

## Task difficulty: ignoring, attending to, and discriminating a visual stimulus yield progressively more activity in inferior temporal neurons

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**Summary.** To study the influence of task difficulty on the stimulus-elicited responses of inferior temporal (IT) neurons, the stimulus-elicited responses of 64 neurons were recorded from IT cortex of three rhesus monkeys while they performed three behavioral tasks - an irrelevant-stimulus task, a stimulus detection task, and a stimulus discrimination task. The monkey could ignore the stimulus entirely in the irrelevant-stimulus task, was required only to detect stimulus dimming in the stimulus detection task, and was required to attend to specific properties of the stimulus in the discrimination task. The excitatory responses in the discrimination and stimulus detection tasks were larger than those in the irrelevant-stimulus task (61% and 33%, respectively, of the individual differences were significant), and excitatory responses in the discrimination task were larger than those in the detection task (49% of the individual differences reached significance). Twenty percent of the stimulus presentations elicited inhibitory responses that were followed by off-responses. The off-responses were modulated by the tasks in the same order as the excitatory on-responses. Assuming that the off-response strengths indicate the depth of the stimulus-induced inhibition, these results suggest that inhibitory responses were influenced across these tasks in a manner similar to the excitatory responses. When the neuronal responses were related to the difficulties of these tasks, both the response strength and errors were seen to be least during the irrelevant-stimulus task and greatest during the discrimination task. This relationship suggests that the visual responsiveness of IT neurons is related to the degree of attention the animal pays to the stimulus. Based on this and findings from several related studies, a more refined hypothesis can be formulated, namely, visual responsiveness of IT neurons is related to the degree of attention the animal pays to stimulus pattern, specifically.

**Key words:** Single neurons – Inferior temporal cortex – Task difficulty – Vision – Attention – Monkey

### Introduction

In monkeys bilateral inferior temporal (IT) cortex lesions are followed by severe deficits in visual pattern discrimination (Iwai and Mishkin 1969; Mishkin et al. 1982). Thus, inferior temporal neurons are frequently studied to elucidate mechanisms that underly visual pattern discrimination. These neurons show two properties that may be related to this lesion effect. First, some IT neurons give their strongest responses only when stimulated with complex stimuli such as faces, hands, or brushes (Gross et al. 1972; Rolls et al. 1977; Desimone and Gross 1979; Perrett et al. 1982; Desimone et al. 1984). Second, the strength of their stimulus-elicited responses are frequently modulated by the behavioral context of stimulus presentation (Gross et al. 1979; Mikami and Kubota 1980; Fuster and Jervey 1981; Richmond et al. 1983; Moran and Desimone 1985; Richmond and Sato 1987; Sato 1988).

In an effort to isolate different factors that contribute to this behavioral modulation a recent study compared the responses of single IT neurons across three tasks, one of which was a pattern discrimination task (Richmond and Sato 1987). The stimulus-elicited responses were strongest during this pattern discrimination task, whereas they were actually mildly suppressed below an irrelevant-stimulus baseline in a stimulus detection task in which both the location and luminance of the stimulus were relevant but the stimulus pattern was irrelevant. Those results suggested that IT neurons are enhanced during pattern discrimination and suppressed during purely spatial tasks. Here we extended that study to learn more about the influence of attentional parameters, and we have found that the amount of response enhancement in these neurons is graded according to the amount of

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attention the animal must pay to the stimulus pattern in the task. A brief report of these results has already appeared (Spitzer and Richmond 1985).

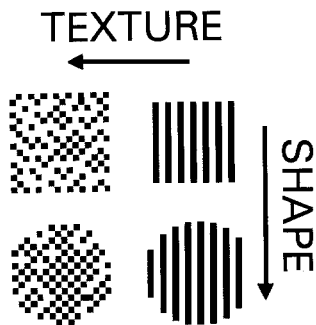
## Methods

### Visual stimulation conditions

Three trained rhesus monkeys were used in these experiments. They were seated in primate chairs in front of a translucent tangent screen (Polacoat, 3M Co.) with their heads immobilized. The image of a black and white television monitor (Electrohome Corp.), controlled by either a VIC-20 or Commodore C64 microcomputer, was rear-projected onto the screen through a television projection lens (Edmund Scientific). The TV display was set to its brightest luminance, 3 candela/sq. meter on the tangent screen, and each edge of the projected image subtended  $40^\circ$  of visual angle. Groups of the  $3/8^\circ$  square picture elements (pixels) that made up the image were darkened to produce visual stimuli. High contrast images were produced by assigning the appropriate pixels the darkest possible luminance, 0.05 candela/sq. meter (97% contrast), and lower contrast images were produced by assigning the pixels a brighter luminance, 0.8 candela/sq. meter (58% contrast). The microcomputers were programmed to produce a fixation spot and four patterned stimuli. The fixation spot was a square  $2 \times 2$  pixels in size. Each of the four patterned stimuli, a striped circle, a dotted circle, a striped square, and a dotted square, was constructed within a  $16 \times 16$  pixel grid, and all contained the same number ( $\pm 5\%$ ) of darkened pixels (Fig. 1). This same set of visual stimuli was used in all of the experiments.

### Animal preparation

**Initial training.** The monkeys were first trained to respond to a change in the contrast of the fixation spot (Wurtz 1969). In this task, after the monkeys touched a small bar attached to the primate chair, the fixation spot appeared at high contrast (against the background) for 1700–2400 ms and then its contrast decreased for 500 ms. If the monkey released the bar during this 500 ms period, a 0.1 ml water or juice reward was delivered.



**Fig. 1.** Four compound visual stimuli. The visual stimuli were either squares or circles with textures of stripes or dots. Each pattern was constructed with a  $16 \times 16$  pixel square grid. The stimuli were 6 degrees on a side when projected onto the tangent screen. The number of darkened pixels were approximately the same in all stimuli (within 5%). The rows differentiate the stimuli by their textures, stripes and dots, whereas the columns differentiate the stimuli by their shapes, squares and circles. Thus, each of these compound stimuli can be differentiated by either of two attributes, shape or texture

**Surgical preparation.** After extensive training in this task, the monkeys were deeply anaesthetized with sodium pentobarbital, and both a single unit recording chamber and a head fixation device were anchored to the skull with orthopedic bone screws surrounded by dental cement (Evarts 1966). The recording cylinder was placed in the stereotaxic plane at coordinates AP + 15 mm relative to the ear bars and 22 mm lateral to the midline. In the same operation, a scleral magnetic search coil was implanted under Tenon's capsule for eye position monitoring (Robinson 1963; Judge et al. 1980).

**Experimental training.** After several weeks of postsurgical recovery, the three tasks used during the recording experiments were taught in the order described below (Fig. 2). In each task, the monkey initiated trials as before by touching the bar attached to the primate chair. This caused the fixation point to appear on the tangent screen, and the trial continued only after the monkey achieved accurate fixation. In each task, a trial was automatically terminated if the monkey did not maintain eye position within  $0.5^\circ$  of the fixation spot throughout the trial. **Irrelevant-stimulus task** (fixation point dims, stimulus irrelevant). After the monkey achieved fixation, one of the four compound stimuli appeared  $3^\circ$  to  $10^\circ$  lateral to the fixation point. This peripherally located stimulus remained on the tangent screen for 400–500 ms and then disappeared. Three hundred milliseconds after the stimulus disappeared, the fixation point's contrast decreased for 500 ms and then the fixation point disappeared. If the monkey released the bar during this period of decreased contrast, a drop of water or fruit juice was delivered. **Stimulus detection task** (fixation point constant, stimulus dims). The peripherally located stimulus came on for 400–500 ms as it did in the irrelevant-stimulus task, but, instead of then simply disappearing, its contrast was decreased for 500 ms before it disappeared. The monkey was rewarded for releasing the bar while the stimulus was at low contrast. The fixation spot remained unchanged during the whole trial and it disappeared together with the stimulus. **Stimulus discrimination task** (fixation point constant, stimulus discriminated from another). The monkeys were taught to associate one response with one stimulus feature, e.g. circle, and another response with the other feature, i.e., square. The two behavioral responses were: (1) delay bar release until the stimulus dimmed as above, or (2) release the bar immediately when the stimulus appeared. Thus, in one block of trials, the monkey would be rewarded only if it released the bar immediately (i.e., within 300 ms) upon the appearance of a square, and only if it delayed its release upon the appearance of the other shape, the circle, until its contrast decreased. In another block of trials, the stimulus-response association would be reversed, such that an immediate bar release was required when the circle appeared and a delayed release when the square appeared. In still other blocks, texture became the relevant stimulus dimension, i.e., stripes vs dots, and again both possible stimulus-response associations were in force at different times.

To facilitate the shift from one discrimination rule to another while a neuron's activity was being recorded, a transition task was used. In this transition task, the monkey was presented repeatedly with one pair of stimuli, say the striped patterns, and was rewarded for delaying bar release to both, thereby priming the monkey to delay bar release to this stimulus feature in the upcoming discrimination task. The other pair of stimuli, the two dotted patterns, would then also be presented repeatedly, the monkey being rewarded for immediate bar release to both, thereby priming the monkey for immediate bar release to these stimuli in the upcoming discrimination task.

Single unit recording was started when the monkey was able to discover within just a few trials which dimension was relevant and which stimuli were to be associated with immediate and which with delayed bar release responses. Data collection, stimulus timing, and behavioral control were carried out at 1 ms time resolution by a laboratory minicomputer (Digital Equipment Corp., PDP 11/34A) programmed with a flexible real-time software system (Hays et al. 1982).

### Single-unit recording

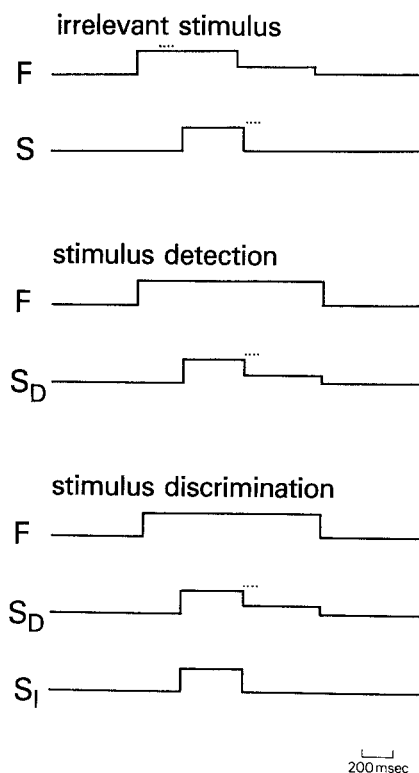
For single-unit recording, thin, tungsten microelectrodes (Frederick Haer & Co., no 1535X) were moved up and down with a hydraulic microdrive through a guide tube placed transdurally 5–8 mm above the cortex of interest. Single units were isolated according to spike amplitude and rate of voltage rise with a time-amplitude window discriminator, and spikes that met the isolation criteria were signaled by TTL pulses sent to the computer. Near the end of the recording period, electrolytic marking lesions were made in the recording region by passing 10  $\mu$ A of current through the microelectrode for 60–120 s. At the end of the experiment, the monkey was given a lethal dose of sodium pentobarbital intravenously and perfused through the left ventricle of the heart with saline followed by 10% formalin. The locations of the electrolytic lesions were determined by examination of histological sections stained with cresyl violet or thionin. These lesions were found to be in the cortex of the middle third of the lower bank of the superior temporal sulcus and on the inferior convexity of the temporal lobe, both of which fall within the area labeled TE by Bonin and Bailey (1947).

### Data display and analysis

Data from the first five trials after each task or rule change were excluded to ensure that the data analyzed were collected after the monkey had discovered which task and, if the task was the discrimination task, which rule, was in effect. The responses collected from the immediate bar release trials of the discrimination task were also excluded because, in these trials, stimulus durations, being dependent on the monkey's reaction time, were variable. To quantify the responses, spikes were counted during a 400 ms period. This was adjusted to begin at the end of the neuron's latency period; the investigators set this latency by examining the rasters and spike densities and estimating the point at which the ongoing activity changed from the ongoing level. This latency was defined to be the earliest response across all conditions and was determined for each neuron. The latencies varied over the range of 70–120 ms. Differences between spike counts for trials with identical stimulus, response, and reward conditions across the three different tasks were tested for significance by means of the two-tailed t-test with corrections for differences in sample size and variance. Confidence level was set at  $p < 0.05$ . When appropriate, the Bonferroni correction for multiple comparisons was used (Miller Jr. 1966).

### Results

In 24 electrode penetrations through IT cortex of the three rhesus monkeys, sixty-four neurons showed a response to at least one of the four visual stimuli (Fig. 1). Sixty-three of these neurons were excited by the appearance of at least one stimulus, and twenty-six were inhibited by the appearance of one or more of the other stimuli. One neuron gave only inhibitory responses. Of the 26 neurons that were inhibited, 13 showed excitation when the stimulus disappeared, i.e., they showed an excitatory off-response. Further, all such excitatory off-responses were preceded by inhibitory on-responses. Seventeen of the neurons we recorded, were recorded in all three tasks, and gave responses to stimuli in all three tasks. All of these neurons gave their strongest response to at least one stimulus in the discrimination task. Fifteen of these gave their strongest average response across all stimuli in the discrimination task, and the weakest in the irrelevant-stimulus task. Because of the complexity of this experiment, i.e., there were several patterns, each

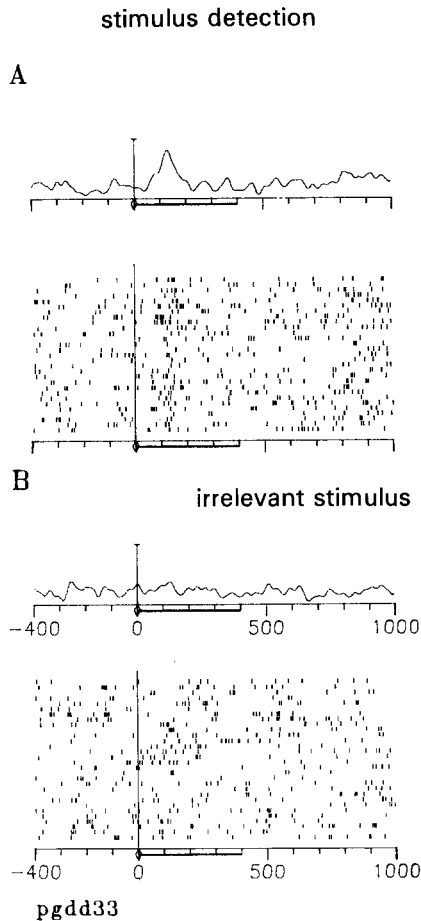


**Fig. 2.** Schematic illustration of the time sequence of events for each behavioral paradigm. The upper line in each set represents the fixation point. The lower lines in each set represent the visual stimulus. The time sequence within a trial is represented by advancing along the lines from left to right. Each line has three possible levels. The lowest indicates the stimulus is absent, the highest indicates the stimulus is on at the highest contrast, and the middle level indicates the stimulus is on at a low contrast, i.e., the stimulus appears to be dim. The times of contrast changes are indicated by changes in the level of a line. Changes in line thickness indicate periods of randomly varied timing. In the irrelevant-stimulus and stimulus detection tasks, one of four stimuli came on. In the irrelevant-stimulus task, the fixation point dimmed as a signal to respond, whereas in the stimulus detection task the stimulus dimmed. The particular stimulus that appeared was of no behavioral significance in either task. In the discrimination task, however, the monkey was required to respond differentially depending upon intrinsic stimulus properties. The monkey discriminated the stimuli either by delaying bar release until the stimulus dimmed, or by releasing the bar immediately upon stimulus onset. These two different stimulus conditions are shown by the lines labeled  $S_I$  and  $S_D$  (immediate and delayed). Correct release of the bar was rewarded in all the paradigms. A change in eye position greater than  $\pm 0.5^\circ$  from the position of the fixation point led to automatic termination of any trial

eliciting a different response, the average response elicited by those stimuli may not indicate what is occurring in a population of neurons. Therefore, our results below are based on the responses to individual stimuli.

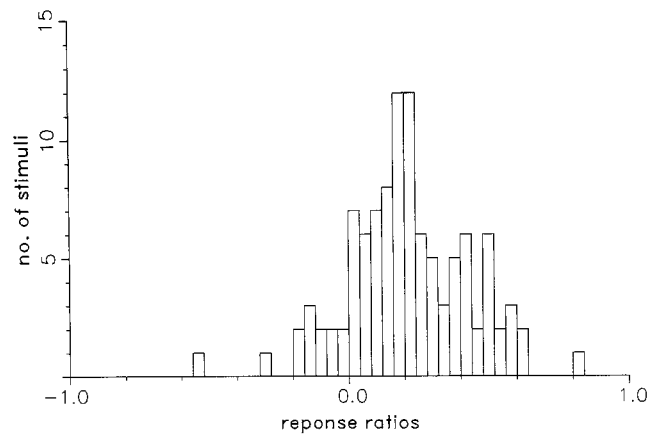
#### *Irrelevant-stimulus vs detection*

When the stimulus-elicited responses from the stimulus detection and irrelevant-stimulus tasks were compared, responses were frequently larger in the stimulus detection task, although only twenty-nine out of eighty-nine (33%) comparisons reached significance for individual cases. An example is shown in Fig. 3.



**Fig. 3A, B.** Responses of an IT neuron to the dotted square during the stimulus detection and irrelevant-stimulus tasks. The responses are displayed in both a raster and a spike density diagram. The histograms and raster diagrams in panel **A** illustrate the response of this neuron to the stimulus during the stimulus detection task, and those in panel **B** the responses during the irrelevant-stimulus task. The time marks are labeled in panel **B**. The raster displays the times of neuronal discharge during each trial as a row of dots. The time of stimulus appearance is shown by the vertical line. The first five trials are not shown (see Methods). Above each raster is its associated spike density diagram. The spike density shows the average of all trials. For this display the spike train from each trial was convolved with a Gaussian pulse ( $\sigma = 10$  ms), quantized at 1 ms resolution to produce an estimate of the probability density function for spike occurrence (MacPherson and Aldridge 1979; Richmond et al. 1987). These individual spike densities were summed to produce the mean spike density which is the Parzen estimate of the probability of spike occurrence in each one millisecond epoch (Sanderson and Kobler 1976; Richmond et al. 1987). The height of the vertical bar in the histogram represents 50 spikes/s/trial or a probability of spike occurrence of 0.05 per ms. The dots in each horizontal row in a raster diagram show the times of neuronal discharge during one successfully completed behavioral trial. The trials represented in the raster are displayed in the order in which they were completed, with the most recent at the bottom. Only successfully completed trials were included in the spike density diagrams. In all diagrams the time of stimulus onset is shown by the vertical line. The heavy horizontal bar under the rasters and spike densities covers 400 ms, the period during which the stimulus remained bright in all paradigms. This figure illustrates activity of a neuron for which the response was significantly more vigorous when the monkey was attending to the visual stimulus than when the monkey was attending to the fixation spot. The stimuli were located 3 degrees peripheral to the fixation point in the field contralateral to the recording site for this neuron

#### IRRELEVANT STIMULUS vs. STIMULUS DISCRIMINATION



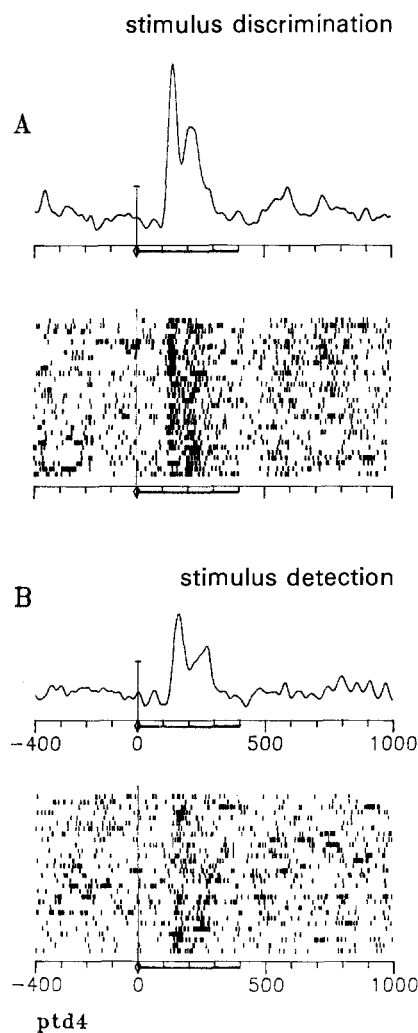
**Fig. 4.** Ratios of stimulus elicited responses during the stimulus detection and irrelevant-stimulus tasks. Each ratio is calculated from responses to the same visual stimulus presented during the two tasks. The abscissa shows these ratios. Each bar shows the number of stimuli over 64 cells that gave a ratio in the range represented by the bar. The ratios were calculated as response indices as described in the results. The right side of the histogram displays the ratios when the responses during the stimulus detection task were larger and the left side displays the ratios when the responses in the irrelevant-stimulus task were larger. Only stimuli that elicited an excitatory response to the stimulus during both tasks are shown in this histogram. The values for the visual responses were averaged over the repeated blocks of the same trial type

To obtain an overview of relative response strength across neurons and stimuli during these two tasks regardless of the significance in an individual case, a relative response index  $R1 - R2 / R1 + R2$  (where  $R1$  is the response for the detection task and  $R2$  for the irrelevant-stimulus task) was calculated for each stimulus that evoked an excitatory response in both tasks. Each neuron could yield a maximum of four data points, one for each of the four stimuli. When tasks were repeated during the course of recording from a single neuron, the response index was based on the trials from all the blocks of a particular task.

Again all the response indices from the stimulus detection and irrelevant-stimulus tasks are shown in the histogram in Fig. 4, regardless of the significance for individual cases. Indices greater than zero indicate instances in which responses were stronger during the stimulus detection than during the irrelevant-stimulus task, and vice versa. Ratios greater than zero occurred significantly more frequently than ratios less than zero ( $\chi^2 = 48.1$ ,  $\text{dof} = 1$ ,  $p < 0.001$ ). Thus, even though many of the individual response differences failed to reach statistical significance (Student *t*-test), there was a reliable group tendency for detected stimuli to elicit a stronger response than irrelevant stimuli across repeated blocks of trials.

#### *Stimulus detection vs discrimination*

Those discrimination trials in which the monkey was required to delay bar release until the stimulus dimmed

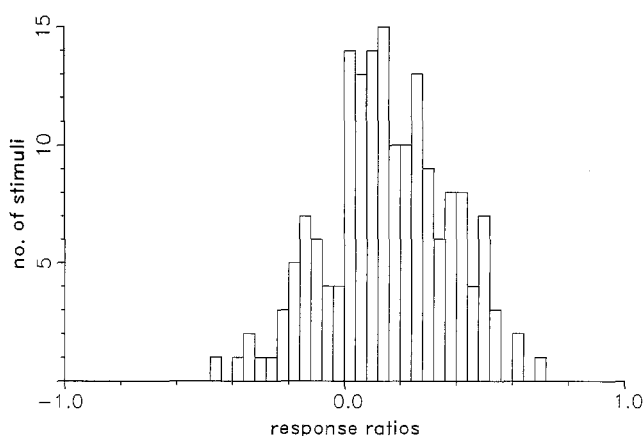


**Fig. 5A, B.** Example of an IT neuron showing stronger responses during the discrimination than during the detection task. Panel **A** shows the responses to the dotted square during the visual discrimination task and panel **B** shows the responses to the same stimulus during the stimulus detection task. For the responses from the discrimination task (**A**), the stimuli were discriminated according to their textures, and the monkey had to wait for the dotted circle to dim before releasing the bar. The responses were taken only from delayed bar release trials in the discrimination task. The stimulus was located 3 degrees peripheral to the fixation point in the field contralateral to the recording site. Fiducial marks and other conventions are as described for Fig. 3

were identical in design to all trials in the stimulus detection task. Comparison revealed that the neuronal responses were significantly larger in the discrimination than in the detection task for 47/96 (49%) of the individual differences (Fig. 5).

The response indices for each stimulus that elicited an excitatory response from a neuron in both tasks are shown in Fig. 6. Significantly more ratios were greater than zero ( $X^2 = 60.5$ ,  $\text{dof} = 1$ ,  $p < 0.001$ ), again indicating a highly reliable group tendency for neurons to give a stronger response to a stimulus during pattern discrimination than during the stimulus detection task. For this analysis, the responses from all presentations of a particular stimulus in stimulus dimming trials of the discrimi-

## STIMULUS DETECTION vs. STIMULUS DISCRIMINATION



**Fig. 6.** Ratios of stimulus elicited responses during the discrimination and stimulus detection tasks. The right side of the histogram displays the ratios when the responses during the discrimination task were greater and the left side displays the ratios when the responses in the stimulus detection task were greater. The value for the discrimination task was calculated from the average values of the visual responses during the shape and texture discriminations. Both were taken from the delayed type of trials only. The fiducial marks and conventions are as described for Fig. 4

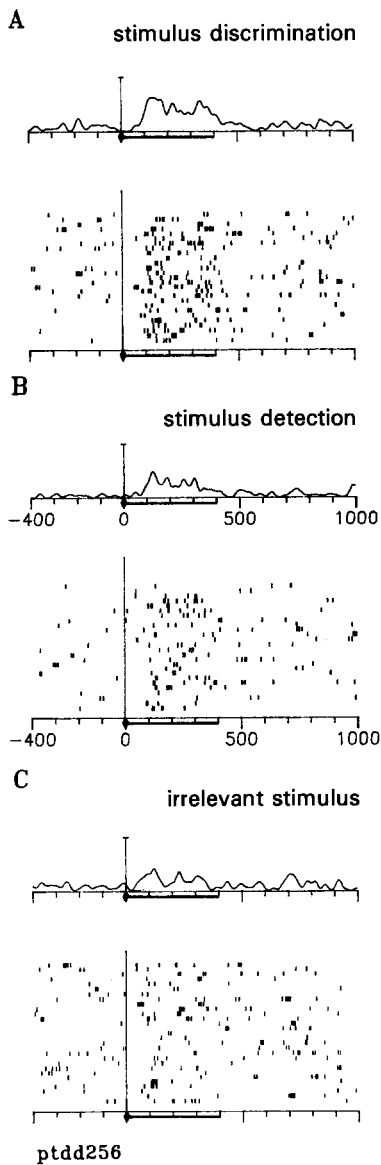
mination task were averaged regardless of the rule. (An analysis of the data separated according to which discrimination rule was in force yielded essentially the same result.)

### *Irrelevant-stimulus vs discrimination*

Since the changes in response strength appeared to be progressive on the basis of the previous two-way comparisons – that is, irrelevant-stimulus < stimulus detection < discrimination – direct comparison between responses from the irrelevant-stimulus and discrimination tasks might appear redundant. However, not all neurons were isolated long enough for their activity to be recorded during all three tasks, and so there were occasions when a neuron was examined only in the irrelevant-stimulus and discrimination tasks. In 65 out of 106 such comparisons (61%), the responses were significantly greater during the discrimination task than during the irrelevant-stimulus task (Fig. 7). As expected, analysis showed that significantly more indices were greater than zero (Fig. 8,  $X^2 = 60.4$ ,  $\text{dof} = 1$ ,  $p < 0.001$ ).

### *Off-responses*

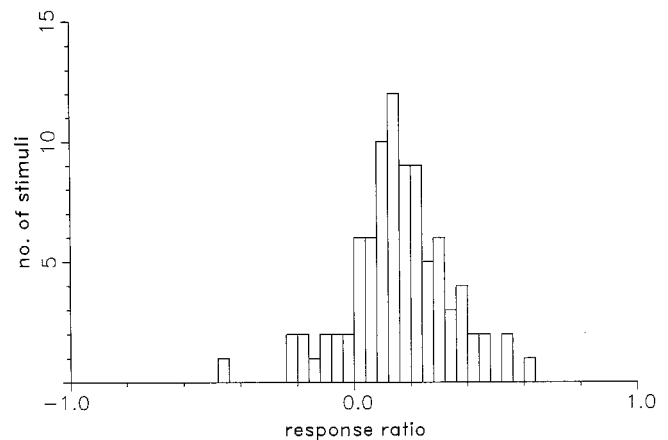
Thirteen of sixty-four neurons that showed inhibitory responses to the appearance of one or more stimuli also showed an excitatory off-response when the inhibiting stimulus disappeared. For inhibited neurons, the inhibition was strong enough to prevent the appearance of any spikes during stimulus presentation in all of the tasks (Fig. 9). Therefore, the intensity of inhibition ap-



**Fig. 7A–C.** Responses of an IT neuron to the dotted circle during the discrimination, stimulus detection, and irrelevant-stimulus tasks are shown in A–C, respectively. The responses were strongest in the discrimination task, intermediate in the stimulus detection task, and weakest in the irrelevant-stimulus task. In this example, the difference between the responses in the stimulus detection and irrelevant-stimulus tasks did not reach statistical significance. Conventions are as in Fig. 3

peared to be equivalent across the different tasks. However, the strengths of the off-responses, which may reflect the depth of the preceding inhibition, showed a systematic variation across tasks similar to that found for the on-responses. The two histograms in Fig. 10 show the distributions of off-response ratios for the irrelevant-stimulus and stimulus detection tasks, and the discrimination vs stimulus detection tasks, respectively. The off-responses for these calculations were defined as beginning at the time of stimulus offset in the irrelevant-stimulus task and at the time of stimulus dimming in the other two tasks. The comparisons show a greater number of off-responses for the stimulus detection than

#### IRRELEVANT STIMULUS vs. STIMULUS DETECTION



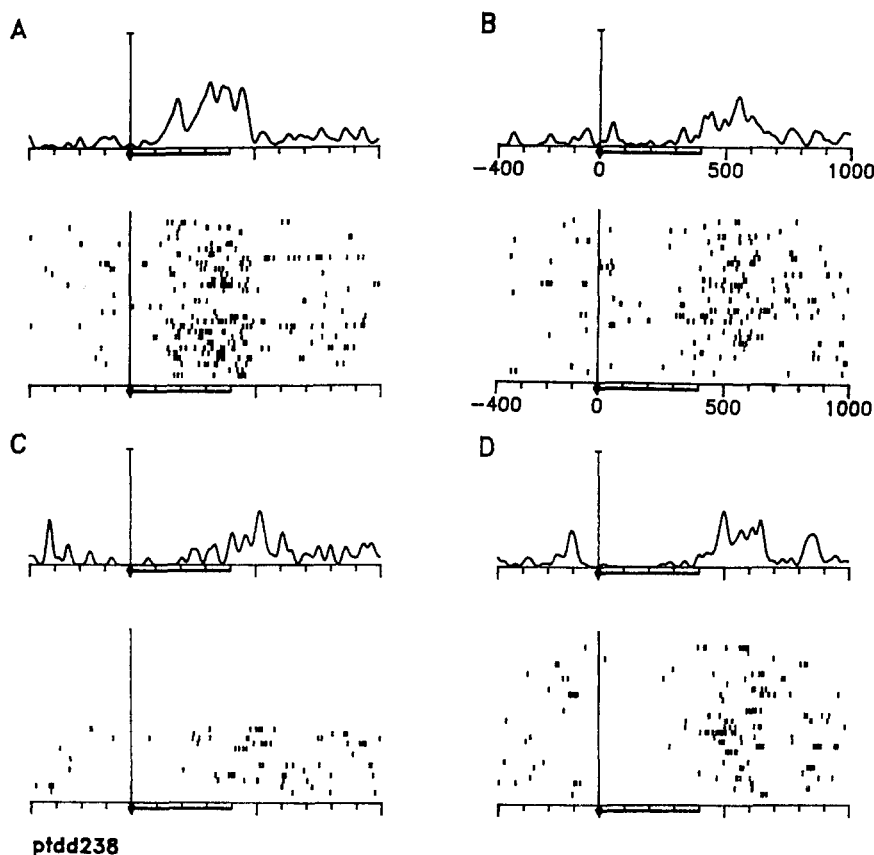
**Fig. 8.** Distribution of IT ratios of stimulus elicited responses during discrimination and irrelevant-stimulus tasks. The right side of the histogram displays the ratios when the responses during the discrimination task were larger, and the left side displays the ratios when the responses in the irrelevant-stimulus task were larger. The value for the discrimination task was calculated from the average values of the visual responses during the shape and the texture discriminations. Both were taken from the delayed type of trials only. Only stimuli that evoked an excitatory response during both tasks are shown in this histogram. The conventions remain as described for Fig. 4

for the irrelevant-stimulus tasks (Fig. 10A,  $X^2=3.0$ ,  $\text{dof}=1$ ,  $p>0.05$ , n.s.), and, also, for the discrimination than for the stimulus detection tasks (Fig. 10B,  $X^2=4.0$ ,  $\text{dof}=1$ ,  $p<0.05$ ). Thus, the inhibitory on-responses appear to reflect the same influences as the excitatory on-responses.

#### Behavioral performance

For ten neurons whose activity was recorded in all three tasks we tabulated the number of errors that the animal made in each. Two types of errors were examined: failure to release the bar within the specified time interval, and movement of gaze farther than  $0.5^\circ$  away from the fixation point. The samples of behavioral performance obtained while these 10 neurons were recorded are shown in Fig. 11 (each line represents a different neuron). The performances when both bar release and eye position errors were included are shown in Fig. 11A, and for bar release errors only in Fig. 11B. These two methods of measurement gave virtually identical results both for the irrelevant-stimulus task, which was performed almost without errors ( $98.2\% \pm 0.47$  SE and  $98.0\% \pm 0.47$ ), and for the stimulus detection task ( $84.8\% \pm 2.12$  and  $84.6\% \pm 2.44$ ). The greatest number of errors occurred in the discrimination task, and here the two methods of calculating behavioral performance gave slightly but not significantly different results ( $75\% \pm 2.46$  and  $80.6\% \pm 2.41$ ).

The neuronal responses and the behavioral responses were compared across tasks and across neurons by transforming both types of responses to relative measures.



**Fig. 9A–D.** Neuron showing off-responses to some stimuli during discrimination. The four panels show the responses of a single neuron to all four stimuli during pattern discriminations. Panels **A**, **B** show responses from the delayed type of trial, whereas panels **C** and **D** show responses from the immediate type of trial. Two of the stimuli elicited inhibitory responses followed by clear off-responses (panels **B**, **D**), and one stimulus, the dotted square, elicited excitatory responses (panel **A**). The fourth stimulus elicited no clear response of any type (panel **C**). The upper row displays responses from immediate bar release trials. Conventions are as in Fig. 3

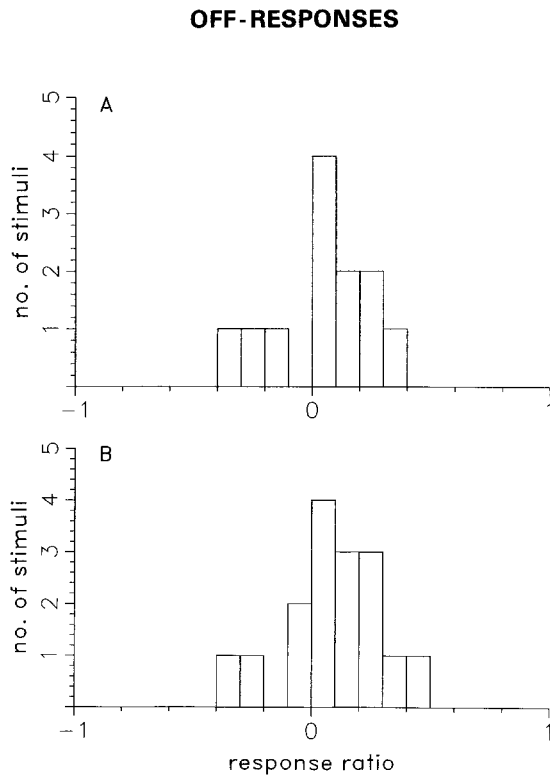
The relative neuronal response was defined as the neuron's response to a stimulus in a given task divided by that neuron's average response to the same stimulus across all three tasks. Relative behavioral performance was derived using an analogous procedure. These values for relative neuronal activity and behavioral performance for each of the 10 neurons are plotted against each other in Fig. 12 and were found to be significantly correlated,  $r_{xy} = -0.67$  ( $p < 0.05$ ).

The strengths of the neuronal responses on trials in which the monkey performed correctly were not significantly different from those in which the monkey made errors.

## Discussion

In these experiments we found that the stimulus-elicited responses of inferior temporal (IT) neurons became stronger as the stimulus pattern became more significant and difficulty increased across three behavioral tasks. Although the increases in response strength were not always significant for any one or all of the four patterns for single neurons, the visual responses across these neurons that showed an increase in response strength was significant, which shows that an ensemble code could carry a reliable message. Either factor, stimulus significance or task difficulty, could have been related to the response changes that were seen. Our study does not provide any means to differentiate between the roles of pattern significance and task difficulty since here they varied together across the tasks.

In other experiments, Richmond and Sato (1987) also found that IT neurons were more highly activated during pattern discrimination than during detection. However, they found that the responses during the irrelevant-stimulus task, the easiest one, were actually stronger than during the more difficult stimulus detection task, whereas we have found the opposite result. There are at least two possible explanations for the discrepant results. First, in Richmond and Sato's study, the length of stimulus presentation as well as the time between stimulus presentations varied across tasks, whereas they were constant here. Such differences in the timings within the paradigms in the previous study could have affected the task difficulty for the monkeys, and, this factor could change the direction of the neuronal enhancement, although Richmond and Sato addressed this point in their analysis and failed to find any clear influence of either variable. The potential effect of this methodological difference between the two studies cannot be dismissed without further investigation. Second, the response strength in IT neurons may be related to pattern significance and not to task difficulty, per se (Spitzer and Richmond 1985). The latter explanation would be consistent with the differing functional roles that have been proposed for the various portions of the cortical visual system, i.e., a dorsal, occipito-parieto-prefrontal system that emphasizes the processing of spatial relationships, and a ventral, occipito-temporal system that emphasizes the processing of stimulus patterns (Ungerleider and Mishkin 1982). This proposed functional division suggests, in turn, that the stimulus-elicited activity of single

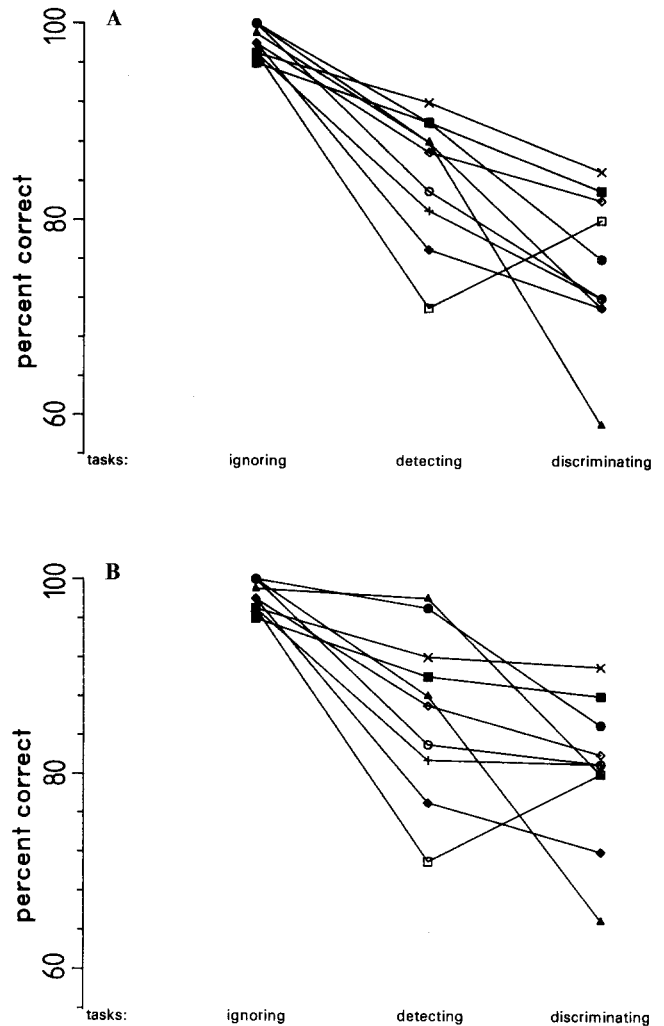


**Fig. 10A, B.** Distributions of off-response ratios calculated like the on-response ratios described in Figs. 4 and 6. The ratios for the stimulus detection and irrelevant-stimulus tasks are shown in A, and the ratios for the off-responses for the discrimination and stimulus detection tasks are shown in B. These histograms show similar tendencies to those seen in Figs. 4 and 6, that is, the response strengths were lowest in the irrelevant-stimulus task, intermediate in the stimulus detection task, and greatest in the discrimination task

neurons in the ventral cortical visual system might be selectively enhanced by attention to visual patterns, whereas that in the dorsal system might be selectively enhanced instead by attention to spatial relationships among stimuli.

Based on this second interpretation, one could give a single explanation for the previous results and ours by hypothesizing that these dorsal and ventral cortical systems interact, with the dorsal or spatial system having the potential to inhibit or suppress the ventral or pattern system. Our monkeys were taught to differentiate quickly among four complex stimuli, rather than just identify whether a bar appeared, whereas the monkeys had only been trained to indicate the presence of one particular stimulus in the previous experiments (Richmond and Sato 1987). If, because of their intensive discrimination training and the changing stimulus patterns, our monkeys paid even a little attention to the stimulus patterns in the stimulus detection task, IT cortex could have been activated, rather than suppressed as seen previously, in keeping with its role in pattern perception. To be valid, this hypothesis would require that IT neurons increase their responsiveness with increasing attention to stimulus pattern specifically.

For our tentative conclusion, i.e., that task difficulty modulates the stimulus-elicited responses of IT neurons

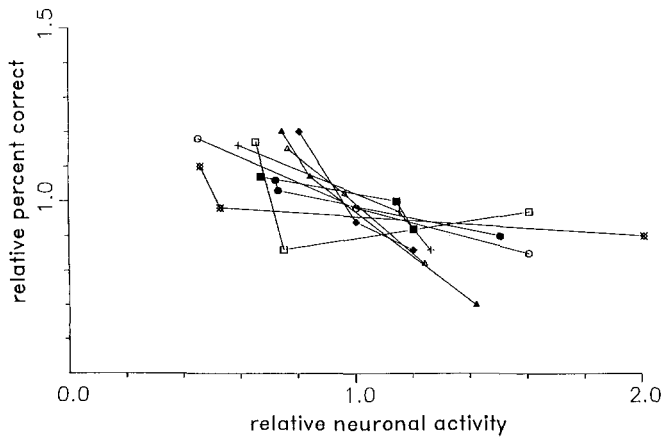


**Fig. 11.** Behavioral performances by the monkeys during the three tasks, irrelevant-stimulus, stimulus detection, and discrimination. The behavioral performance was monitored while single neurons were recorded. These two panels display the percentage of correct trials while 10 neurons were recorded. The total number of trials was calculated in two ways. A Displays the percentages of correct trials when both bar release errors and failure to maintain gaze were included in the total. B Displays the percentage of correct trials when bar release errors only were included in the total. The percentage of errors was greatest in the discrimination task, intermediate in the stimulus detection task, and lowest in the irrelevant-stimulus task

to be valid, our measure of task difficulty must be reliable. However, inferring degree of attention to stimulus pattern from a measure of task difficulty such as error rate has a flaw. In principle, when confronted by a difficult task a subject could adopt either of two strategies: either raise the level of attention sufficiently to reduce errors, or, alternatively, maintain a level appropriate for an easier task and accept an increased number of errors. Thus, although it may seem plausible to believe that the number of errors is related to the task difficulty here, we regard our conclusion relating task difficulty and neuronal response as tentative.

The circumstances under which the relationship between neuronal activity and attentional effort is studied can be improved by adopting a behavioral paradigm in





**Fig. 12.** Correlation between the neuronal activity and the behavioral performance during the three tasks. The relative neuronal activity and the relative performance were taken from the data shown in Fig. 11

which attentional effort is an independent variable. One way to accomplish this is by measuring the response of a neuron to the same constant stimulus when an animal is discriminating it from stimuli that may be more or less similar, according to some objective criterion. When such an approach was taken to study neurons in area V4, an area in the visual system from which IT cortex receives visual input, the neuronal activity was found to vary with degree of attention to stimulus pattern, as inferred from pattern discrimination difficulty (Spitzer et al. 1988). Thus, based on the results here and those from V4, we suggest that attentional effort applied to visual patterns modulates neuronal activity in two successive areas of the visual system known to be important for pattern vision.

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