Low-Frequency Oscillations Arising From Competitive Interactions Between Visual Stimuli in Macaque Inferotemporal Cortex

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Some neurons in the inferotemporal cortex (IT) of the macaque monkey respond to visual stimuli by firing action potentials in a series of sharply defined bursts at a frequency of about 5 Hz. The aim of the present study was to test the hypothesis that the oscillatory responses of these neurons depend on competitive interactions with other neurons selective for different stimuli. To test this hypothesis, we monitored responses to probe images displayed in the presence of other already visible backdrop images. Two stimuli were used in testing each neuron: a foveal image that, when displayed alone, elicited an excitatory response (the “object”) and a peripheral image that, when displayed alone, elicited little or no activity (the “flanker”). We assessed the results of presenting these images separately and together in monkeys trained to maintain central fixation. Two novel phenomena emerged. First, displaying the object in the presence of the flanker enhanced the strength of the oscillatory component of the response to the object. This effect varied in strength across task contexts and may have depended on the monkey’s allocating attention to the flanker. Second, displaying the flanker in the presence of the object gave rise to sometimes strong oscillations in which the initial phase was negative. This was all the more striking because the flanker by itself elicited little or no response. This effect was robust and invariant across task contexts. These results can be accounted for by competition between two neuronal populations, one selective for the object and the other for the flanker, if it is assumed that the visual responses of each population are subject to fatigue.

INTRODUCTION

Neurons of inferotemporal cortex (IT) are highly selective for visual images, differentiating among them in a way that cannot be accounted for merely by selectivity for low-level features (Baker et al. 2002; Desimone et al. 1984; Logothetis and Pauls 1995; Rollenhagen and Olson 2000; Tanaka et al. 1991). The information about images carried by neuronal activity in IT is, to a first approximation, in the form of a rate code: the spike count throughout the response period is greater in the presence of a preferred image than of a nonpreferred image. However, the temporal pattern of the response, as distinct from its net strength, can also vary across stimuli (Optican and Richmond 1987; Richmond and Optican 1987; Richmond et al. 1987). One example of this principle is the tendency of IT neurons to respond to some stimuli with a series of discrete bursts of action potentials. Neuronal visual responses in the form of damped initially positive oscillations at a frequency of around 5 Hz were first described in IT by Nakamura et al. (1991, 1992). Such responses, although not a major focus of other studies, are evident in several published poststimulus-time histograms. Two clear examples are contained in Fig. 5A of Sheinberg and Logothetis (1997). Less dramatic but still convincing instances of oscillation, in the form of a peak, followed by a trough, followed by rebound, appear in histograms accompanying several other papers (Fig. 3E in Sato 1989; Fig. 3, A and B in Sato et al. 1980; Figs. 3 and 4 in Tamura and Tanaka 2001). The functional significance of this low-frequency oscillatory activity is uncertain. Nakamura et al. (1991) reported that oscillatory responses were elicited more commonly by familiar than by unfamiliar images. However, 5-Hz oscillations have not emerged as a distinguishing feature in subsequent studies comparing responses elicited by learned or familiar stimuli to responses elicited by unlearned or novel ones (Baker et al. 2002; Booth and Rolls 1998; Erickson and Desimone 1999; Erickson et al. 2000; Kobatake et al. 1998; Logothetis and Pauls 1995; Xiang and Brown 1998, 1999).

The central idea investigated in the present study is that oscillatory activity in IT arises from competition among neurons selective for different images. Networks in which neurons compete with each other and are subject to fatigue can alternate between states in which antagonistic populations are active (Wilson et al. 2000). Oscillatory visual responses therefore might occur in IT through a process in which neurons responsive to an image are initially excited by it, then succumb through fatigue to suppression by other neurons not responsive to the image, then recover and fire again, and so on. Intrinsic inhibitory connections mediated by GABAergic interneurons, a well-known feature of IT (Wang et al. 2000), may play a role in the competitive interactions among stimuli that have been described by several groups (Chelazzi et al. 1993, 1998; Desimone 1998; Miller et al. 1993; Missal et al. 1999; Moran and Desimone 1985; Sato 1989, 1995). The notion that IT neurons are subject to fatigue is compatible both with the fact that excitatory cortical neurons give adapting responses to prolonged electrical stimulation (Connors and Gutnick 1990) and with the observation that IT neurons commonly respond to prolonged visual stimulation with a phasic burst that tapers off to a tonic plateau (Tamura and Tanaka 2001).

If oscillatory visual responses in IT depend on competition between neurons selective for different patterns, then the ten-
dency for an excitatory stimulus to elicit an oscillatory response from a neuron should be subject to influence by the presence of other images—images to which the neuron is not responsive but to which its competitors do respond. The aim of the experiment described here was to test that prediction and thus to elucidate the nature of mechanisms underlying oscillatory visual responses in IT. A preliminary description of the results has been presented in an abstract (Olson and Rollenhagen 1999).

**METHODS**

**Subjects**

We collected data from three adult male 5.5- to 7.5-kg rhesus monkeys (*Macaca mulatta*), referred to in the text as monkeys 1, 2, and 3 (laboratory designations: Op, Fi, and Ph, respectively). Experimental procedures were approved by the Carnegie Mellon University Animal Care and Use Committee and were in compliance with the guidelines set forth in the United States Public Health Service Guide for the Care and Use of Laboratory Animals.

**Preparatory surgery**

At the outset of the training period, each monkey underwent sterile surgery under general anesthesia maintained with isoflurane inhalation. The top of the skull was exposed, bone screws were inserted around the perimeter of the exposed area, and a continuous cap of rapidly hardening acrylic was laid down so as to cover the skull and embed the heads of the screws. A head-restraint bar was embedded in the cap and scleral search coils were implanted on the eyes, with the leads directed subcutaneously to plugs on the acrylic cap (Remmel 1984; Robinson 1963). After initial training, a vertically oriented recording chamber with a 2-cm-diameter bore was implanted in the acrylic cap overlying the intact dura exposed by a craniotomy. Chambers were located approximately 13 mm anterior to the Horsley–Clarke interaural plane and approximately 19 mm lateral to the midline.

**Single-neuron recording**

At the beginning of each recording session, a sharp 23-gauge guide tube was advanced downward through the dura to a depth of nearly 1 cm beneath the hemispheric surface. A varnish-coated tungsten microelectrode with an initial impedance of several megohms at 1 kHz (FHC, Bowdoinham, ME) was then advanced through the guide tube into IT. The guide tube and electrode could be placed reproducibly at track locations forming a square grid with 1-mm spacing (Crist et al. 1988). The action potentials of a single neuron were isolated from the multineuronal trace by means of an on-line spike-sorting system using a template-matching algorithm (Signal Processing System, Prospect, Australia). The spike-sorting system, on detection of an action potential, generated a pulse the time of which was stored with 1-ms resolution.

**Behavioral apparatus**

All aspects of the behavioral experiment, including presentation of stimuli, monitoring of eye movements, monitoring of neuronal activity, and delivery of reward, were under the control of a Pentium-based computer running Cortex software provided by R. Desimone, Laboratory of Neuropsychology, National Institute of Mental Health. Eye position was monitored by means of a scleral search coil system (Riverbend Instruments, Birmingham, AL). Stimuli were presented on a 14-in. monitor 38 cm from the monkey’s eyes. Reward in the form of about 0.1 ml of juice was delivered through a spigot under control of a solenoid valve on successful completion of each trial.

**Identification of an effective stimulus**

Before collecting data from a neuron, we monitored its activity during foveal presentation of a series of moderately complex white shapes, not exceeding $3 \times 3°$ in extent, selected from a library of 107 images. During this phase of testing, the monkey was required merely to maintain central fixation. We selected one shape that elicited dependable excitatory responses, hereafter referred to as the “object,” for further study of each neuron.

**Peripheral-attention task**

This task was designed for another study. One of its incidental features—onset of an image against the backdrop of another already present image—resulted in our discovering the phenomena at the heart of the present report. Events during representative trials under three critical conditions are shown in Fig. 1, A–C. While the monkey maintained central fixation, waiting for a target to appear, various visual stimuli were presented, all centered on the fovea. Possible stimuli included the 0.6° blue fixation spot; a $3.3 \times 3.3°$ gray square; a flanker array consisting of two $1.5 \times 0.6°$ blue rectangles with their centers at an eccentricity of $3.3°$; and an “object,” an image centered on the fovea and selected to elicit an excitatory response from the recorded neuron. The flankers never overlapped the object. In three conditions, the object and the flankers appeared in different temporal relations. In the “object-alone” condition, the object appeared in the absence of the flanker (Fig. 1A). In the “flanker-then-object” condition, the object appeared against the backdrop of the already present flanker (Fig. 1B). In the “object-then-flanker” condition, the flanker appeared against the backdrop of the already present object (Fig. 1C). The three conditions were imposed in separate blocks, each containing 192 successful trials. At the end of each trial, regardless of the prior sequence of stimuli, a target appeared. This was a 0.7° red disk placed 5° from the center of the screen at one of four locations: up and to the right, up and to the left, down and to the right, or down and to the left. The monkey had to respond by moving one of two levers affixed to the primate chair forward or backward (Fig. 2). If he moved the right (or left) lever forward (or backward) then the right (or left) flanker moved upward (or downward). If the monkey moved a flanker so that it hit the target (Fig. 2), a drop of juice was delivered as reward. This late phase of the trial is relevant to the present study only insofar as it presumably induced the monkey to allocate attention to the flankers even during the earlier phase of the trial.

**Fixation task**

This task required the monkey simply to maintain central fixation during the presentation of task-irrelevant visual stimuli. Successful maintenance of fixation was rewarded with a drop of juice at the end of each trial. Four conditions were imposed in a pseudorandom interleaved sequence until 16 trials had been completed successfully under each condition. In the “object-alone” condition, the object was displayed in isolation for 600 ms (Fig. 1D). In the “flanker-then-object” condition, the flanker was visible for 600 ms and then the object was displayed against its backdrop for an additional 600 ms (Fig. 1E). In the “flanker-alone” condition, the flanker was displayed in isolation for 600 ms (Fig. 1F). In the “object-then-flanker” condition, the object was visible for 600 ms and then the flanker was displayed against its backdrop for an additional 600 ms (Fig. 1G). There was a slight difference in timing between the fixation task and the peripheral attention task insofar as the second stimulus was displayed for 600 ms in the fixation task as contrasted to 700 ms in the peripheral attention task. The use of a 600-ms duration in the fixation task was motivated by our intent to equalize the duration of the period when the first stimulus alone was visible and the duration of the period when both stimuli were visible together. The object was selected to elicit an excitatory response from the recorded neuron.
The flanker was a red annulus with an inner radius of 7.1° and an outer radius of 7.5°. The centers of both coincided with the center of the screen.

**Data analysis: assessment of visual responsiveness**

To determine whether each neuron was visually responsive, we compared firing rates before and after onset of the object in the object-alone condition (paired \( t \)-test with criterion of \( P < 0.05 \)). In the peripheral-attention task, the prestimulus epoch occupied the 200 ms immediately before object onset, whereas the poststimulus epoch extended from 100 to 300 ms after object onset. In the fixation task, the prestimulus epoch occupied the 550 ms immediately before object onset, whereas the poststimulus epoch extended from 50 to 600 ms after object onset.

**Data analysis: curve-fitting**

For each visually responsive neuron under each experimental condition, we assessed the oscillatory component of the response by means of a curve-fitting procedure carried out with a commercially available package (Origin, MicroCal Software). The period under consideration, as defined relative to stimulus onset, was 100–710 ms for the peripheral-attention task and 100–610 ms for the fixation task. A function was fit to points representing mean firing rate versus time in 10-ms bins. The function was \( F(t) = F_a(t) + F_b(t) + F_c(t) \), where \( t \) represents time, with \( t = 0 \) at 100 ms poststimulus onset, and where the individual terms are as follows.

**Adapting nonoscillatory component**

\[
F_a(t) = K_1 + \frac{K_2}{\exp\left(\frac{t - K_3}{K_4}\right)} + \frac{K_5}{\exp\left(\frac{t - K_6}{K_7}\right)}
\]

**Gain and adaptation of oscillatory component**

\[
F_b(t) = \frac{K_3}{\exp\left(\frac{t - K_4}{K_5}\right)}
\]

**Oscillatory component**

\[
F_c(t) = 2 + \cos\left(\frac{t - K_4}{K_5}\right) + K_6^n
\]

Beginning the period of observation at a time close to the peak of the visual response (100 ms after stimulus onset) obviated having to model the onset of the response. Term \( F_a(t) \) captured the tendency for the response to wane exponentially even in the absence of any oscillatory component. Term \( F_b(t) \) allowed for independent adaptation of the oscillatory component. In term \( F_c(t) \), adding 2 to the cosine function constrained the oscillation to vary between 1 and 3. Taking the resulting value to a variable power allowed us to control the sharpness of the peaks compared with the troughs. This function gave a good fit to obviously oscillatory responses (Fig. 3).
CORRELATION BETWEEN OSCILLATORY TERM AND HISTOGRAM. For each visually responsive neuron under each experimental condition, the curve-fitting procedure yielded a solution including parameters $K_{9}$, $K_{10}$, and $K_{11}$ of $F_{u}(t)$, the oscillatory term. We classified a response as potentially oscillatory if the frequency of the oscillatory term of the best-fit equation was $\geq 4$ Hz. We imposed this conservative criterion to rule out cases in which the fit might have arisen from an approximate match (within the 610- or 510-ms measurement epoch) between the oscillatory function and a phasic but nonperiodic peak or trough in the response. To rate the degree of fit to the data afforded by the best-fit oscillatory term, we computed, for each neuron under each condition, the coefficient of correlation between this term and the histogram. We began with raw 10-ms–binned measures of mean firing rate: $Y(0), Y(10), \ldots, Y(T)$, where $Y(t)$ represents the mean firing rate in the interval between times $t$ and $t + 10$ and where $T = 600$ and 500 for the peripheral-attention task and the fixation task, respectively. Then we conditioned the binned measures by removing variance that could be accounted for by the nonoscillatory $F_{b}(t)$ terms of the best-fit function. To do this, we used the formula: $Y'(t) = [Y(t) - F_{b}(t)]/F_{u}(t)$, with parameters $K_{9}-K_{11}$ set to the values that had yielded an optimal fit. Then we measured the correlation across $t$ between $Y'(t)$ and the oscillatory function $F_{u}(t)$, with parameters $K_{9}-K_{10}$ of this function set to the values that had yielded an optimal fit. The resulting correlation coefficient was used for two purposes. First, it provided an indication of the goodness with which the oscillatory term fitted the data. Second, it served as a criterion for including or rejecting data in subsequent steps of analysis aimed at parametric characterization of oscillatory activity. If, for a given neuron under a given experimental condition, the correlation coefficient was $>0.25$ (in the peripheral-attention task with 61 binned firing rate measures) or 0.27 (in the fixation task with 51 binned firing rate measures), then the response was classified as oscillatory and the data were included in subsequent stages of analysis. The threshold values were those that would, in a standard correlation analysis based on the respective numbers of observations, have yielded a significance level of $P < 0.05$. This significance level should not be taken literally because the observed and fitted measures were not independent. It was simply used as a means for equating the goodness-of-fit thresholds used in the two experiments.

COMPARISON OF DISTRIBUTIONS OF PARAMETERS. To determine whether a measure of oscillatory activity (frequency, amplitude, or damping time constant) differed significantly between experimental conditions, we carried out the following steps of analysis. First, we computed the distribution of values obtained in all visually responsive neurons that met the criterion for oscillatory activity under a given condition. Then we compared the distributions, obtained under planned pairs of conditions. If the two distributions were not significantly different from normal (KS–Lilliefors test) then they were compared by a $t$-test. Otherwise, they were compared by a Mann–Whitney $U$ test. A layered Bonferroni correction took into account the occurrence of multiple pairwise comparisons. This was not a within-neuron analysis. A given neuron might meet the criterion for oscillatory activity under one experimental condition and fail to meet it under another with the result that between-condition comparisons involved nonidentical sets of neurons.

Data analysis: Fourier analysis

Construction of an autocorrelogram representing the activity of a given neuron under a given experimental condition proceeded according to the following steps. Consideration was restricted to a limited duration of the sampling period was 510 ms.

FIG. 2. In the peripheral-attention task, subsequent to the sequence of visual stimuli depicted in Fig. 1, A–C, a target appeared on the screen and the monkey made a lever response contingent on the target’s location. While the monkey (seated upright and drawn as seen from above) fixated the center of an upright screen and grasped 2 levers, the target appeared at one of 4 locations relative to the center of the screen: 1) up and to the left, 2) up and to the right, 3) down and to the left, or 4) down and to the right. To the 4 targets, respectively, the monkey had to respond with the following actions on the screen. Anticipation of these events may have affected neuronal activity during the previous part of the trial by inducing attention to the visual-field periphery.
period 100–700 ms after stimulus onset (in the peripheral-attention task) or 100–600 ms after stimulus onset (in the fixation task). Proceeding one trial at a time, and considering every pairwise combination of spikes within the measurement period, we accumulated counts of interspike intervals in 1-ms bins ranging from the minimal measurable interval (1 ms) to the maximal measurable interval (600 ms in the peripheral-attention task and 500 ms in the fixation task). Even in the absence of low-frequency oscillations, an autocorrelogram constructed by measuring spikes in a finite temporal window will not be flat. For example, in the case of a neuron firing regularly at 1,000 Hz, measuring interspike intervals in a 500-ms measurement period will result in 500 counts in the 1-ms bin, one count in the 500-ms bin, and a linear decline from 500 to 1 in the counts assigned to intervening bins. To compensate for this effect, we normalized the count in each bin to the value \( (w - i + 1) \), where \( w \) was the duration of the measurement window and \( i \) was the duration of the interspike interval associated with the bin. After this normalization, any deviation from flatness must reflect either noise or the presence of low-frequency oscillatory activity. Before computation of the power spectrum, we conditioned the histogram so as to minimize the impact of the oscillatory activity induced when the object was presented against the backdrop of the flanker.

**Localization of recording sites**

The mediolateral and anterior–posterior coordinates of each vertical track were noted relative to a 1-mm-square grid centered on the recording chamber. Grid coordinates were translated into brain coordinates by means of structural magnetic resonance (MR) images (Fig. 4) showing the brain relative to MR-visible fiducial markers placed at known grid locations.

**RESULTS**

**Recording sites**

Recording sites were reconstructed by analysis of structural MR images showing the vertical chamber in relation to serial 2-mm frontoparallel slices spanning the entire anterior–posterior extent of temporal lobe (Fig. 4). Recording was carried out in anterior IT in the right hemisphere of two monkeys (monkeys 1 and 2) and in the left hemisphere of a third monkey (monkey 3). In all three animals, recording sites were located lateral to the anterior medial temporal sulcus. Recording in monkey 1 was confined to frontal levels in the range anterior 18–22 mm as defined with respect to the interaural plane. The corresponding range in monkey 2 was 17–20 mm and 13–16 mm in monkey 3. With respect to depth, recording sites in monkey 1 were limited to the ventral aspect of the inferotemporal gyrus, whereas recording sites in monkeys 2 and 3 were localized to the lower bank of the superior temporal sulcus as well as the ventral aspect of the inferotemporal gyrus. There was no obvious trend toward variation in neuronal properties with respect to the location of the recording site.

**Overview of experimental design**

**PERIPHERAL-ATTENTION TASK.** The motivation for the present study arose from an observation made in monkey 1 during performance of a task designed for another purpose but possessing the incidental feature that visual stimuli were turned on in succession under some conditions. During steady fixation, an object effective at eliciting neuronal activity was presented at the fovea (Fig. 1A). On some trials, flanking bars were already present on the screen at the time when the object appeared (Fig. 1B). These presumably attracted attention because they served as proxies for the manipulanda by means of which the monkey responded to a target presented at the end of the trial (Fig. 2). We noted on several occasions that the neuronal visual response to the foveal object, as rendered on the audio monitor, developed an obvious “chatter” whenever the flanks were present on the screen at the time of object onset. We proceeded to document and extend this observation by monitoring neuronal activity under three separate conditions presented in blocks. 1) **Object-alone.** The purpose of this condition (Fig. 1A) was to characterize the baseline visual response to the object. 2) **Flanker-then-object.** The purpose of this condition (Fig. 1B) was to characterize oscillatory activity induced when the object was presented against the backdrop of the flanks. 3) **Object-then-flanker.** The purpose of this condition (Fig. 1C) was to explore the possibility that oscillatory responses might also occur when the flanker was presented against the backdrop of the object. We collected data from 65 neurons in monkey 1 under all three conditions. The results confirmed our initial observation that presenting an object against the backdrop of a flanker could induce or enhance an initially positive oscillatory response. Furthermore, they revealed that presenting the flanker against the backdrop of the object could induce an initially negative oscillatory response. Having characterized these phenomena in the context...
of a task containing complex features some of which were undoubtedly irrelevant to the elicitation of oscillatory responses, we proceeded to examine whether similar phenomena could be observed in a simpler context.

**FIXATION TASK.** We trained monkeys 1 and 2 simply to maintain central fixation while an object and a flanker were presented in various sequences. A new flanker (an annulus centered on fixation) was used to prevent any association with the first task. The square that had appeared before the object in the peripheral-fixation task (Fig. 1A, A2) was eliminated. A new condition (flanker-alone) was included as a baseline for the analysis of oscillatory activity elicited when the flanker was presented against the backdrop of the object. The sequence of events occurring under each of four interleaved conditions of the fixation task is portrayed in Fig. 1, D–G. In the context of this task, we recorded from 75 neurons in monkey 1 and 103 neurons in monkey 2. In addition, we collected data from a small sample of neurons (n = 21) in monkey 3. Data from this monkey were included in the Fourier-based analysis but were excluded from the curve-fitting analysis because this focused on a subset of neurons satisfying stringent criteria for oscillatory activity, with the result that the number of neurons would have been too small for meaningful statistical analysis. On one hand, results obtained in the context of the fixation task confirmed that presenting an object against the backdrop of a flanker could induce or enhance an initially positive oscillatory response. However, the effect was weak and variable compared with the effect observed in the context of the peripheral-attention task. On the other hand, the tendency for a flanker presented against the backdrop of an object to induce an initially negative oscillatory response was at least as robust in the fixation task as in the peripheral-attention task.

**Examples of oscillatory visual responsiveness**

**PERIPHERAL-ATTENTION TASK.** Data collected from one neuron during the peripheral-attention task are shown in Fig. 5, A–C. The presence of the flanker clearly enhanced the oscillatory component of the visual response to the preferred object. When the object was presented alone, this neuron gave a response in which there was a slight oscillatory tendency as indicated by the occurrence of a second peak around 200 ms after the first peak (Fig. 5A). When the object was presented against the backdrop of an already present flanker, the oscillatory tendency was markedly enhanced. This was evident by an increase in the peak-to-trough amplitude and a prolongation such that up to four peaks were discernible (Fig. 5B). When the flanker appeared against the backdrop of the already present object, a dramatic oscillatory response also occurred, but in this case took the form of an initial phase of suppressed activity followed by a series of peaks and troughs (Fig. 5C). The robust oscillations occurring under this condition are all the more striking by contrast to the complete lack of any oscillatory tendency in the response to onset of the flanker and square in the absence of the object (event B2 in Fig. 5B).

**FIXATION TASK.** Data from a neuron studied in the context of the fixation task are presented in Fig. 5, D–G. Presentation of the object in isolation elicited a strong response in which there was little or no oscillatory tendency (Fig. 5D). When the object was presented against the backdrop of the flanker, a moderately oscillatory pattern emerged (Fig. 5E). Presentation of the flanker in isolation elicited a weak excitatory response, lacking any oscillatory component (Fig. 5F). The response to the isolated flanker (event E2 in Fig. 5E and event F3 in Fig. 5F) occurred at a latency (around 200 ms) that was long but still within the range reported for IT in previous studies (Baylis et al. 1987). In dramatic contrast to the weak, nonoscillatory response elicited by the flanker in isolation, an intense initially negative oscillatory response occurred when the flanker was displayed against the backdrop of the already present object (Fig. 5G).

These examples make clear that presenting one image against the backdrop of another could, in either task context, elicit oscillatory activity substantially stronger than that elicited by onset of the same image in isolation. Under the flanker-then-object condition, oscillations in the peripheral-attention task were stronger than in the fixation task (Fig. 5, B vs. F). Under the object-then-flanker condition oscillations in the fixation task were at least as strong as in the peripheral-attention task (Fig. 5, C vs. G). Because the data are from different neurons, these disparities could reflect either interneuron or intertask differences.

**Curve-fitting analysis: selection of neurons possibly exhibiting oscillatory responses**

The aim of the first step of analysis was to remove from the database all cases in which there was clearly no oscillatory visual response. By case, we mean data obtained from a given neuron under a given task condition. A case remained in the database only if two criteria were met: 1) that the neuron gave a statistically significant visual response under the object-alone condition (see METHODS for procedure) and 2) that the oscillatory component of the best-fit function obtained by a curve-fitting procedure applied to the case had a frequency of >4 Hz (see METHODS for procedure and rationale and Fig. 3 for an example).

**PERIPHERAL-ATTENTION TASK.** Of the 65 neurons from which data were collected (Table 1, row 1), 62 gave statistically significant visual responses to the object in the object-alone condition (Table 1, row 2). A curve was fit to the visual-response histogram of each of the 62 neurons under each of the three experimental conditions. Thus curves were fit to 186 histograms in all (62 neurons × three conditions). The criterion that the frequency of the oscillatory term of the best-fit function be >4 Hz was met by 54, 53, and 59 cases under the object-alone, flanker-then-object, and object-then-flanker conditions, respectively (Table 1, row 3). Only these cases were considered further.

**FIXATION TASK.** In monkeys 1 and 2, respectively, 58 and 71 neurons gave statistically significant visual responses to the object in the object-alone condition (Table 1, row 2). In monkey 1, under the object-alone, flanker-then-object, flanker-alone, and object-then-flanker conditions, 46, 49, 34, and 57 out of 58 neurons met the criterion that the frequency of the oscillatory term of the best-fit function be >4 Hz (Table 1, row 3). In monkey 2, under the same four conditions, the criterion was met by 52, 55, 54, and 56 out of 71 neurons (Table 1, row 3).
Curve-fitting analysis: goodness of fit between best-fit oscillatory function and histogram

The aim of this step was to determine whether the fit between the oscillatory term of the best-fit function and the histogram representing the neuronal visual response was consistently better under one condition than that under another. If it were, then we would take this as evidence that oscillatory activity was more robust under the condition consistently...
yielding a better fit. We took as a measure of fit the correlation coefficient reflecting the correlation between the histogram and the oscillatory term of the best-fit function (see METHODS).

PERIPHERAL-ATTENTION TASK. Flanker-then-object versus object-alone. The aim of this step of analysis was to determine whether the oscillatory response to the object was more robust in the presence of an already visible flanker than in its absence. In 49 neurons, data were available for both of these conditions. The results of a within-neuron comparison of the correlation coefficients are presented in Fig. 6A. In this figure, each point represents data from one neuron. The point’s location with respect to the horizontal (or vertical) axis represents the correlation coefficient obtained under the object-alone (or flanker-then-object) condition. That some correlation coefficients were negative reflects the curve-fitting procedure’s having stopped short of an optimal solution in cases where a large amount of the variance in the histogram could be accounted for by the nonoscillatory terms. The correlation coefficient tended to be greater under the flanker-then-object condition, as reflected by the preponderance points above the identity line. This tendency was significant in monkey 1 (paired t-test, \( P < 0.005 \)) but not in monkey 2. Object-then-flanker versus flanker-alone. The aim of this step of analysis was to determine whether the oscillatory response to the flanker was more robust in the presence of an already visible object than in its absence. Neurons in which data were available for both conditions numbered 33 in monkey 1 and 41 in monkey 2. For these neurons, the scatter plot of Fig. 6D compares correlation coefficients obtained under the flanker-alone condition (horizontal axis) to correlation coefficients obtained under the object-then-flanker condition (vertical axis). There was a marked tendency for the correlation coefficient obtained under the object-then-flanker condition to be greater than that under the flanker-alone condition. This effect was significant in both monkeys (paired t-test; monkey 1, \( P < 0.01 \); monkey 2, \( P < 0.05 \)).

In summary, the robustness of oscillatory activity, as reflected by the correlation between the oscillatory term of the best-fit function and the visual-response histogram, clearly tended to be stronger when an image was presented against the backdrop of another already present image than when it was presented alone. The results obtained in the peripheral-attention and fixation tasks were subtly different, however. 1) Responses to the object. Presenting the object against the backdrop of the flanker significantly enhanced the robustness of oscillatory activity in monkey 1, as studied in both tasks, but not in monkey 2, studied only in the fixation task. This might reflect either intermonkey or intertask differences. 2) Responses to the flanker. Presenting the flanker against the backdrop of the object significantly enhanced the robustness of oscillatory activity in monkey 1, as studied in both tasks, and in monkey 2, studied only in the fixation task. However, the comparison on which this conclusion was based differed between tasks. In analyzing data from the fixation task, we compared the response elicited by the flanker when it was presented against the backdrop of the object to the response

### Table 1: Counts of neurons satisfying a series of successively more stringent criteria in the curve-fitting analysis

<table>
<thead>
<tr>
<th>Monkey</th>
<th>Attention task</th>
<th>Monkey 1</th>
<th>Fixation task</th>
<th>Monkey 2</th>
</tr>
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<tbody>
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<td>Task</td>
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<td>O-F</td>
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</tr>
<tr>
<td>4) ( r &gt;0.25 ) or ( 0.27 )</td>
<td>13</td>
<td>18</td>
<td>47</td>
<td>33</td>
</tr>
</tbody>
</table>

**Task:** peripheral-attention (“attention”) or fixation. Condition: object-alone (O), flanker-then-object (F-O), flanker-alone (F), or object-then-flanker (O-F). **Rows 1–4** contain counts of neurons meeting progressively more stringent criteria for oscillatory visual responsiveness. Recorded: neurons from which a full set of data was collected under all conditions in a given task. Visual: neurons satisfying the above condition and giving a significant visual response to the object in the object-alone condition. Frequency >4 Hz: neurons satisfying the above condition and in which the frequency of the oscillatory term of the best-fit function was >4 Hz, \( r >0.25 \) or 0.27: neurons satisfying the above condition and in which the coefficient of correlation between the best-fit oscillatory term and the histogram was >0.25 (in the peripheral-attention task) or 0.27 (in the fixation task). These coefficients represent the degree of correlation expected by chance at a probability of 0.05 in light of the numbers of bins in the histograms (61 in the peripheral-attention task and 51 in the fixation task). “Curve-fitting analysis: goodness of fit between best-fit oscillatory function and histogram” (see text) involved cases “possibly exhibiting oscillatory responses” in the row marked “Frequency >4 Hz.” Subsequent steps in the curve-fitting analysis involved cases of “robust” oscillatory activity in the row marked “\( r >0.25 \) or 0.27.”

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elicited by the flanker when it was presented alone. However, we had to deviate from this ideal in analyzing data from the peripheral-attention task because, in this task, there was no flanker-alone condition. Instead, we compared the response elicited by the flanker when presented against the backdrop of the object to the response elicited by the object when presented alone. This comparison at least possessed the virtue of being conservative: the object, when presented alone, elicited a significant visual response, in which an oscillatory component might be present, whereas the flanker when presented alone usually did not.

**Curve-fitting analysis: selection of cases in which oscillatory responses were robust**

As a preliminary to carrying out a parametric analysis of oscillatory activity, we removed from the already reduced database those cases in which oscillatory activity was not robust. By case, we mean data obtained from a given neuron under a given task condition. A case remained in the database at this stage only if the coefficient of correlation between the oscillatory term of the best-fit function and the visual-response histogram was >0.25 in the peripheral-attention task or 0.27 in the fixation task (see METHODS for rationale). **Peripheral-attention task.** The criterion for robust oscillatory activity was met by 13, 18, and 47 neurons in the object-alone, flanker-then-object, and object-then-flanker conditions, respectively (Table 1, row 4). **Fixation task.** In monkey 1, the robustness criterion was met in 33, 39, 25, and 49 neurons in the object-alone, flanker-then-object, flanker-alone, and object-then-flanker conditions, respectively. In monkey 2, the corresponding counts were 33, 35, 29, and 37 (Table 1, row 4).

**Curve-fitting analysis: population histograms**

For all neurons remaining in the database, we created population histograms representing the average firing rate as a function of poststimulus time under each condition (Fig. 7). It is important to note that these histograms do not represent the responses of the entire sampled population but rather represent the responses of subpopulations of neurons that met the robustness criterion for oscillatory activity under the given condition. By inspection of the histograms, it is possible to determine whether oscillatory activity, when robustly present, was qualitatively different across conditions.

**PERIPHERAL-ATTENTION TASK.** Under the object-alone condition, oscillatory activity was restricted to a subtle dip in firing rate after the initial phasic component of the visual response (Fig. 7A). In contrast, oscillatory activity was pronounced under the flanker-then-object (Fig. 7B) and object-then-flanker
(Fig. 7C) conditions. Between these conditions, however, it differed in phase, beginning with a peak under the flanker-then-object condition (Fig. 7B) and with a trough in the object-then-flanker condition (Fig. 7G).

**FIXATION TASK.** Under the object-alone condition, oscillatory activity was restricted to a subtle dip in firing rate after the initial phasic component of the visual response (Fig. 7D). This pattern was slightly more pronounced under the flanker-then-object condition (Fig. 7E). Under the flanker-alone condition, there was a weak phasic excitatory response followed by a dip and rebound (Fig. 7F). In contrast, under the object-then-flanker condition, oscillatory activity was pronounced and began with a trough rather than a peak (Fig. 7G).

In summary, even with consideration restricted to cases in which oscillatory activity was robustly present, as judged by a goodness-of-fit criterion, oscillatory activity was more robust under some conditions than under others. In particular, the oscillatory component of the population response was stronger when an image was presented against the backdrop of another image than when it was presented in isolation, although there were differences between tasks and conditions. **Between-task difference.** The oscillatory component of the response to the...
object was enhanced to a substantially greater degree by the presence of the flanker in the peripheral-attention task (Fig. 7, A and B) than in the fixation task (Fig. 7, D and E). Between-condition difference. Oscillatory activity elicited by presentation of the object against the backdrop of the flanker began with a peak (Fig. 7, B and E), whereas oscillatory activity elicited by presentation of the flanker against the backdrop of the object began with a trough (Fig. 7, C and G).

Curve-fitting analysis: oscillatory frequency

It appears from inspection of the population histograms that oscillatory activity, when present, always had a frequency close to 5 Hz. However, averaging across neurons might have masked trends that would be evident at the single-neuron level. To assess this possibility, we estimated the frequency of the oscillatory component of the visual response in each case meeting the goodness-of-fit criterion for robust oscillatory activity (see METHODS). We then compared the distribution of frequencies between planned pairs of conditions.

PERIPHERAL-ATTENTION TASK. The distributions of best-fit frequencies are shown in Fig. 8, A–C. The means of the distributions for the object-alone, flanker-then-object, and object-then-flanker conditions were 5.8, 5.8, and 5.2 Hz, respectively. Comparison of the distributions 1) in object-alone and flanker-then-object conditions and 2) in object-alone and object-then-flanker conditions revealed no significant differences.

FIXATION TASK. The distributions of best-fit frequencies are shown in Fig. 8, D–G. The means of the distributions were between 5 and 6 Hz in both monkeys under all conditions. In monkey 1, the means were 5.7, 5.5, 5.2, and 5.2 Hz under the object-alone, flanker-then-object, flanker-alone, and object-then-flanker conditions, respectively. In monkey 2, the corresponding values were 5.6, 5.3, 5.7, and 5.1 Hz. Comparison of the distributions 1) in flanker-then-object and object-alone conditions and 2) in object-then-flanker versus flanker-alone conditions revealed no significant differences.

On inspection of the distributions, it appears that the distribution of frequencies is shifted toward lower values for onset of the flanker against the backdrop of the object (Fig. 8, C and G) than for onset of the object against the backdrop of the flanker (Fig. 8, B and E). Post hoc analysis revealed that the distributions indeed differed significantly (χ² test; peripheral-attention task: P < 0.02; fixation task: P < 0.02). The significance of this observation is not immediately clear. However, it may provide a useful constraint on future efforts to understand the mechanisms of oscillatory activity.

We conclude that if oscillatory activity occurred then its frequency was in a range centered between 5 and 6 Hz regardless of the presence or absence of a visible backdrop at the time of stimulus presentation.

Curve-fitting analysis: amplitude and damping time-constant

It appears from inspection of the population histograms (Fig. 7) that two effects might account for the enhanced robustness of the oscillatory response elicited when an image was presented against the backdrop of another already present image: 1) an increase in the amplitude of the oscillatory activity and 2) greater prolongation of the oscillatory activity. To characterize the contribution of each effect, we compared between selected pairs of conditions the values of parameters extracted from the best-fit model that represented 1) oscillatory amplitude and 2) the time constant that controlled damping of the oscillation (see METHODS). This analysis was confined to cases in which oscillatory activity met the robustness criterion.

PERIPHERAL-ATTENTION TASK. Flanker-then-object versus object-alone. The mean amplitude was significantly greater under the flanker-then-object condition (Mann–Whitney U test, P < 0.02). Object-then-flanker versus object-alone. The damping
time constant was significantly greater under the object-then-flanker condition (Mann–Whitney U test, \( P < 0.02 \)).

**FIXATION TASK.** Flanker-then-object versus object-alone. Neither the mean amplitude nor the damping time constant was significantly different between these conditions in either monkey. Object-then-flanker versus flanker-alone. The mean amplitude was significantly greater under the object-then-flanker condition in monkey 1 (Mann–Whitney U test, \( P < 0.0002 \)). The damping time constant was significantly greater under the object-then-flanker condition in monkey 2 (Mann–Whitney U test, \( P < 0.05 \)).

In summary, effects involving the amplitude of the oscillatory activity and its damping time constant were equally common. All of the significant effects were in the expected direction: when an image was presented against the backdrop of another image, then the amplitude, if changed, was greater, and the damping time constant, if changed, was longer. Only one comparison (flanker-then-object vs. object-alone in the fixation task) yielded no significant difference. This is not surprising because the oscillatory activity was comparatively weak under both of the conditions being compared (Fig. 7, D and E).

### Fourier analysis

The curve-fitting approach described above took as its starting point the assumption that oscillations were time-locked to the onset of the stimulus and so could be analyzed by fitting a curve to a histogram representing a neuron’s firing rate relative to the time of stimulus onset as averaged across multiple trials. This assumption was well founded in that it was apparent on examination of data from neurons with strong oscillatory activity that oscillatory peaks did indeed occur at consistent times relative to stimulus onset across multiple trials. Making the assumption enhanced the power that we could bring to bear on the analysis of oscillatory activity because averaging the data across multiple trials before carrying out the analysis eliminated, at the outset, the considerable noise associated with cross-trial variability. However, it might be argued that by averaging across trials, we reduced our ability to detect changes in oscillatory activity induced by presenting an image against the backdrop of another image.

Accordingly, we explored an alternative approach based on the analysis of data from individual trials. The sole criterion for inclusion in this analysis was that a neuron be visually responsive as indicated by a standard measure based on comparing prestimulus to poststimulus activity (METHODS). This allowed meaningful inclusion of data from neuron 3, in which we had collected data from a relatively small number of neurons. For each visually responsive neuron, and for each trial condition, we first constructed an autocorrelogram representing the interspike intervals measured during the visual-response epochs of all trials. Then, by Fourier analysis, we computed the autocorrelogram’s power spectrum. Comparing power spectra obtained under different experimental conditions allowed us to determine whether oscillatory activity at particular frequencies varied across conditions without any reference to whether oscillations were in phase or out of phase between trials (see METHODS for further details).

The results of this approach as applied to two representative neurons are shown in Fig. 9. Autocorrelograms and power spectra of data collected from a neuron studied in the context of the peripheral-attention task (Fig. 5, A–C) are presented in Fig. 9, A–D. Equivalent displays for a neuron studied in the context of the fixation task (Fig. 5, D–G) are presented in Fig. 9, E–I. Note the tendency for peaks in the autocorrelograms (Fig. 9, A–C and E–H) to occur at around \( \pm 200 \) ms, the period associated with 5-Hz oscillations. Note the tendency for peaks at around 5 Hz in the power spectra to be 1) greater under the flanker-then-object than under the object-alone condition (green vs. red curve in Fig. 9, D and I), 2) greater under the object-then-flanker than under the object-alone condition (blue vs. red curve in Fig. 9D), and 3) greater under the object-then-flanker than under the flanker-alone condition (blue vs. yellow curve in Fig. 9I). All of the noted differences reflect the tendency for oscillatory activity at 5 Hz to be stronger when an image was presented against the backdrop of another already present image than when it was presented alone.

### PERIPHERAL-ATTENTION TASK. To characterize trends present across the entire population of neurons, we examined the population power spectrum. For all 62 visually responsive neurons, we computed average power as a function of frequency for each of the three conditions. The results are shown in Fig. 10A. Red, green, and blue curves represent data from object-alone, flanker-then-object, and object-then-flanker conditions, respectively. Because there were no obvious differences in the power spectra for the three conditions at frequencies \( >15 \) Hz, including frequencies in the gamma range, the power spectra are shown for frequencies only \( \leq 15 \) Hz. The average power for low-frequency oscillations in the range of 5–6 Hz was greater in the flanker-then-object (green) and object-then-flanker (blue) conditions than the object-alone (red) condition. Thus low-frequency oscillations were more pronounced when stimuli were turned on in the presence of other stimuli than when they were turned on in isolation.

To assess the statistical significance of these trends, we compared the power at low-frequencies between appropriate pairs of conditions. Flanker-then-object versus object-alone. For 57 neurons, the power spectra contained a true maximum between 4 and 7 Hz (see METHODS) under both the flanker-then-object and object-alone conditions. We carried out a within-neuron comparison of the values of power in these cases. The results are presented in Fig. 11A, in which each point represents a neuron and in which the point’s location with respect to the horizontal (or vertical) axis represents the peak spectral power in the 4- to 7-Hz range for the object-alone (or flanker-then-object) condition. The spectral power was significantly greater for the flanker-then-object condition, as reflected by the preponderance of points above the identity line (paired \( t \)-test, \( P < 0.000001 \)). Object-then-flanker versus object-alone. For 59 neurons, the power spectrum contained a peak between 4 and 7 Hz under both the object-then-flanker and object-alone conditions. For these neurons, the scatter plot of Fig. 11B compares the peak spectral power in the 4- to 7-Hz range for the object-alone condition (horizontal axis) to the peak spectral power in the 4- to 7-Hz range for the object-then-flanker condition (vertical axis). The spectral power was significantly greater for the object-then-flanker condition, as reflected by the preponderance of points above the identity line (paired \( t \)-test, \( P < 0.000001 \)).
FIXATION TASK. For all 149 visually responsive neurons (monkey 1: \( n = 58 \); monkey 2: \( n = 71 \); monkey 3: \( n = 20 \)), we created a population power spectrum representing average power as a function of frequency for each of the four conditions. These are shown in Fig. 10B. Red, green, yellow, and blue lines represent average power spectra for object-alone, flanker-then-object, flanker-alone, and object-then-flanker conditions, respectively. The power for low-frequency oscillations in the range of 5–6 Hz was greater in the flanker-then-object (green) than in the object-alone (red) condition and was greater in the object-then-flanker (blue) than in the flanker-alone (yellow) condition. Thus low-frequency oscillations were more pronounced when stimuli were turned on in the presence of other stimuli than when they were turned on in isolation.

To assess the statistical significance of these trends, we carried out comparisons between pairs of conditions. Flanker-then-object versus object-alone. For 107 neurons, the power spectrum contained a peak between 4 and 7 Hz under both the flanker-then-object and object-alone conditions (monkey 1: \( n = 46 \); monkey 2: \( n = 44 \); monkey 3: \( n = 17 \)). We carried out a within-neuron comparison of the values of power in these cases for each monkey separately. The results are presented in Fig. 11C, in which each point represents a neuron and in which the point’s location with respect to the horizontal (or vertical) axis represents the peak spectral power in the 4- to 7-Hz range for the object-alone (or flanker-then-object) condition. Although there was a trend toward greater power at low frequencies for the flanker-then-object condition compared with the...
object-alone condition, this trend was not significant for any of
the three monkeys (paired t-test; monkey 1: \( P > 0.1 \); monkey 2: \( P > 0.5 \); monkey 3: \( P > 0.6 \)). Object-then-flanker versus
flanker-alone. For 95 neurons, the power spectrum contained a
peak between 4 and 7 Hz under both the object-then-flanker
and object-alone conditions (monkey 1: \( n = 44 \); monkey 2: \( n = 39 \); monkey 3: \( n = 12 \)). For these neurons, the scatter plot
of Fig. 11D compares the peak spectral power in the 4- to 7-Hz
range for the flanker-alone condition (horizontal axis) to the
peak spectral power in the 4- to 7-Hz range for the object-then-
flanker condition (vertical axis). The spectral power was sig-
nificantly greater for the object-then-flanker condition for mon-
keys 1 and 3 (paired t-test; monkey 1: \( P < 0.006 \); monkey 2:
\( P > 0.3 \); monkey 3: \( P < 0.02 \)).

![Graph A](image1.png)  
**A** Peripheral-attention Task  

![Graph B](image2.png)  
**B** Fixation Task  

**FIG. 10.** Population power spectra averaged across 62 neurons in the peripheral-attention task (A) and 149 neurons in the fixation task (B). There was greater power at low frequencies when stimuli were turned on in the presence of other stimuli (green and blue lines) than when stimuli were turned on in isolation (red and yellow lines). Red, green, yellow, and blue lines represent power spectra of data collected in the object-alone, flanker-then-object, flanker-alone, and object-then-flanker conditions, respectively.

![Graph C](image3.png)  
**A**: flanker-then-object vs. object-alone.  

![Graph D](image4.png)  
**B**: object-then-flanker vs. object-alone.  

**C**: flanker-then-object vs. object-alone.  

**D**: object-then-flanker vs. flanker-alone.  

**FIG. 11.** Within-neuron comparisons of spec-
tral power in the frequency range of 4–7 Hz.  
Comparisons were made for conditions in the peripheral-attention task (A–B) and fixation task (C–D). Each point represents a neuron. Position of each point with respect to a given axis is the power of the highest peak in the power spectra within the frequency range of 4–7 Hz for the corresponding condition. A: flanker-then-object vs. object-alone. B: object-then-flanker vs. object-alone. C: flanker-then-object vs. object-alone. D: object-then-flanker vs. flanker-alone.  

Power at low frequencies tended to be greater under conditions in which an image was presented against the backdrop of another image. This effect achieved significance for both comparisons in the peripheral-attention task and for monkeys 1 and 3 in the comparison between object-then-flanker and flanker-alone in the fix-
tation task (D).
In summary, the approach based on Fourier analysis confirmed observations obtained with the curve-fitting approach by showing that low-frequency oscillatory activity was significantly stronger when the object was presented against the backdrop of the flanker (in the peripheral attention task) and when the flanker was presented against the backdrop of the object (in both tasks). The failure to demonstrate a significant effect of presenting the object against the backdrop of the flanker in the fixation task was concordant with the conclusion arising from the curve-fitting approach that oscillatory enhancement was very weak in this case.

The effect of the flanker: competition versus inhibition

Oscillations elicited by presenting the flanker against the backdrop of the object began with a trough (Fig. 7, C and G). From this observation, one might be tempted to infer that the effect of the flanker was purely inhibitory and that the oscillations arose from alternating inhibition and rebound. To test this idea, we constructed histograms representing the activity of all neurons that gave oscillatory responses under the object-then-flanker condition in the fixation task. The population responded with early suppression to the object-then-flanker display (Fig. 12, thin curve) and yet responded with early excitation to the flanker-alone display (Fig. 12, thick curve). This observation suggests that the initially suppressive response in object-then-flanker arose from a form of competition in which the flanker, when presented against the backdrop of the object, drew population activity toward the lower (but still excitatory) firing rate elicited by the flanker in isolation. Effects of this sort can occur if two pools of neurons receive excitatory input from two stimuli, with each stimulus exciting one pool more strongly than the other, and if the two pools inhibit each other (Moldakarimov et al. 2003, 2005). In the rare case of a neuron more responsive to the flanker than to the object, it follows from this model that the oscillatory response under the object-then-flanker condition should have an initially positive phase. This we indeed observed in the one such case that we could identify (Fig. 13).

Eye movements

Throughout all data collection sessions, eye position was continuously monitored and monkeys were required to maintain fixation within a window approximately 2° in diameter. Microsaccades were tolerated so long as they did not take the eye outside the window. Several general considerations mitigate against the notion that microsaccades could have given rise to oscillatory activity in IT. First, oscillatory eye movements have never been described as accompanying fixation in normal monkeys. Second, oscillatory eye movements even when they do occur—in congenital nystagmus in humans—are at a frequency <5 Hz (Bifulco et al. 2003). Third, although there have been descriptions of neuronal activity in IT yoked to large voluntary saccades (Ringo et al. 1994; Sobotka et al. 1997), recent reports have indicated that the impact of large saccades is minor (DiCarlo and Maunsell 2000) and that there is virtually no effect of microsaccades (Leopold and Logothetis 1998). Nevertheless, we considered the possibility that oscillatory activity could have been locked to microsaccades. To test this idea, we examined data from sessions in which both oscillatory activity and eye position data had been stored. We found no relation between the two. Data supporting this point are presented in Fig. 14. This neuron displayed initially positive oscillations under the object-alone condition and initially negative oscillations under the object-then-flanker condition (Fig. 14A). Oscillatory activity was at least as strong and well defined when the period of oscillatory activity was devoid of microsaccades (Fig. 14C) as on trials in which microsaccades occurred (Fig. 14B). This example makes clear that robust 5-Hz oscillatory activity can occur in the absence of microsaccades.

Discussion

Overview

Some neurons in IT, presented with an effective foveal image, respond to it with a series of bursts at a frequency of about 5 Hz. The study reported here has yielded two novel observations related to this phenomenon. First, the strength of oscillatory activity is enhanced if the foveal stimulus is presented against the backdrop of an already present peripheral flanking stimulus (although the degree of enhancement is variable and may depend on task context). Second, presenting the peripheral stimulus against the backdrop of an already present foveal stimulus elicits an initially negative oscillatory response. A robust oscillatory response can occur even in a neuron responding little or not at all to the presentation of the peripheral stimulus in isolation.

Consistency of the results

The tendency for the flanker (although ineffectual as a stimulus in its own right) to elicit a strong initially negative oscillatory response when presented against the backdrop of the already present object was consistently present in the peripheral-attention and fixation tasks. The pattern obviously present in the population histograms (Fig. 7, C and G) was confirmed by most statistical measures. The effect was statistically significant in data collected from monkey 1 during performance of the peripheral-attention task, as determined both by a curve-fitting approach (Fig. 6B) and by Fourier analysis (Fig. 11B). It was also statistically significant in data collected during performance of the fixation task, as determined by the curve-fitting approach in both monkeys (1 and 2).
to which it was applied (Fig. 6D) and by Fourier analysis in two of three monkeys (1 and 3) to which it was applied (Fig. 11D).

Results obtained in the context of the two tasks were only partially consistent with respect to the tendency for the object to elicit a stronger oscillatory response when presented against the backdrop of the already present flanker than when presented in isolation. This tendency is dramatically evident in the population histograms representing data from the peripheral-attention task (Fig. 7, B vs. A) but is only marginally evident in data from the fixation task. That there was a trend even in the fixation task is indicated 1) by the numbers of cases in which oscillatory activity met the goodness-of-fit criterion for robustness (74 under the flanker-then-object condition vs. 66 in the object-alone condition) and 2) by the depth of modulation in the population histograms for these neurons (deeper for flanker-then-object in Fig. 7E than for object-alone in Fig. 7D). Nevertheless, the effect was small and achieved significance by only one statistical test: the test based on curve fitting in monkey 1 (Fig. 6C). The curve-fitting approach applied to data from monkey 2 (Fig. 6C) and Fourier analysis applied to data from all three monkeys (Fig. 11C) yielded only insignificant results. The difference in outcome between the two tasks may have been related to the fact that the monkey allocated attention to the visual-field periphery in the peripheral-attention but not in the fixation task. However, it might also have arisen from other unrelated differences in task design, including the use of different flanking stimuli, or from our having sampled a population of neurons with subtly different properties.

Relation to previous studies demonstrating oscillatory activity

Previous microelectrode recording studies of IT have revealed that some neurons respond to visual stimuli by firing rhythmically at a frequency of around 5 Hz. Nakamura et al. (1991, 1992), recording from the temporal pole, in subdivisions of TE and TG anterior to those studied here, documented oscillatory visual responses within this frequency range and observed a trend whereby familiar objects elicited stronger oscillations than unfamiliar ones (Nakamura et al. 1991). Cases of IT neurons with oscillatory activity in roughly this range have also been presented incidentally in Fig. 5A of Sheinberg and Logothetis (1997), Fig. 3E of Sato (1989), Fig. 3, A and B of Sato et al. (1980) and Figs. 3 and 4 of Tamura and Tanaka (2001). Tovee and Rolls (1992), searching explicitly for oscillatory activity in IT, failed to obtain evidence for it; they focused on gamma-range oscillations, however, and do not show results for frequencies <10 Hz.

In a recent study of area V4, Lee et al. (2005) found that energy in the theta (4–8 Hz) range of the local field potential was enhanced during the delay period of a visual working memory task after presentation of a high-contrast sample image, that each neuron tended to fire at a preferred phase of the theta cycle, and that neuronal selectivity for preferred images was maximal at this phase. This set of findings is related to ours in the general sense that both concern oscillatory activity in the theta range. However, it remains unclear whether the underlying mechanism is the same. As a means for resolving this issue, it would be of interest to know whether oscillatory activity in V4 was confined within the same range of
frequencies as in our study and whether it was phase-locked to the stimulus as in our study.

Relation to previous studies demonstrating stimulus–stimulus interactions

Several previous studies assessed the impact on neuronal activity in IT of presenting a neuron’s preferred image simultaneously with another image, either a different image or a duplicate of the preferred image (Miller et al. 1993; Missal et al. 1999; Rolls and Tovee 1995; Sato 1989, 1995). The essential finding is that supplementing an effective image with a second image leads to reduced responsiveness. In no case was oscillatory activity noted. In most cases the onset of the two images was simultaneous, rather than staggered as in the present study. However, in one case, even staggered presentation did not yield oscillatory activity (Sato 1995). The discrepancy between that result and ours might be related to various factors. The stimulus set used in the former study (consisting of seven geometric figures and four colored spots) was more limited than ours (consisting of 107 relatively complex images) with the result that we might have been able to match more closely the stimulus preferences of recorded neurons. Moreover, the stimuli in that study were both located in the peripheral visual field, whereas, in our study, a small preferred stimulus at the fovea was balanced against a large nonpreferred stimulus at an eccentric location. Outstanding questions relevant to this issue include the following: 1) Do oscillations occur even at relatively posterior levels in IT? 2) Do oscillations depend on displaying one image at an eccentric location and another at a central location? and 3) Do oscillations depend on displaying two images with different featural content?

A potential mechanism

Oscillatory activity of the sort observed in this study could arise from many sources including intracellular processes, interactions among neurons in IT, and area-to-area interactions. None of these possibilities is clearly to be preferred to the others. However, it is worth noting that simple interactions at the network level, either confined to IT or involving other areas, could produce the effects described here in a comparatively straightforward manner. Networks consisting of fatiguing neurons with reciprocal inhibitory connections are well known to give rise to oscillatory activity (Wilson et al. 2000). Furthermore, the ability of such networks to produce oscillatory activity qualitatively like that observed in our study can be demonstrated in terms of a model incorporating only two neurons, one responsive to the object and the other to the flanker, which give exponentially fatiguing responses and which inhibit each other (Fig. 15A). These can be thought of as pyramidal neurons inhibiting each other by inhibitory interneurons not explicitly represented in the figure. We modeled these neurons as simple nodes with linear activation functions subject to fatigue. The state of neuron $i$ ($i = 1, 2$) was characterized in terms of three time-dependent variables: $N_i(t)$ (net
Why do single stimuli sometimes elicit oscillatory responses?

Oscillatory visual responses occasionally occur even in response to presentation of a single image in isolation. This has been described previously (Nakamura et al. 1991, 1992) and was observed in the present study (Fig. 5A). The ability of a single image to elicit an oscillatory response may seem to contradict the view that competition between neuronal populations representing different stimuli is at the heart of oscillatory activity. However, it fits easily within the framework of the model presented in the preceding section if neuronal populations selective for different images are assumed to fire spontaneously even in the absence of their preferred stimuli. To see that this is so, one need merely imagine that visual input from the flanker in Fig. 15A has been replaced with an endogenous drive of equal strength. Presentation of the object in isolation would now elicit an oscillatory response identical to that shown in Fig. 15C. This line of argument is reasonable because neurons in IT do commonly have spontaneous activity. For example, in the present study, in the context of the fixation task, neurons fired at an average rate of around eight spikes/s because neurons in IT do commonly have spontaneous activity.

Why do only some neurons exhibit oscillatory activity?

Under the conditions of this experiment, some neurons gave extremely robust oscillatory visual responses, whereas others revealed not even a hint of oscillatory activity. This can be explained by reference to the theoretical framework laid out above. In systematic modeling studies based on the concept

\[ N_i = w_e E_i + w_i I_i; \]
\[ \frac{dF}{dt} = \left[ m N_i - F_i \right] \tau; \]
\[ O_i = N_i - F_i \text{ if } [N_i - F_i] > 0 \text{ else } O_i = 0; \]

where \( w_e \) and \( w_i \) represent the weights of excitatory and inhibitory synapses respectively, \( \tau \) is the time-constant of fatigue, and \( m (0 \leq m \leq 1) \) determined the strength of fatigue at asymptote. \( E_i(t) \), the excitatory input to neuron \( i \), was set to one or zero as the visual stimulus for which that neuron was selective was turned on or off. \( I_i(t) \), the inhibitory input to neuron \( i \), was set to the value of the other neuron’s output. In this model, fatigue acted at the stage of input; however, the results were qualitatively unaltered by making fatigue activity dependent. In the simulation depicted in Fig. 15, the values of the constants were: \( w_e = 40, \ w_i = 20, \ \tau = 100 \text{ ms}, \) and \( m = 0.7 \). Figure 15, \( B-D \) represents activation as a function of time for the object-selective neuron (neuron 1 in Fig. 15A) under object-alone (Fig. 15B), flanker-then-object (Fig. 15C), and object-then-flanker (Fig. 15D) conditions. Under the flanker-alone condition, this neuron was not active. The behavior of the flanker-selective neuron (analogous to the neuron of Fig. 13) is not shown. Because all connections were symmetrical, it responded to any combination of object and flanker just as the object-selective neuron responded to the corresponding combination of flanker and object. We conclude that neurons adapting to visual stimulation at roughly the rate at which IT neurons adapt (Fig. 15B) can give rise, through mutual inhibition, to oscillations at around 5 Hz and at the phases observed in this experiment. In a subsequent more thorough and systematic study, we have extended these findings by demonstrating that comparable phenomena are observed under a specific range of conditions in large networks consisting of realistic neurons (Moldakarimov et al. 2003, 2005).

\[ \text{FIG. 15. A simple model of oscillatory activity arising from reciprocal inhibition between neurons selectively responsive to different visual stimuli and subject to fatigue.} \ A: \ \text{neurons 1 and 2 selectively responsive to the object and the flanker respectively.} \ B-D: \ \text{responses of neuron 1 under object-alone, flanker-then-object, and object-then-flanker conditions.} \]
depicted in Fig. 15, we have found that the occurrence of oscillatory activity depends on the precise balance of excitatory and inhibitory influences brought to bear on the neuron (Moldakarimov et al. 2003, 2005). The balance of excitatory and inhibitory inputs to different neurons in our sample might well have differed either because their connectional anatomy was different or because our particular stimuli induced excitation and inhibition to different degrees in different neurons. Whether one could induce oscillatory activity in any IT neuron by an appropriate choice of stimuli or, alternatively, whether certain neurons exhibit oscillatory behavior over a wide range of stimulus conditions is an interesting question for future study. Whatever the answer turns out to be, the fundamental point made in this study, that oscillatory activity depends on competitive interactions between neurons representing different stimuli, will remain valid.

**Relation to principles of visual processing**

The model proposed above provides a framework for understanding the relation between oscillatory activity and basic principles of visual processing. It suggests that oscillations are related to a competitive process by which different stimuli vie for representation in IT. Desimone and colleagues (Desimone and Duncan 1995; Reynolds et al. 1999) have proposed a model of competitive effects in IT and other visual areas according to which simultaneously presented visual stimuli compete for neuronal representation. Competition in this model is proposed to arise from a combination of excitation and shunting inhibition such that two active afferents elicit a response intermediate in strength between the responses that those afferents would elicited independently (Reynolds et al. 1999). We will refer to this as an “averaging” response. It would be parsimonious to assume that the same competitive mechanism underlies both averaging responses and oscillatory responses. However, the mechanism based on shunting inhibition (Reynolds et al. 1999) has no obvious potential to produce oscillatory responses because it involves no feedback loop. This observation raises the question of whether a network-based (as distinct from dendrite-based) mechanism could account for averaging responses and, if so, whether oscillatory responses could arise as an emergent property of the network. The idea that biased competition might involve reciprocal inhibition has been put forward before (Deco and Lee 2002; Usher and Niebur 1996) as has the idea that inhibitory circuits are capable of producing averaging responses (Carandini and Heeger 1994; Carandini et al. 1997). We have extended this approach recently by demonstrating that a circuit incorporating reciprocal inhibition between neurons selective for different stimuli can give rise both to averaging responses and to low-frequency oscillations (Moldakarimov et al. 2003, 2005). If oscillatory activity is indeed an emergent property of a circuit evolved to mediate biased competition, then this is of interest because it implies that the mechanism underlying biased competition is based on a network process (reciprocal inhibition) rather than on a cellular process (shunting inhibition).

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**References**


