity between flash and sample.

Responses to color sample. The initial responses of most unit sets to the color light were excitatory (Figs. 3 and 4). As in the case of the flash responses, distribution into response pacquets and dominance of unimodal responses (66%) were also observed after sample onset (Table 1). However, the response latencies, though variable, were substantially longer (by about 30 ms on the

TABLE 1

Unit Response Categories: Classification of Unit Records According to Response to the Stimulus

	Occipital (111)	Inferotemporal (59)[a]
Flash		
Inhibitory	2 (1.8%)	21 (36%)
Unimodal	79 (71.2%)	12 (20%)
Bimodal	14 (12.6%)	1 (1.7%)
Multimodal	3 (2.7%)	1 (1.7%)
Unresponsive	13 (11.7%)	24 (40.6%)
Sample[b]		
Inhibitory	5 (4.5%)	2 (3.4%)
Unimodal	73 (65.8%)	17 (28.8%)
Bimodal	10 (9%)	15 (25.4%)
Multimodal	3 (2.7%)	6 (10.2%)
Unresponsive	20 (18%)	19 (32.2%)

[a] Single units accounted for 14 of these 59 records.

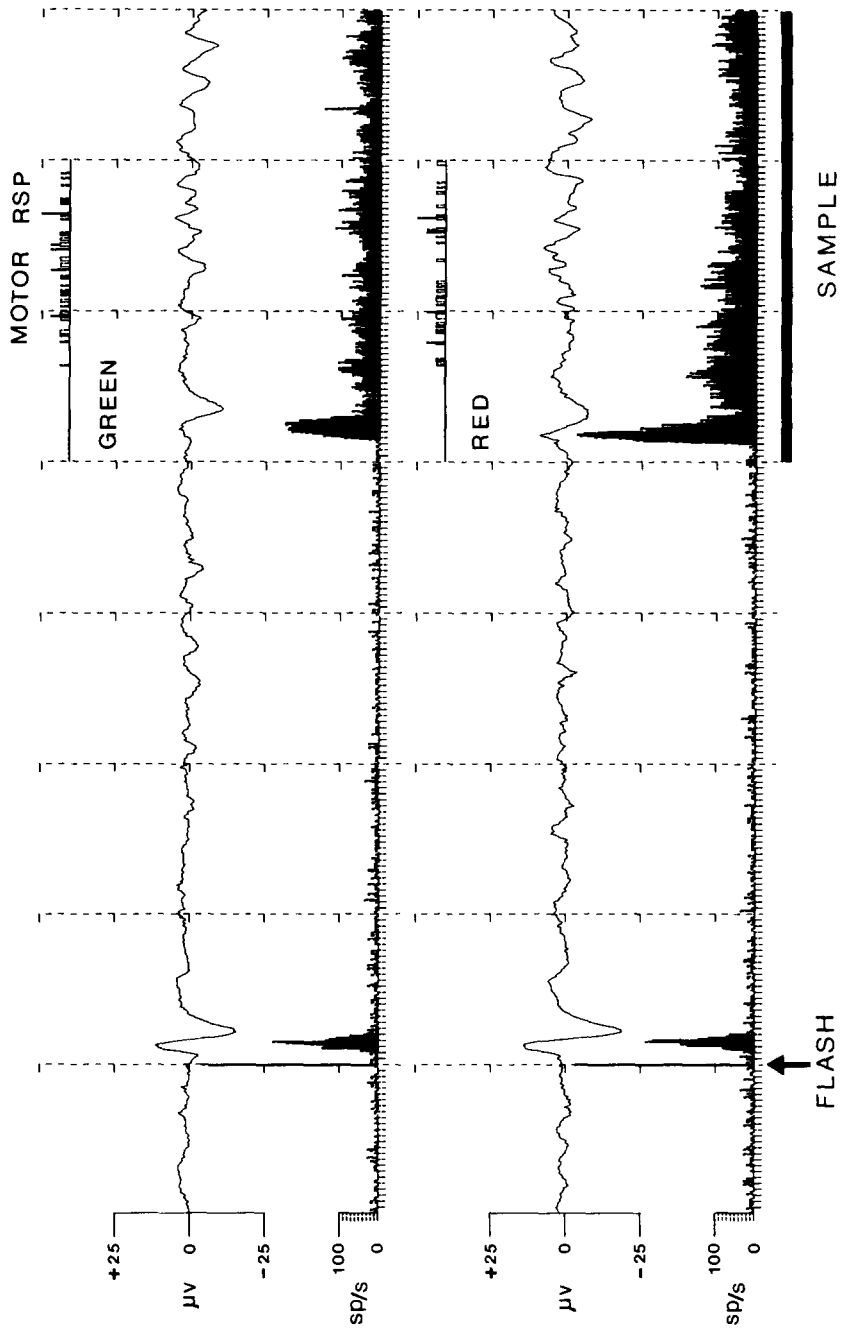
[b] Where the response to the two colors differed in amplitude, the largest was used for classification.

average; Table 2). Green-responses had longer latencies than red-responses (average difference, about 10 ms). The responses were often sustained for the duration of the stimulus. The majority of responsive cells showed a large transient burst after the flash, another after sample onset, and sustained activity for as long as the sample was present. The sample responses of unit sets from across the cortical breadth combined into a unimodal distribution in similar manner as after the flash.

The field potential generated by the sample had longer latency characteristics than that generated by the flash, as well as a smaller amplitude. The green–red difference seen in unit sets could also be observed in field potential latencies. The major power of the sample field potential response again occurred during the initial overall unimodal burst of unit response, in a relationship similar to that noted after the flash.

Inferotemporal Cortex. The spontaneous firing frequencies of inferotemporal units were similar to those of occipital units, both in range and average. The baseline inferotemporal EEG records also showed low-voltage, fast activity. As seen in the course of occipital penetrations, unit responsiveness in the inferotemporal region clustered along specific tracts.

Responses to alerting flash. In striking contrast with occipital units, most inferotemporal units showed either an inhibition (Fig. 5) or no apparent reaction (Fig. 6) after the alerting flash. Only about one-fourth of all inferotem-


MOTOR RSP
GREEN
RED
SAMPLE
FLASH
+25
0
-25
μv
100
0
sp/s
+25
0
-25
μv
100
0
sp/s

poral cells examined showed excitatory responses (Table 1), and these tended to be minor (Fig. 7).

Unit response latencies after the flash were generally longer in inferotemporal than in occipital cortex. Little change of activity was observed before 40 ms. The inhibitory responses, which were more numerous and of greater magnitude than the excitatory ones, had an average onset latency of about 100 ms. Sums of unit activity across inferotemporal cortex showed that inhibition dominated the overall reaction of the region and was sustained until at least 500 ms after the flash (Fig. 8). In many cells, initial changes of activity were followed by periods of variable inhibition or excitation which lasted until the color sample appeared. In contrast, no such protracted deviations from baseline were observed in occipital cortex.

The inferotemporal field potential evoked by the flash, although also biphasic, was generally slower than the occipital one (Figs. 4 and 8; Table 3). Due to the predominance of unit inhibition in the presence of relatively discrete field potentials, a clear relationship between the time courses of unit responses and those of the field potential responses could not be established as in the occipital cortex.

Responses to color sample. Unlike the responses to the flash, the responses of inferotemporal unit sets to the sample commonly manifested initial excitation (Figs. 5–7), although not of as great magnitude as that of most occipital cells. However, multimodal response pacquets were also observed in inferotemporal cortex (Table 1). The unit responses of this region were generally more variable in terms of onset and peak latency, as well as time course, than those of occipital cortex. Although unit sets were found in inferotemporal cortex which responded with as short a latency to the color sample as occipital cells (Figs. 3 and 6), the average onset latency of evoked activity in the inferotemporal cortex was longer (by approximately 8 to 28 ms; Table 2). Peak latency was, likewise, somewhat longer in inferotemporal cortex.

As in the occipital region, the inferotemporal unit responses to the color added to form an initially unimodal distribution (Fig. 8), but that distribution did not show as discrete a temporal demarcation as the one from the occipital region (Fig. 4). Nevertheless, the two temporal distributions (occipital and temporal) of the initial unit response were largely overlapping. After that

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FIG. 3. Average field-potential records and spike-frequency histograms from a supragranular locus in the occipital cortex during 50 green-sample and 50 red-sample trials. Motor responses (RSP) are indicated on the right above the potential records. The field-potential calibration is at left in microvolts (μV); the polarity indicated is for the (surface) reference electrode. The histograms are scaled in spikes per second (sp/s). Hash marks are 20 ms apart; vertical dash lines are 0.5 s apart.

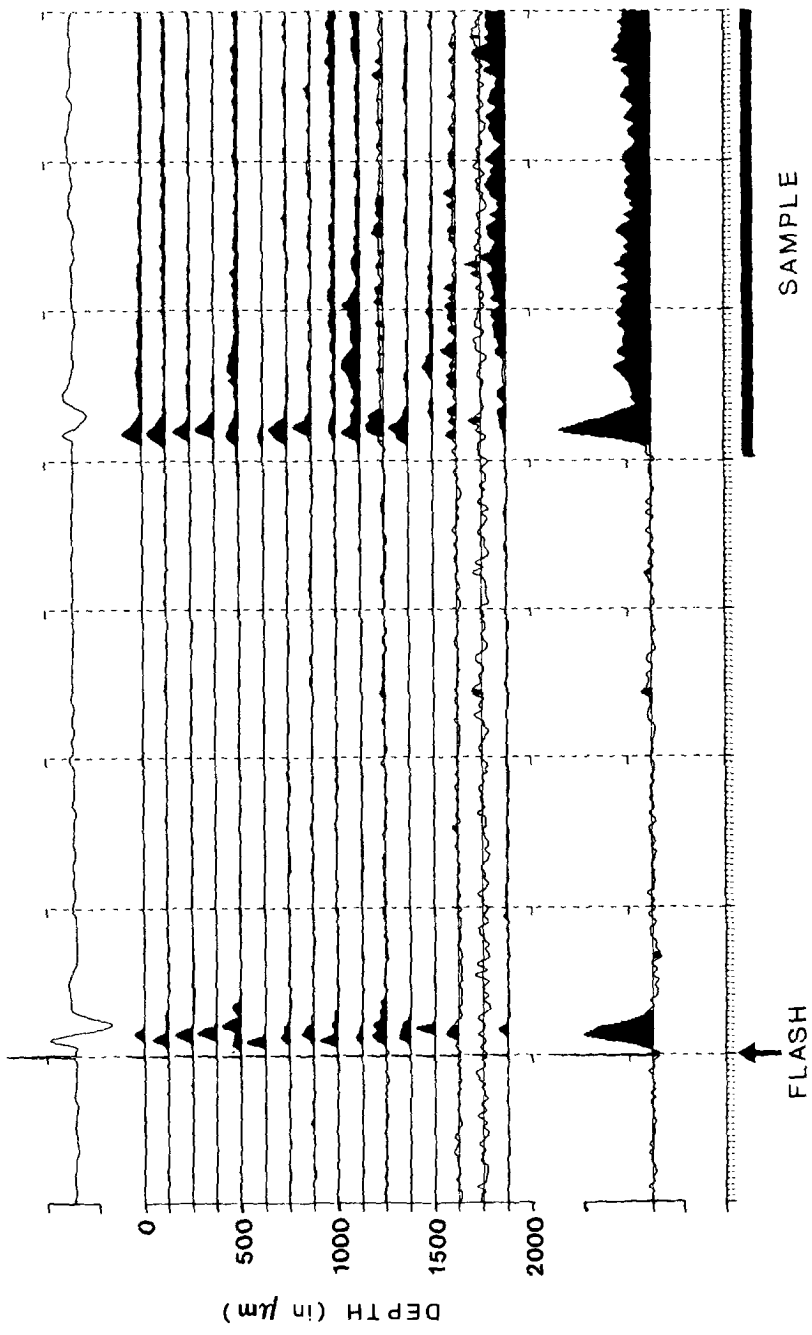
SAMPLE
FLASH
0
500
1000
1500
2000
DEPTH (in μm)

TABLE 2

Range of Unit Response Latencies in Two Monkeys Performing a Discriminative Task[a]

	Onset		First peak	
	Occipital	Inferotemporal	Occipital	Inferotemporal
Flash				
OH4	16–72 (20)	(Inhibition)	36–92 (72)	(Inhibition)
OH5	24–72 (22)	(Inhibition)	36–92 (68)	(Inhibition)
Green				
OH4	48–104 (48)	48–148 (76)	76–144 (102)	52–176 (96)
OH5	56–104 (52)	64–168 (72)	84–156 (120)	80–180 (108)
Red				
OH4	44–80 (48)	52–168 (60)	64–132 (84)	72–188 (96)
OH5	52–76 (52)	48–132 (60)	80–128 (96)	56–168 (100)

[a] The variation in unit response latencies (in ms) for onset and first peak in occipital and inferotemporal cortices of the two animals, OH4 and OH5. The numbers in parentheses represent the values for unit response sums like those shown at the bottom of Figs. 4 and 8.

initial response, both cortices showed concurrent and sustained discharge, though of lesser magnitude, until the termination of the colored light.

The field potential response of the inferotemporal cortex to the colored light was nearly as large in amplitude as the response to the flash. Most latency measures of sample-evoked potentials were slightly longer in inferotemporal than in occipital cortex, none were shorter (Table 3). As in the occipital region, initial unit response and field potential response seemed to occur, for the most part, concurrently.

Relationships to Behavioral Reaction. Reaction time, measured from sample-on to button press, varied between about 0.2 and 1 s (reactions after 1 s were excluded). Unit and field potential responses were divided into two groups: one associated with fast (less than median) and the other with slow (greater than median) reaction time. No differences in electrical response latencies were observed between the fast and slow groups in either occipital or

FIG. 4. Plots of activity of 16 cell groups selected from the occipital cortex of monkey OH5. The plots are stacked in order of depth (approximate depth indicated at left, between 0 and 2000 μm). Each plot represents a digitally smoothed and separately scaled crest of the frequency histogram from red-sample trials. The horizontal line through each record marks the mean pretrial baseline frequency. The blackened portions of the record denote deviation from the 0.5-s preflash or the 0.5-s presample baselines by at least three standard deviations. The bottom plot represents a summation of all the histogram crests. On top, a local field-potential record is shown.

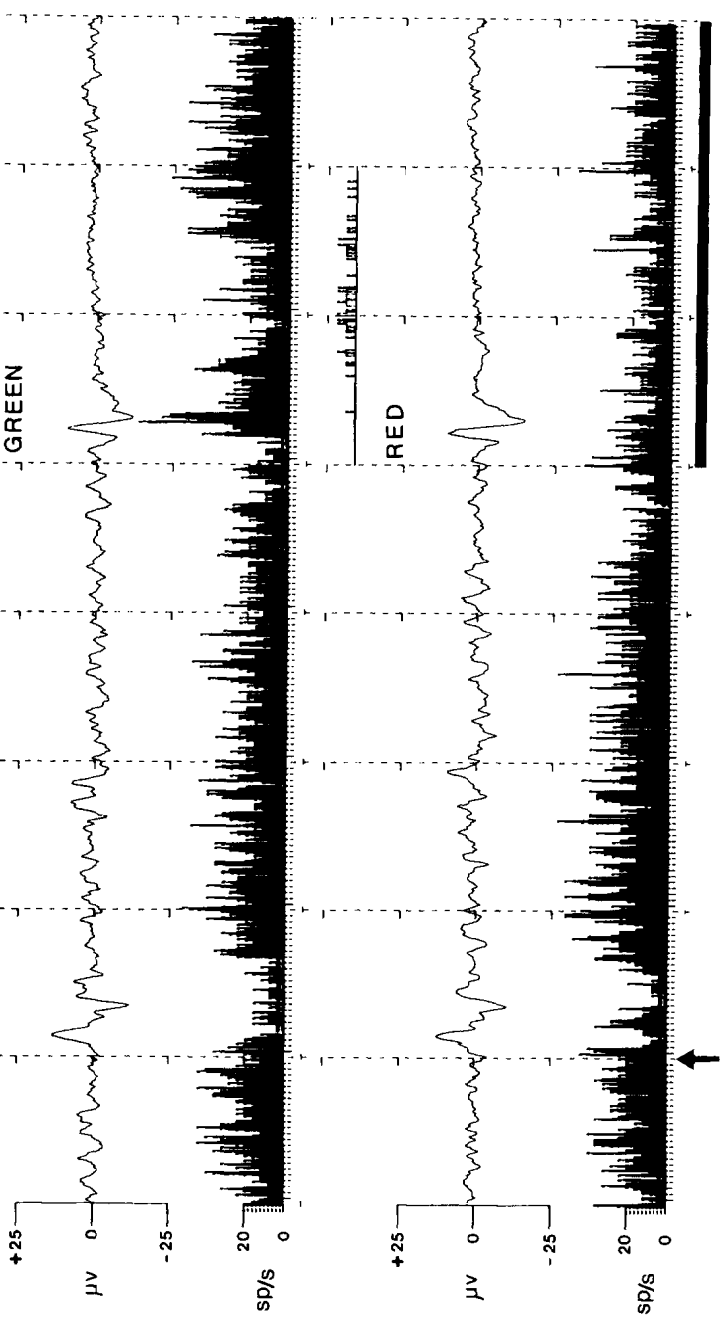

FIG. 5. Average field potentials and frequency histograms from inferotemporal cortex (60 green and 60 red trials). Graphic format as in Fig. 3. Note inhibition of cell activity after the flash and excitation after green sample.

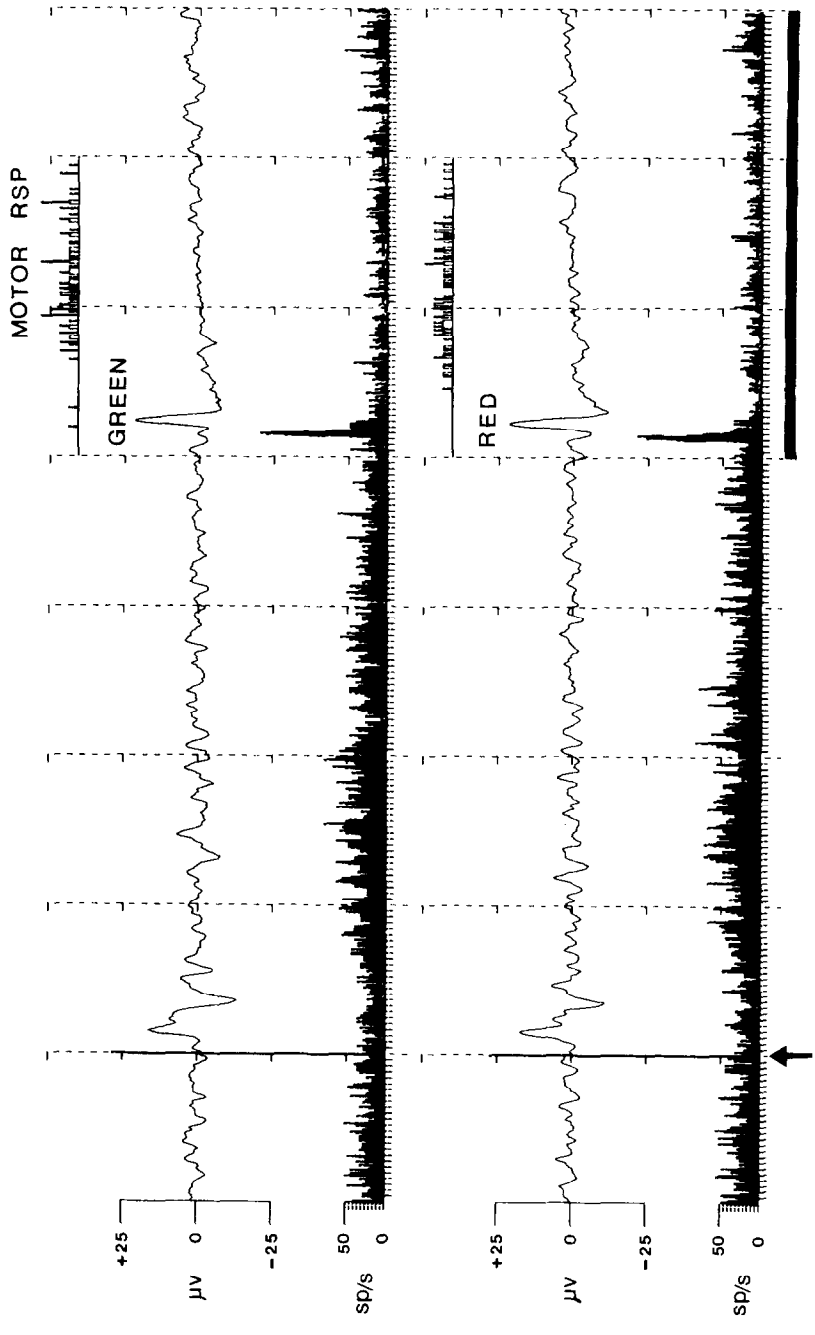

FIG. 6. Records from inferotemporal cortex (90 green and 90 red trials). Graphic format as in Fig. 3. Note the lack of initial unit response to the flash and the brisk response to both sample colors.

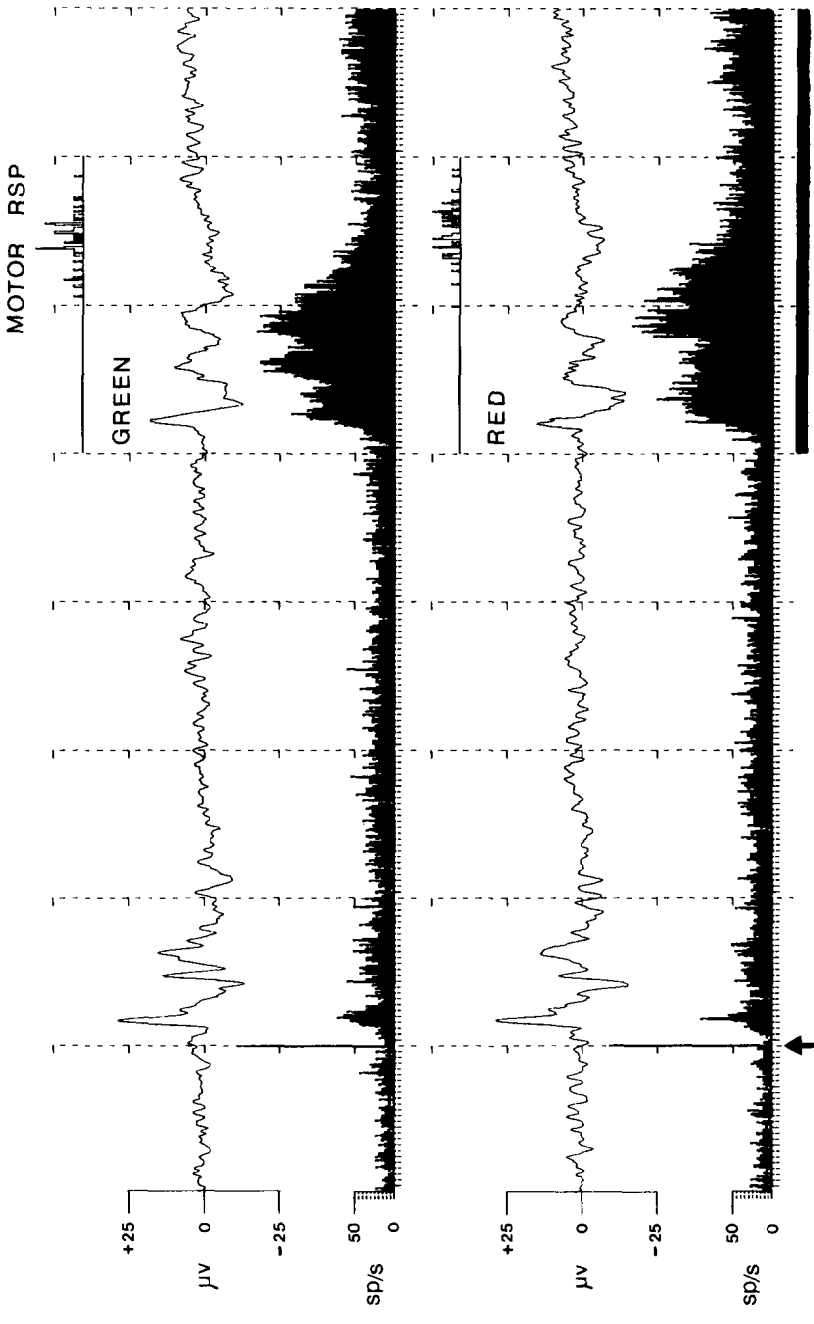

FIG. 7. Records from inferotemporal cortex (50 green and 50 red trials). Graphic format as in Fig. 3. Note small excitatory unit response to flash in comparison with that to both colored lights.

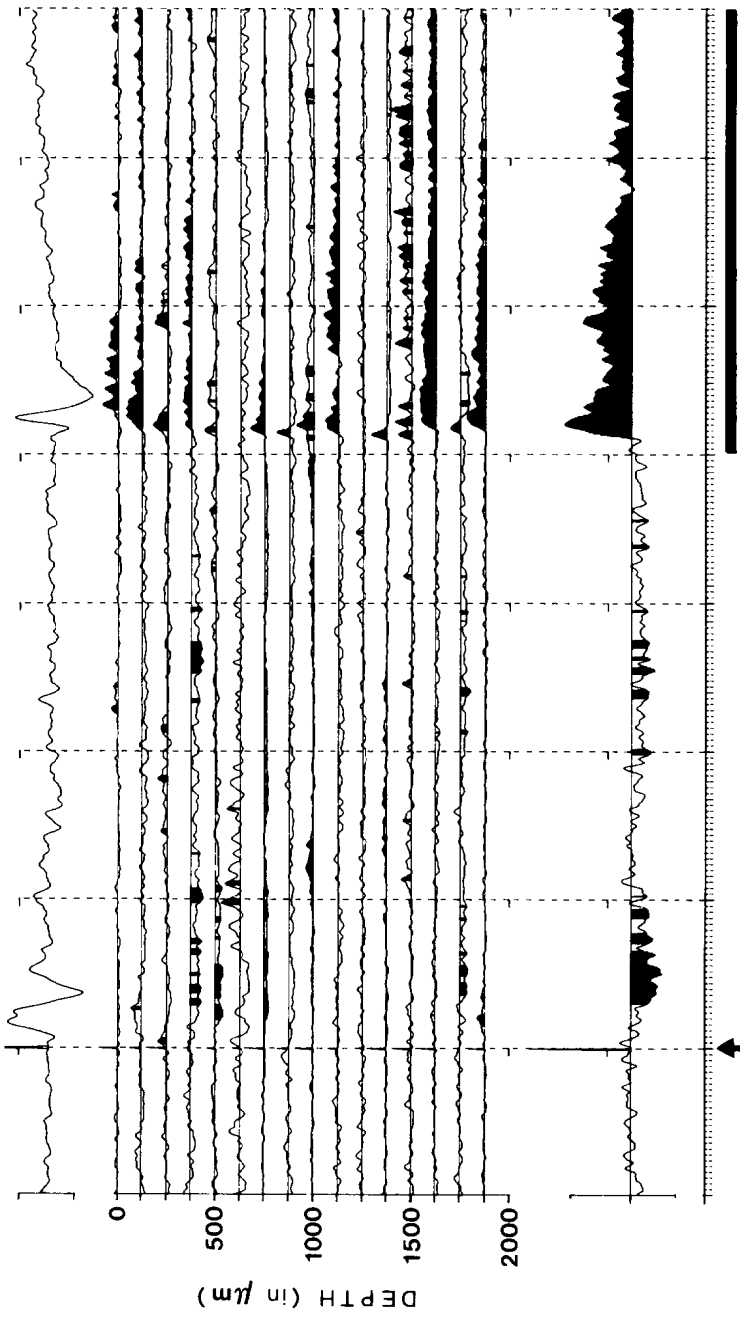

FIG. 8. Selected records from inferotemporal cortex at various depths, monkey OH5. Graphic format as in Fig. 4. Note the predominant inhibition following the flash, contrasting with the occipital response in Fig. 4.

TABLE 3

Evoked Field Potential Latencies in Two Performing Monkeys[a]

	Onset of first deflection		First surface-positive peak	
	Occipital	Inferotemporal	Occipital	Inferotemporal
Flash				
OH4	20	62	40	84
OH5	30	50	66	82
Green				
OH4	60	92	112	112
OH5	80	80	112	120
Red				
OH4	52	72	68	100
OH5	72	72	88	112

[a] Values are milliseconds.

inferotemporal cortex. However, fast motor reactions were generally associated with larger initial responses (units and field potentials) than were slower motor reactions (Fig. 9). When unit and potential response averages were time-locked to the instant of the hand press, the unit activity patterns showed little discrete clustering (pacquets) and the field potentials showed little deviation from baseline, suggesting that the electrophysiologic activity of the cortical regions examined was time-locked to the onset of the sample light rather than to the resulting motor reaction.

DISCUSSION

In acute, anesthetized animals, the responses of striate cortex neurons to temporally discrete visual stimuli have been found to be generally uniform in terms of latency and time course (18). By contrast, the results of this study show that the responses of striate units to one such stimulus—the alerting flash—in the unanesthetized monkey vary considerably, especially in latency (3). The increased complexity and variability of unit reactions in the alert animal may be due to greater diversity of presynaptic inputs (48), as must be the case in the behavioral context. The similarity of latencies between field potentials and summated unit responses suggests that a causal relationship links these two orders of phenomena, although the relationship is obscure (7). In any event, because of the observed variability of responses between cells, the "statistical envelope" that the field potential represents (12, 18) appears to reflect unit activity patterns with a broad range of different temporal characteristics.

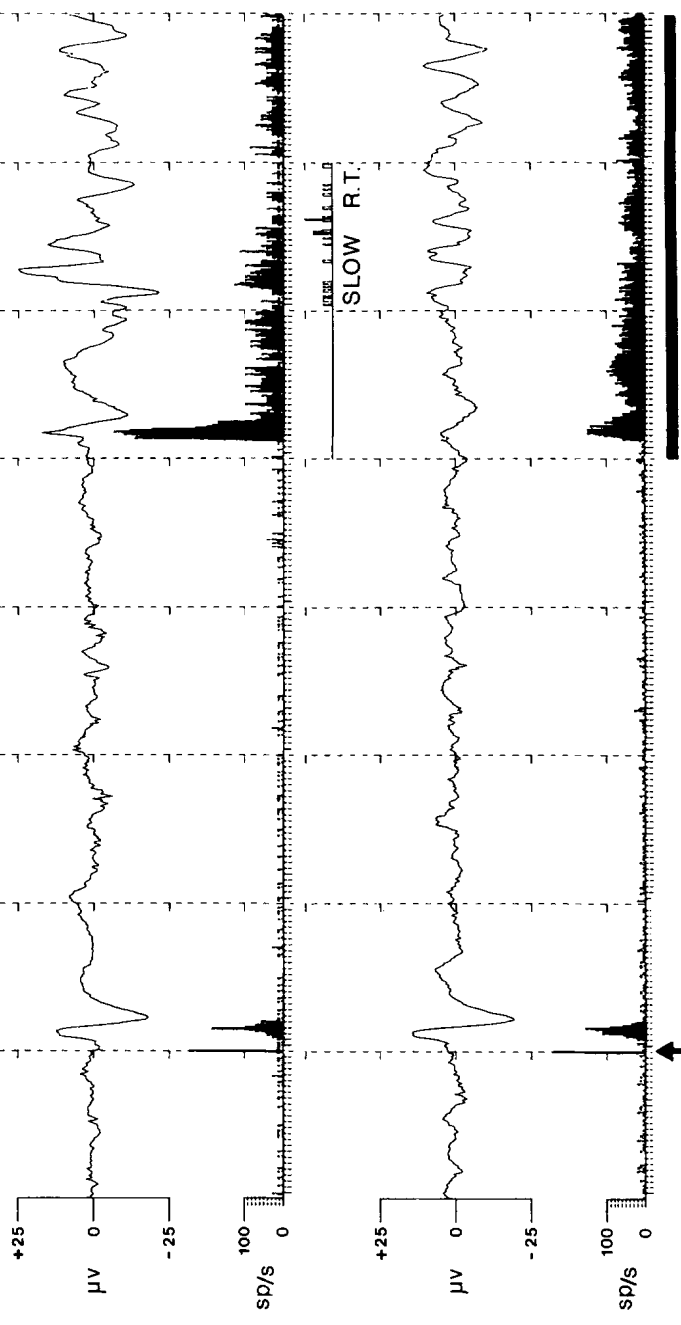

FIG. 9. Same (red-sample trial) records and graphic format as in Fig. 3, here grouped by speed of reaction time (R.T.). Above, records from trials with reaction time between 300 and 500 ms (17 trials); below, reaction time between 500 and 1000 ms (33 trials). Note the larger unit and field-potential responses to the sample before fast behavioral reaction.

The longer latencies of striate unit and field potential responses to the sample, compared with those to the flash, is probably attributable to differences in stimulus intensity (7); intensity-latency relationships may be determined precortically in the visual system (56). As in anesthetized preparations, the prolonged color stimuli in this experiment induced—in addition to transient ON-responses—sustained unit responses (35). Although some cells showed differential responses to the two colors, color-opponent reactions were not observed, presumably because the colored stimuli, as used in our behavioral task, were not adequate to elicit them (14).

In anesthetized preparations, neurons in inferotemporal cortex are known to respond to a great variety of visual stimuli, including diffuse flashes (30), and appear to have large receptive fields that include the fovea (10, 29). However, inferotemporal neuron responses are greatly influenced by behavioral factors (23, 27, 41, 52). This accords with the evidence from lesion experiments indicating that the inferotemporal region is specialized in processing discrete visual information (37, 44). A remarkable finding in our behavioral experiment is that, after the alerting flash, and while occipital neurons undergo substantial firing increases, inferotemporal neurons predominantly undergo inhibition. Inferotemporal units are not excited probably because that signal does not require detail analysis. One could further speculate that inferotemporal cortex is inhibited by the flash because this cortical region is somehow actively disengaged from processing that undifferentiated signal. In spite of the prevalence of cell inhibitions, an evoked field potential can be observed in the inferotemporal cortex, although its characteristics are somewhat different from those of the occipital potential (26, 46). The sustained changes of inferotemporal unit activity taking place after the flash, including continuation of the above mentioned inhibitions, may reflect some form of priming of the inferotemporal region for processing the upcoming sample stimulus.

The reaction of inferotemporal cells to the sample, in sharp contrast to their reaction to the undifferentiated flash, has a major transient ON component. The average of the earliest excitatory unit responses to the sample in inferotemporal cortex follows that in striate cortex by 8 to 28 ms. This lag is in accord with conventional understanding of the cortical flow of visual information (33, 38, 43). However, the cumulative inferotemporal unit reaction has a peak latency similar to that of striate units. The latter finding indicates that, during the initial epoch of sample presentation, the processing of the information contained in the colored stimulus occurs to a large extent simultaneously in the two cortical regions. A similar inference may be drawn from the temporal coincidence of field potentials. In this regard, one cannot ignore the possibility that some of the neural activity elicited by the stimulus is transmitted to both regions synchronously by a collateral pathway involving the superior colliculus (11, 19). That might be the case, in particular, for input

concerning the gross initial detection of the signal (45). Beyond the initial responses, the greater variability of sustained unit-activity patterns in inferotemporal cortex, in comparison with striate cortex, is very likely related to the more complex nature of neuronal transactions in the associative region.

Our data show that the latencies of visual electrophysiologic responses were not correlated with the speed of behavioral reactions, although, as others have found (13, 54), larger early response amplitudes were associated with faster reactions. That inverse relationship between amplitude of electrical response and reaction time agrees with the presumption that these two measures covary as a function of the level of alertness of the animal. Level of alertness is in turn determined, at least in part, by the state of the reticular structures of the brain stem. Indeed, as earlier experiments have demonstrated, the magnitude of cortical responses to visual stimuli (21, 22), as well as the accuracy and speed of behavioral reaction in visuomotor tasks (20, 24), vary as a function of the level of excitability in the mesencephalic reticular formation. During the initial response to the sample, it is therefore possible that the striate and inferotemporal cortices are subject to brain stem modulation and that modulation is reflected in our data by the covariations of amplitude and reaction time.

A critical issue for understanding the function of the cerebral cortex is the relationship between those regions long identified as primary in sensory function and the adjacent regions referred to as associative (17). Hubel and Wiesel (33) suggested that the primary visual cortex is the first cortical step in a sequential series of information processing stages; progressively more complex analysis would occur at each successive stage. Object discriminations would be completed in the inferotemporal region (43). This hierarchical concept of visual processing is supplemented by the theory of "efferent control" (51), stating that the associative regions direct to some extent the processing in primary regions. Anatomically, axonal connections pass in both directions between striate and inferotemporal cortex through the prestriate belt (53, 59), suggesting that information flows both ways. As noted above, our data indicate that, under appropriate conditions, primary and associative regions of visual cortex can be active in processing the same material at the same time. This evidence supports the possibility of reciprocal and cooperative interactions between them.

The simultaneous recruitment of selected, discrete regions of cortex is consistent with the notion of a distributed system of central representation (15) which incorporates both the serial and efferent-control theories. That notion is more sophisticated than simple serial or parallel linear models. The different stages of the cortical organization for visual processing may be viewed as representing a wide range of signal qualities, from the most elementary to the most complex, a "structural map" containing several levels of representation

(32) and allowing dynamic reciprocal interactions between levels. Accordingly, each level of cortex may be considered a component of the system (42, 60), several orders of complexity thus coexisting and interacting (50). Not only would each cortical region process distillates of external information received from lower centers, but that processing would be guided by inputs from higher centers. In this way, both the striate visual area and the inferotemporal association area, and possibly all visual subregions in between, would participate in the integration of the current scene with past experience. That integration is presumably the essence of visual perception.

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