EFFECTS OF SPATIAL ATTENTION ON MACAQUE PRIMARY VISUAL CORTEX

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ABSTRACT

Does spatial attention affect neuronal responses in primary visual cortex? This question has been addressed in several previous studies, either with negative results or with modest positive results that do not rule out the possibility of experimental artifacts. The present study addressed three critical facets of this question: are responses in V1 affected by whether spatial attention is engaged, are they affected by where attention is directed, and does attention influence the modulatory effects of stimuli shown in the non-classical surround? Answering these questions requires establishing the following: whether V1 responses vary with attentional condition; whether any response changes are attributable to systematic offsets in eye position; and whether any responses changes are due to direct modulation of visually evoked responses or whether they are indirectly due to changes in baseline activity.

Responses from isolated single cells in V1 were recorded in two awake behaving monkeys. The monkeys were trained to perform a same-different orientation discrimination task while maintaining fixation. There were three attentional conditions, as determined by a cue: attending *to* the cell's classical receptive field (CRF); attending *away* from the CRF; and a *passive* condition, where no cue was shown and the animals had to maintain fixation throughout the trial's duration. In all three conditions, stimuli were presented both in the CRF and in the opposite hemifield. These stimuli were shown either alone, surrounded by parallel-oriented bars, or surrounded by orthogonal oriented bars.

59 cells were recorded under all three attentional conditions. 11/59 (19%) cells showed a significant effect of attentional condition on responses; no cells showed a significant effect of attentional condition on surround modulation. This was evident over the population of mean responses, as well, and could not be attributed to systematic

biases in eye position. Compared to passive fixation, responses were suppressed, on average, by 7% when attention was engaged away from the CRF; compared to when attention was directed away from the CRF, moving attention to the CRF facilitated responses by 15%, back to passive fixation levels (similar results were obtained for the set of all 99 cells recorded with attending-away and attending-to conditions). Analyzing baseline activity showed that these response differences were modulations of the stimulus-evoked responses themselves and not of the baseline firing rates. This was confirmed by analyzing the time course of these attentional effects; modulations began about 80 ms after stimulus onset, 30-50 ms beyond the onset times for the responses. In addition, the response onset times were unchanged between attentional conditions. These results are discussed both in the context of previous studies that have investigated attentional modulation in V1 and in the context of computational models that attempt to describe the neurobiological underpinnings of spatial attention.

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1 Introduction

It is widely recognized that primary visual cortex (V1) performs a low-level analysis of the visual world, leading to response tuning along a number of feature dimensions, including orientation, disparity, motion, color, size, spatial frequency, and temporal frequency. It has also become increasingly clear that responses in V1 can be modulated by visual context, where stimuli outside the classical receptive field (CRF) affect responses to stimuli within the CRF. What is less clear, though, is whether responses in V1 can be affected by behavioral state. Relatively early evidence indicated general behavioral modulations, such as changes in excitability with changes in arousal; however, evidence of V1's involvement with cognitive processes, such as figure-ground segregation and selective attention, has been only indirect, as in the former, or incomplete, as in the latter.

The purpose of the present study is to investigate whether V1 responses are significantly affected by spatial attention. One issue is whether responses in V1 are affected by whether spatial attention is engaged, relative to a passive fixation task. A second issue is whether responses are affected by the locus of spatial attention, i.e., towards vs. away from a cell's CRF. A third issue is whether attention influences the modulatory effects of stimuli shown in the non-classical surround. The results indicate that attention significantly modulates responses to stimuli presented in the CRF but does not affect the interactions with the non-classical surround. While the magnitude of these effects are modest, they provide evidence that the effects of visual attention are apparent at the earliest stage of cortical visual processing.

WHAT ARE ATTENTIVE AND PREATTENTIVE PROCESSING?

The visual world comprises an enormous amount of information. Proper visual function depends upon extracting only a small fraction of this information at any given moment. This is the role of attention, first described by James (1890) as "the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought."

Our understanding of visual attention has grown dramatically over the last century. James's definition of attention relates to selectively processing one object to the exclusion of others. While attention can be directed to objects, per se (Baylis and Driver, 1993), there is considerable evidence that selective attention can also be directed to stimulus features, such as orientation, spatial frequency, color, motion, or size (Vogels et al., 1988; Corbetta et al., 1991). The most often studied – and arguably the most compelling – form of attention, though, is that which is directed to spatial locations, independent of other stimulus properties.

The form of spatial attention that conforms most with our everyday experience is known as *overt attention*. It involves moving the center of gaze to the attended location, and attempts to study it have focused primarily on visual search experiments (see Kinchla, 1992, for a review). In these experiments, a subject reports the presence or absence of a target stimulus embedded in a field of distracters. If the target comprises two conjoining features present separately in the distracting stimuli (such as a red vertical bar in a field of red horizontal bars and blue vertical bars), the time it takes to perform the search is linearly dependent upon the number of distracters in the array. This linear dependence is often taken as evidence that the subject searched the display serially until the target was found (Treisman and Gelade, 1980). While the presence of an overt serial search is debatable for smaller stimulus arrays (Kinchla, 1992; Desimone

and Duncan, 1995), eye movement measurements in monkeys show that a target embedded in a large array of distracters is not detected until it is brought near the center of gaze (Motter and Belky, 1996; Motter and Belky, 1997).

While overt attention relates most directly to our everyday experience of visual attention, it combines the underlying attentional mechanism with an associated oculomotor orienting response. *Covert attention* entails attending to a spatial location without changing the direction of gaze. This provides a means of studying the attentional mechanism independent of physical orientation. A number of early studies used covert attention tasks to investigate the physiological underpinnings of visual attention (Eason et al., 1969; Wurtz and Mohler, 1976; Von Voorhis and Hillyard, 1977). It was Posner et al. (1978), though, who introduced the now classic paradigm to show, behaviorally, how shifting attention towards a location in space without changing the center of gaze enhances visual processing at that location. Subjects were told to maintain fixation on the center of a monitor and press a response key when a stimulus appeared in the periphery. A cue preceded the stimulus, and this cue either directed the subject's attention to where the stimulus would appear (valid cueing), directed the subject's attention to the opposite hemifield (invalid cueing), or did not direct attention to any peripheral location (neutral cueing). Reaction times for detecting the target were significantly faster for the valid cueing trials than for either the invalid or the neutral cueing trials. This provided strong evidence that visual attention could be directed about the visual field without changes in gaze.

In addition to increasing detection sensitivity, covert attention also enhances stimulus discriminability. Downing (1988) had subjects perform luminance detection, brightness discrimination, orientation discrimination, and form discrimination after cueing one spatial location. She found that stimulus discriminability (d′) varied dramatically as a function of stimulus distance from the attended location. This was

most true for orientation and form discriminations, where d´ was almost three-fold higher at the cued location than during neutral-cueing trials. In addition, d´ in the orientation discrimination task dropped from about 0.8 at the cued location and to almost zero at one degree eccentric to the cued location. This study thus described how spatial attention could have dramatic effects on form-related processing, suggesting a process that may involve changes in the form-related ventral visual cortical stream.

While spatial attention significantly enhances visual processing at the attended location, the detection of feature contrast, such as a vertical bar in a field of horizontal bars, can be processed *preattentively*. That is, the time it takes to detect the presence of a popout target does not depend upon the number of distracters present, and thus appears to be independent of spatial attention (Treisman and Gelade, 1980; Bergen and Julesz, 1983). Braun and Sagi (1990, 1991) showed subjects a single stimulus array with which subjects had to perform both a discrimination (spatial attention) task and a texture contrast detection (preattentive) task before the onset of a mask. Instructing subjects to treat the discrimination task as primary, they showed that feature contrast detection is not significantly affected by performance of a concurrent orientation discrimination at the fovea (Braun and Sagi, 1990) or by a concurrent letter identification at the fovea or in the periphery (Braun and Sagi, 1991). This provided further evidence that preattentive processing occurs outside the realm of attention-related processing.

There is some evidence, though, that preattentive and attentive processing are not entirely separable. Joseph et al. (1997), for example, used rapid serial visual presentation to display a stream of black letters at a rate of 12 letters per second; subjects were instructed to report the identity of an oddball white letter. As a concurrent secondary task, a field of oriented Gabor stimuli were displayed for 150 ms, before being masked, and the subject had to report whether there was an orthogonally oriented Gabor – a popout stimulus – present in the array. Performance on this popout detection

task was drastically reduced if the stimulus array was presented up to 400 ms after the white letter target. This suggests that spatial attention can be engaged in such a way so as to preclude visual processing of feature contrast.

While many issues about the relationship between preattentive and attentive processing remain to be elucidated, both are distinct and important means of processing information used by the visual system. This leads to questions of how visual system carries out these processes, and what role, if any, V1 might play.

V1 is the primary cortical recipient of visual information from the thalamus, and it is the primary source of visual information for the rest of cerebral cortex. From V1, visual information flows through two principal cortical pathways: the dorsal (parietal) stream, which processes location-related information, and the ventral (inferotemporal) stream, including V2, V4, and IT, which processes feature-related and object-related information (Ungerleider and Mishkin, 1982). Given the central role of V1 in visual processing, what role it might play in preattentive and attentive mechanisms relates directly to the broader underlying question of what neuronal circuitry, in general, is involved in their mediation.

PREATTENTIVE PROCESSING: CONCEPTUAL MODELS AND V1

Conceptual models

Koch and Ullman (1985) posit that the primary role of preattentive processing is to draw the locus of spatial attention to the most perceptually salient stimulus. In this model, each principal feature dimension, such as orientation or color, has an associated feature map. These feature maps retinotopically represent salient stimuli within a given feature; these, in turn, converge to a saliency map, upon which a winner-take-all network acts to

relay the properties of only one of these stimuli to a central representation. If there is only one striking peak in the saliency map, the winner-take-all network converges upon that stimulus automatically and routes it to the central representation; this would correspond to preattentive popout. If there are a number of peaks in the saliency map, the winner-take-all network converges upon each of these peaks in turn; this would correspond to spatial attention.

For the feature maps, they propose representations in relatively early visual areas (as examples, they suggest MT for motion, V4 for color). For the saliency map, they propose two alternatives: first, the feature maps project to some higher cortical area, which in turn interacts directly with the winner-take-all network, and second, these feature maps project back to a saliency map represented in V1 or the LGN.

Evidence of V1 involvement

The role of V1 in preattentive processing is suggested most strongly its responses to orientation contrasts. This was first studied in relation to how V1 responses to a stimulus inside the CRF can be modulated by stimuli outside the CRF.

Blakemore and Tobin (1972) first showed that surround stimuli can modulate V1 responses in anesthetized cats. This modulation was dependent upon the orientation of the surround stimuli (Blakemore and Tobin, 1972; Maffei and Fiorentini, 1976), and most often resulted in response suppression (Fries et al., 1977). This suppression was apparent even when the surround stimuli were entirely outside the classical receptive field (Nelson and Frost, 1978).

Knierim and Van Essen (1992) showed that this orientation-dependent extra-CRF suppression is prevalent in V1 of awake fixating monkeys, as well. About one third of the cells they recorded from showed stronger suppression when the stimulus in

the receptive field was surrounded by parallel-oriented bars than when it was shown alone or surrounded by orthogonal-oriented bars. Put another way, these cells, termed "orientation contrast cells," responded most strongly when the stimulus in the CRF was perceptually salient and most weakly when it was part of a homogeneous texture.

These V1 orientation contrast cells may provide the physiological underpinnings of the orientation popout effect, an example of preattentive processing. V1 may also be important for motion popout, since Kastner et al. (1997) reported that 36% of cells recorded in V1 responded preferentially to motion contrasts.

Whether these orientation and motion contrast responses indicate two separate feature maps in V1 or whether they reflect a saliency map in V1 remains undetermined. It seems likely, though, that some feature contrasts are explicitly represented in V1 – either through feedback interactions with higher cortical areas such as V2 (Bullier et al., 1996) or through horizontal interactions within V1 (c.f. Knierim and Van Essen, 1992) – and that these feature contrasts are then projected to parietal cortex where saliency and associated changes in the locus of attention can be determined.

ATTENTIVE PROCESSING: CONCEPTUAL MODELS

While V1 is likely to play a role in preattentive processing, its role in attentive processing is less clear. As visual information flows from V1 through the ventral stream, attention must act, at some point, to affect how this information is processed. A priori, this modulation might occur either at the beginning (early selection), at any number of stages throughout the ventral stream (multistage selection), or at the highest stages, in anterior inferotemporal cortex (late selection).

Corbetta (1998) has drawn a useful distinction between two principal forms of attention-related activations: source signals and site signals. Source signals are those

activations in the brain related to controlling the direction of attention, whereas site signals are those activations that reflect attention's effects on visual processing. He argued that parietal cortex and, perhaps to a lesser degree, frontal cortex are attentional sources which act upon the ventral stream, the attentional site. This general framework is well supported by the literature; however, the mechanism by which information flow in the ventral stream is affected by this attentional source remains unknown, and different models make distinct predictions about whether responses in V1 would be affected, as well.

Early selection

An early selection model spatial attention would change feedforward visual processing at its earliest stage, via the so-called attentional spotlight. One of the earliest hypotheses was suggested by Crick (1984), who proposed that connections between an assembly of LGN relay cells and their targets in V1 are momentarily strengthened by a short, intense burst of activity. This would enhance the cortical processing related to this assembly of LGN cells, and thus their associated region of space. This is often referred to as a spotlight model of attention because all processing associated with the attended region of space is non-selectively enhanced.

The short burst that effects this facilitation would ostensibly be caused by a momentary inhibition imposed by the reticular nucleus, which surrounds the dorsal thalamus. Cells in the reticular nucleus are inhibitory, and LGN cells have been shown to exhibit bursty behavior in slices when hyperpolarized (Llinas and Jahnsen, 1982; Jahnsen and Llinas, 1984a and 1984b). Thus, feedback from cortex, which is known to pass through and synapse onto the reticular nucleus of the thalamus, would be responsible for controlling the locus of the spotlight.

One problem with this theory is that the LGN demonstrates bursting behavior principally during sleep (Steriade and Llinas, 1988; McCormick, 1989). A substantial revision of this theory was offered by LaBerge (1990). He cited more recent evidence that the feedback reticular nucleus cells synapse onto the inhibitory interneurons within the thalamus as well as onto the relay cells. But the strength of inhibition on the inhibitory interneurons is at least 20 times that imposed on the relay cells. Thus, when cortical feedback stimulates a section of the reticular nucleus, the underlying region of thalamus becomes disinhibited, since the reticular activity inhibits the corresponding inhibitory interneurons more than it directly inhibits the relay cells. In addition, the activated reticular cells send collaterals to neighboring reticular regions, suppressing their activity, which increases the net inhibition of their associated, underlying relay cells. The resulting pattern of activity in the relay cells of the thalamus, then, would be a facilitation at the attended region and a suppression in the surrounding regions.

Multistage selection

Because of various anatomical constraints, LaBerge modified the early selection model to become a multistage model. This model required an attentional source signal to innervate the thalamic nuclei; however, evidence for such signals innervating the LGN was lacking. He therefore posited a mechanism dependent upon the pulvinar. The pulvinar is reciprocally connected with both the dorsal and ventral stream. This, therefore, provides a plausible site for the two streams to interact. LaBerge proposed a multistage model: visual information from any number of ventral stream visual areas project to nuclei of the pulvinar, where the signals are processed using filtering mechanisms controlled by projections from the parietal cortex. These filtered responses

are then projected back to the ventral stream, modifying the information as it flows anteriorly.

Olshausen et al. (1993) also proposed a multistage model dependent upon the pulvinar. They suggested that visual information is transformed along the ventral stream by a routing, or "shifter," circuit. This model posits that spatial representations of the visual field in successive areas along the ventral stream are increasingly biased towards representing regions of space occupied by the attended stimulus. This would reach its climax in late inferotemporal cortex, where cell responses would be constrained exclusively to that which is being attended. Such a representation would demand that receptive field properties be able to change dynamically with the locus of attention, and they propose that projections from the pulvinar interact multiplicatively on the feedforward ventral stream synapses to effect these changes. The shifter circuit model is necessarily a multistage model, as the fan-in from one cortical area to the next is not sufficient to route a stimulus from anywhere in the visual field to a canonical representation in only one layer of synapses between them.

Late selection

Deutsch and Deutsch (1963) first proposed the idea of late attentional selection by considering the auditory system. Stimuli that are not attended to can still draw attention based upon properties that require a high degree of discrimination, such as one's name. They proposed that all available auditory stimuli are fully processed in parallel, and that attention is then drawn to the one that has the greatest saliency. Allport (1977) showed that semantic processing of unattended stimuli can occur in the visual system, as well, and Duncan (1980) extended the idea of late selection to visual attention, in general.

A neurobiological model of late selection would thus posit that attention acts at a stage after substantial processing in the ventral stream has been completed. Inferotemporal cortex would represent and perform pattern recognition upon every stimulus in the visual field in parallel, and perhaps posterior parietal cortex, which does have direct reciprocal connections with inferotemporal cortex, would then select the activation associated with the attended region of space.

The most likely scenario: multistage selection

Attentional modulations are seen throughout the ventral stream, at least from V2 on (Moran and Desimone, 1985; Chelazzi et al., 1993; Motter, 1993; Luck et al., 1997), providing evidence against a late model of attention. Furthermore, the magnitude of these modulations increase in the later stages of processing, which would not be expected if the only site of modulations were at the beginning of the processing stream. This suggests that multistage attentional selection is the most likely of options. Of these, the shifter circuit model is arguably the most attractive from a computational perspective. It accounts for the increasing classical receptive field sizes in successively higher cortical areas, and it provides a model for transition- and scale-invariant pattern recognition, in which the routing circuit acts to transform sensory signals to an object-centered representation within inferotemporal cortex.

The presence of attentional modulation in V1 would rule out an exclusively late model of attentional selection and the absence of attentional modulation in V1 would rule out the early model of attentional selection; however, these two models are, a priori, the most unlikely, and the multistage models of visual attention do not make hard predictions about V1's involvement. The nature of V1 modulation will, though, help elucidate the mechanisms underlying this probable multistage selection.

HYPOTHESES FOR ATTENTIONAL MODULATION IN V1

Orientation contrast cells in V1 may provide a physiological substrate for the preattentive popout effect. Whether cells play a role in attentive processing, as well, is the principal focus of the present study, which was designed to address three basic questions:

1. Does engaging spatial attention, relative to passive fixation, affect V1 responsiveness?
2. Does moving the locus of attention affect V1 responsiveness?
3. Does attention affect surround modulation?

These three questions derive from considering the possible interactions between preattentive processing – presumably mediated through surround modulation in V1 – and attentive processing. For example, Yantis and Jonides (1990) showed that sudden-onset stimuli, which are normally powerful in automatically capturing attention, are less so when attention is already engaged somewhere else in the visual field. This led to the question of whether surround modulation, and thus the putative popout signal, would be stronger during passive fixation than when attention was engaged, away from the CRF. This, then, generalizes to the more general question of whether attentional task, i.e., the presence or absence of directed spatial attention, modulate responses in V1.

Similarly, if V1 orientation contrast cells mediate the preattentive popout effect, and if the principal role of preattentive processing is to drawn the locus of spatial attention to these very stimuli, then a natural question is whether the responses of these cells change when attention is directed to their receptive fields, when drawing attention

to their spatial locations is no longer necessary. This, too, generalizes to the more general question of whether the location of spatial attention modulates responses in V1.

ATTENTIONAL MODULATION IN V1 (AND THE VENTRAL STREAM)

While there is ample evidence that responses at higher levels of the dorsal and ventral streams are modulated by spatial attention, there is conflicting evidence as to whether responses in V1 are, as well. It is important in reviewing the literature, though, to consider what attentional demands are imposed by a given study's task. Luck et al. (1997), for example, suggests that only the more demanding attentional loads would elicit earlier attentional modulations. In addition, for the shifter circuit model attention-related modulations at multiple levels of visual cortical processing would be most necessary for tasks involving object recognition or pattern discrimination; changes in processing necessary for stimulus detection or localization might be restricted to parietal cortex. Finally, many of the studies investigating attentional modulation of V1 were principally interested in attentional modulations elsewhere in the ventral stream, especially area V4. Thus, discussions of attentional modulations in V1 are often phrased in the context of the rest of the ventral stream.

Single-unit physiology

The first ostensible evidence against spatial attention modulation in V1 came before positive evidence of modulation was reported anywhere in the ventral stream. Wurtz and Mohler (1976) recorded responses in macaque V1 while the monkeys either passively fixated or performed a covert attention task. In the attention task, stimuli were displayed both in the cell's classical receptive field (CRF) and in the opposite hemifield,

and the monkey had to report either of their dimming. Responses were unaffected by whether the dimming stimulus was in the CRF or in the opposite hemifield. Because stimulus conditions were blocked by location, this was taken as evidence against location-related modulation in V1. It is important to note, though, that the animals were engaged in a dimming task. This is a relatively easy task that is unlikely to tax the processing specialization of the ventral stream, pattern recognition. Thus, attention-related changes might be restricted to parietal cortex and may not involve modulations in V1.

While Wurtz and Mohler (1977) did not see spatially specific modulation with the locus of attention, responses of 8/50 (16%) cells in V1 were significantly facilitated relative to fixation when the monkey engaged in the dimming task. This facilitation may have been due to increases in arousal, an explanation consistent with Bartlett et al. (1973), where stimulation of the reticular formation caused greatly increased responsiveness in V1. A similar task-related facilitation was seen by Boch (1986), where responses in V1 were markedly facilitated when the fixation point was removed and the monkey was required to maintain his gaze. This increase in activity can be attributed either to an artifact of higher eye position variance (eye position data were not analyzed) or to an increase in arousal caused by the more difficult task of maintaining fixation without a fixation point. Contrary to its intention, though, Boch (1986) did not manipulate selective attention, *per se*.

Moran and Desimone (1985) first reported modulation of single-unit responses in the ventral stream by selective attention. This study was later extended by Luck et al. (1997). Monkeys performed a simple match-to-sample task at one of two locations, both of which were within a cell's receptive field. Stimuli were displayed at both locations simultaneously, and the attended stimulus was effective in driving the cell while the unattended stimulus was not. This location-specific modulation was apparent

Like Moran and Desimone (1985) and Luck et al. (1997), Haenny and Schiller (1988) also described attentional-related modulation in V4 with inconclusive results in V1. In their task, though, attention was directed to a stimulus feature – orientation – instead of to a spatial location. During each trial, the monkey viewed alternating gratings of mutually orthogonal orientations; the task was to detect when one of these two stimuli was repeated twice in a row. Both in V4 and V1, when the cell's preferred stimulus was repeated, and so becoming a target, the response to the second stimulus in the repeated pair was significantly greater than the response to the first. This appeared to be evidence for modulation in V1 by selective attention to the target orientation. In both areas, though, responses to the preferred stimulus became habituated with its every presentation. To account for this habituation, the response of the second, target stimulus was compared to the first stimulus in the series instead of to the first stimulus in the repeated pair. Using this comparison, the facilitation was still evident in V4, though the response to the second, target stimulus in V1 was indistinguishable from the first stimulus in the series.

Haenny and Schiller interpreted these results as an absence of attentional modulation in V1. There is, though, an alternative explanation. The initial response to the preferred stimulus may have been maximal for a given V1 cell. Thus, attending to that orientation would be unable to facilitate the cell's responses. Habituation, though, decreases the cell's responsiveness and so increases its ability to demonstrate facilitation. The fact that V1 responses are habituated by a repeated stimulus, then, does not detract from selective attention's ability to facilitate the cell's responses to pre-habituation levels.

The strongest indication that spatial attention might modulate responses in V1 comes from Motter (1993). The task was to report whether the orientation of a test bar at a cued location was tilted to the left or tilted to the right. This test bar was imbedded

in an array of distracter bars, making the task relatively difficult. Responses in 34/96 (35%) V1 cells were differentially affected by whether attention was directed to the cell's CRF or to one of the surrounding locations in the stimulus array; the magnitude of these effects, though, were not reported.

Unfortunately, it is not possible to conclude from Motter (1993) whether response in V1 were, in actuality, modulated by the location of spatial attention. In Motter (1993), the CRF was mapped while the animal directed spatial attention to the CRF. In every trial, the monkey was required to fixate within a one degree window about the fixation point. Thus, if the monkey systematically biased his eye position towards the locus of attention yet remained within the one degree fixation window, attending to any stimulus other than the stimulus at the CRF might have resulted in an offset between the CRF and its stimulus, eliciting a consistently different response. Indeed, Luck et al. (1997), who did not see response modulation in V1, suggested that the apparent effects of attention on V1 responses reported by Motter might instead have reflected a systematic bias in eye position.

A related issue is whether small fixational changes in eye position affect V1 responses. Motter and Poggio (1982, 1990) first proposed that the locations of V1 receptive fields are not strictly retinotopic; rather, they are dynamically shifted to account for variability in eye position during fixation. Under this model, while the CRF stimulus would drift across the retina with fixational biases in eye position, the V1 CRF would move right along with it, manifesting the same response as if the eye position had not moved. This could be effected by a dynamic routing circuit, as proposed by Anderson and Van Essen (1987) and Olshausen et al. (1993). Their evidence was drawn from onsets times of responses evoked by drifting bars across the CRF, and it was supported by Kjaer et al. (1997), who show that eye position deviations of up to 12

minutes resulted in no significant change in the pattern selectivity of parafoveal complex cells, even though some of the patterns consisted of relatively high frequencies.

The stimuli shown in Motter (1993), though, were flashed bars, and flashed bars do not seem to demonstrate retinal stabilization (Gur and Snodderly, 1987; Motter, 1995). In addition, Gur and Snodderly (1997) were unable to repeat Motter and Poggio (1982, 1990), failing to show retinal stabilization with drifting bars. Gur et al. (1997) also provided evidence against retinal stabilization, showing that responses in V1 are significantly more variable during small fixational eye position adjustments than during periods where the eye position remains unchanged.

Thus, the evidence that responses in V1 are stabilized during small adjustments in eye position remains inconclusive. Given the possibility, it is not possible to determine whether the changes in firing rate caused by changes in attentional location in Motter (1993) are due to attentional modulation or to concomitant changes in eye position. And importantly, Motter (1993) did not apparently analyze eye position data. It is critical that any study of attentional modulation in V1 take this possibility of a confound into account. The present study has been designed with this very consideration in mind, taking into account the possibility of fixational biases in eye position on apparent attentional modulations of V1 responses.

Event-related potentials (ERP)

Event-related potentials (ERP) experiments, like many of the single-unit experiments described above, often fail to show attentional modulation in V1. While directing spatial attention to one hemifield typically facilitates responses in the contralateral hemisphere (Eason et al., 1969), the earliest components to demonstrate this facilitation are P1 and N1 (Van Voorhis and Hillyard, 1977). These roughly correspond to inferotemporal

cortex (fusiform gyrus: Heinze et al., 1994) and parietal cortex activations, respectively, and peak at 90-140 ms and 160-190 ms (Mangun et al., 1993). The ERP component associated with V1 activity, the C1 component, has not yet been shown to be significantly modulated by the locus of spatial attention (Mangun et al., 1993; Gomez Gonzalez et al., 1994; Clark and Hillyard, 1996).

As with many of the single-unit experiments, the lack of V1 modulation may be due to differences in the attentional tasks. In these ERP experiments, attention was alternately directed from one hemifield to another; however, only one stimulus was ever displayed on the screen at any given time. In single-unit recordings in the macaque, going from a simultaneous-display paradigm to a sequential-display paradigm drops the mean facilitation in visual area V4 from 63% to 6% (Luck et al., 1997). Thus, the asynchronous visual stimulation in these ERP experiments makes the task easier and may eliminate the computational demand for V1 modulation.

Oakley and Eason (1990a, 1990b) claimed to see subcortical modulation of visual responses using a doublet detection task. Single flashes were asynchronously displayed in the left and right hemifields and subjects had to report infrequent (25% to 30%) double flashes in the attended hemifield, ignoring the unattended hemifield. In Oakley and Eason (1990a), an early (40-70 ms) component showed significant facilitation in the hemisphere contralateral to the attended hemifield; however, this facilitation was significant only at frontal recording sites, and not at occipital locations. And because the magnitude of this early component was of comparable magnitude across the scalp, they concluded the facilitation was subcortical in origin. In Oakley and Eason (1990b), the significance of these effects was dependent upon the method of reporting: saccade and counting tasks revealed significant attentional modulations, whereas reporting target doublets with a foot pedal elicited no attentional modulations.

This dependence on reporting method suggests that these modulations are unlikely to reflect changes in the geniculocortical stream due to selective attention.

Functional imaging

In contrast to these ERP studies, recent abstracts of functional magnetic resonance imaging (fMRI) experiments suggest the presence of attentional modulation in human V1 (Worden and Schneider, 1996; Gandhi et al., 1998). In these experiments, attention was periodically shifted from one hemifield to another while stimuli were shown simultaneously in both. In both of these experiments, activity in V1 was modulated with the same periodicity as the attentional shifting. Worden and Schneider (1996) saw attentional modulation only when surround stimuli were displayed on the screen as distracters throughout the task. This modulation was further increased when the distracters shared characteristics with the discriminanda (such as curved or straight lines). Thus, the ability to see attentional modulation in V1 correlated with task difficulty. Similarly, Gandhi et al. (1998) used a motion discrimination task where subjects were constrained to perform near psychophysical threshold. As with the Worden and Schneider (1996), task difficulty may have been important for their seeing early visual cortical modulation.

In addition to these V1 modulations by attentional location, Corbetta et al. (1991) showed task-related changes in V1 activity using PET. Subjects were shown two sequential full-field displays of moving bars and performed either a selective attention task or a divided attention task. In the selective attention task, the subject had to report whether a given stimulus dimension (such as color) had changed, while ignoring changes in the other stimulus dimensions (such as speed and shape). In the divided attention task, the subject merely had to report whether anything about the stimuli had

changed, along any of the stimulus dimensions. The divided attention task is essentially a detection task, and is easier to perform than the selective attention tasks. When the activation during the divided attention task was subtracted from the activation during the shape or speed selective attention tasks, a significant differential activation in V1 was revealed.

Effects on baseline activity

In principle, attention might modulate neural activity in a variety of ways. These include possible effects on baseline firing rates and effects on spike timing, as well as more conventional effects on visually evoked responses.

Evidence for the presence of attentionally related shifts in baseline activity was presented by Luck et al. (1997). As noted already, response magnitudes in their study were not affected by whether spatial attention was directed to the cell's CRF or to the opposite hemifield. However, they did report that baseline activity was facilitated, on average, by 30% in V4 when attention was directed to the cell's CRF, as opposed to the opposite hemifield, and this facilitation was significant in 40/74 (54%) cells; similarly, baseline activity was facilitated by 43% in V2 when attention was directed to the cell's CRF, and this facilitation was significant in 48/65 (74%) cells. This would ostensibly provide a competitive advantage over stimuli presented to unattended locations, where the baseline firing rate is lower (Desimone and Duncan, 1995). This change in baseline firing rate might be a biasing signal for the competition between the two stimuli; as a result, this mechanism is referred to as biased competition.

Rees et al. (1997a) further explored the difference between response changes and baseline changes using PET. Subjects were required to categorize stimuli based upon either simple features or the conjunction of features. These stimuli were shown at

various presentation rates, and the rate-response function was compared between the two tasks. If modulation by the conjunction task were due to a change in stimulus response gain, they hypothesized that the two rate-response functions would have significantly different slopes. If, on the other hand, modulation were due to a biasing signal, one that changed the rate of baseline activity, the two rate-response functions would have significantly different intercepts. Activity in the inferotemporal visual stream showed both changes in response gain and offsets in spontaneous activity, suggesting the presence of a biasing signal; however, neither type of attentional modulation was discernible in V1 using this non-spatial feature conjunction task.

Changing the temporal structure of response-related activity without changing the cells' mean firing rates has been proposed as a means of using attention to bind together stimuli and their associated features across the visual field, giving rise to a single unitary percept (Crick and Koch, 1990). Beyond V1, attention clearly modulates mean firing rates as a way of affecting visual processing. Whether attention modulates the temporal structure of this activity, though, remains unknown. Niebur et al. (1993) propose a model whereby attention-related oscillations within V1 could give rise to the modulations of response magnitude seen in extrastriate cortex.

THE PRESENT STUDY

Responses in V1 correlate with the preattentive popout effect, and responses in V1 can be modulated by attentional task. However, little is known about how attentional state affects V1 preattentive processing. And while there appears to be some evidence for modulation of V1 responses by the locus of spatial attention, how much of this is due to eye position artifacts and how much is due to veridical attentional modulation of stimulus-evoked responses remains unknown.

The present study addresses these issues by recording single-unit responses in V1 while the monkey was in one of three attentional conditions: passive fixation, attending to the cell's receptive field, and attending away from the cell's receptive field. To increase the chances of evoking modulation as early as V1, the behavioral task was an orientation discrimination. V1 is the first visually responsive structure to demonstrate orientation tuning, and its sensitivity to changes in orientation can approach psychophysical thresholds (Vogels and Orban, 1990). Areas downstream from V1 are critical for performing orientation discriminations; for example, lesioning area IT interferes with orientation discrimination (Dean, 1978). And to assess how these attentional conditions affect preattentive popout-related processing in V1, the stimulus in the receptive field was either shown under conditions similar to Knierim and Van Essen (1992): alone, surrounded by parallel bars, or surrounded by orthogonal bars.

2 Methods

SUBJECTS

We used two male Rhesus monkeys (Macaca Mulatta) weighing 5-10 kg in our experiments. These monkeys, housed in separate cages, received dry food (monkey chow and dried fruit) on the same schedule as the other monkeys in the colony; however, they received their daily intake of water via their training and recording regimen. When performing their behavioral tasks, the monkeys were rewarded with water or juice and were typically allowed to work until satiety. Every day, the animal's degree of hydration was assessed by examining body weight, skin dryness, appetite, stools, and coat. Water supplements and fresh fruit were given as was appropriate to ensure their health and comfort.

BEHAVIORAL PARADIGM

Monkeys were trained on a "same-different" orientation discrimination paradigm while maintaining fixation, as schematized in figure 1. The task was to determine whether the reference and test stimuli at the cued location were of same or different orientation. There were three attentional conditions, as determined by the cue: attending to the cell's CRF, attending away from the CRF, and a passive condition, where no cue was shown and the animal's only task was to maintain fixation throughout the trial's duration.

The time course of each trial is shown in figure 2. Once the monkey depressed the response lever, a fixation point appeared in the center of the screen. The trial was

discontinued if the monkey did not fixate within one second and maintain fixation within a specified window (A). This fixation window ranged from 30-40 arc-min., depending upon the state of the monkey's training. For trials where attention was directed to the cell's CRF or to the opposite hemifield (across the vertical meridian), a cue ring was then shown for 200 ms at the appropriate location (B). This determined where the orientation discrimination task was to occur, encouraging the monkey to direct his attention appropriately. After a one second interval (C) reference stimuli were shown for 300 ms at both locations (D). After another one second interval (E), two helper rings were shown at both locations for 200 ms (F), followed immediately by test stimuli for 300 ms (G), shown at each location. These test stimuli could be shown either alone, surrounded by parallel oriented bars, or surrounded by orthogonally oriented bars. To receive a fluid reward, the money was required to respond correctly according to whether the reference and test stimuli *at the cued location* were of same or different orientations. If they were of different orientations, the monkey was rewarded for releasing the response lever between 100 and 700 ms after test stimulus offset (H). If they were the same orientation, he was rewarded for holding the lever down for at least one second after test stimulus offset. In tests that included the passive condition, 20% of trials began without a lever depress and no cue stimulus was displayed. All other stimuli were identical to the cued trials, and the animal's task was to maintain fixation and to avoid pressing the response lever. This latter requirement helped discourage the monkey from trying to perform an attentional task during the passive trials.

STIMULUS PRESENTATION

Texture stimuli

As described above, the test stimuli were shown either alone, surrounded by parallel oriented bars, or surrounded by orthogonal oriented bars (figure 3). These surround stimuli were arrayed in a hexagonal pattern, spaced between 1 degree and 2.6 degrees from one another, often scaled to the size of the oriented bar stimuli. The median hexagonal spacing was 1.9 degrees.

The test and surround stimuli were always of identical color and contrast to one another; however, when present, their orientations were jittered by the amount of the discrimination. Specifically, every surround bar had an equal probability of being at the match orientation or at the non-match orientation (parallel surround condition) or of being orthogonal to the match orientation or to the non-match orientation (orthogonal surround condition). The difference between the parallel and orthogonal surround textures therefore depended upon the difficulty of the discrimination. This jittering of the surround circumvented a confound that would have occurred if the surround bars were oriented identically: the monkey would have been able to obtain a reward based on absolute surround orientation and/or orientation contrast with the test stimulus (for example, in the parallel surround condition the test stimulus would be of the same orientation as the surround in one set of trials, e.g., match trials, but not in the other set of trials, leading to a difference in perceptual salience that could guide behavior; alternatively, if the orientation of the surround stimuli covaried with the match/non-match condition, the monkey would have no incentive to attend to the cued location).

Display parameters and contrast

Stimuli were presented on a Silicon Graphics GDM-1640SG 60 Hz RGB monitor driven by a Silicon Graphics Indigo R4000. The monitor was 36 X 27 cm with a resolution of 1280 X 1024 pixels, viewed at a distance of 40 cm.

Stimuli could be one of six colors (white, yellow, cyan, green, magenta, red, and blue). In most recordings, stimuli were presented at what will be referred to as *standard contrast*. Under standard contrast conditions, the white, yellow, cyan, and green stimuli were of 1-1.3 log units contrast, or 82-88% Michaelson contrast; magenta, red, and blue stimuli, which were used infrequently, were of 0.3-0.7 log units contrast, or 67%, 60%, and 33% Michaelson contrast, respectively (United Detector Technology model 371 photometer). For some cells, very *high contrast* stimuli were used, as well. The stimuli were presented on an unilluminated background, instead of a gray background, and the contrast was limited only by the degree of light scatter; presumably, the stimuli were > 2 log units contrast, near 100% Michaelson contrast.

EXPERIMENTAL CONTROL AND DATA ACQUISITION

The experiment was controlled on the display computer by the Xdowl data acquisition program, developed by Jamie Mazer and adapted for the Silicon Graphics computers by Heather Drury. For every trial, Xdowl ran the behavioral paradigm and acquired incoming neural activity and eye position data. All relevant experimental events (stimulus display times, spike times, eye positions, and pedal responses) were recorded in a single data file and were coordinated with the display refresh to a resolution of ±1 ms.

Pedal input and juicer output were routed through both a custom-built Micromint D/A I/O device and a custom-built pedal/juicer controller. The Micromint was connected to the computer through the serial port and was also responsible for sampling eye position information. Input from the Micromint was read by the computer using software originally written by Ed Connor.

Eye position was monitored with the scleral search coil technique (Robinson, 1963) using a Remmel Labs EM3 eye movement monitor. The output from the eye movement monitor was then digitized by the Micromint and recorded by Xdowl. The Micromint sampled eye positions using 8 bits at approximately 33 Hz, with a resolution ranging from one to three arc-minutes. This resolution depended upon the coil-dependent gain settings, which were checked periodically and which changed with every eye coil.

Single-unit activity was recorded from the operculum of V1 using a 125 μm diameter 1-5 MΩ epoxy-coated tungsten electrode (A-M Systems and FHC Inc.). The electrode was inserted transdurally through a 5 mm craniotomy using a custom guide-tube system. Signals were amplified by a differential amplifier (Bak MDA-4) and were then filtered (Krohn-Hite 3700 analog filter), and spike events generated by a window discriminator (Bak DIS-1) were recorded by Xdowl through the computer's audio port.

SURGICAL PROCEDURES

To prepare monkeys for these experiments, an acrylic cap and triangular headpost were installed using fully sterile conditions. This was done under general anesthesia (isoflurane, 2%-3%) following intubation under ketamine (10 mg/kg), xylazine (1 mg/kg), and atropine (0.04 mg/kg). The acrylic cap was extended from about 1 cm behind the brow (to accommodate the head post) to the occipital ridge (to accommodate a

recording chamber placed over V1). The monkey was always given a minimum of one week to recover following any major surgery before training or recording, and during that time he was maintained on a regimen of antibiotics (Baytril, 2.5 mg/kg BID). An eye coil was also often implanted as a part of this same surgery. If a new eye coil needed to be implanted following the initial cap installation, these same procedures were followed. Recording chambers were added and removed from the acrylic cap under ketamine, alone, since it required manipulating only the acrylic.

Before first recording from a monkey, he was anesthetized using ketamine, xylazine, and atropine (to prevent fluid loss typically induced by ketamine) and, using sterile precautions, a 5 mm hole was drilled through the acrylic and skull within the chamber. This craniotomy was maintained for as long as electrodes would penetrate the dura, typically three to four weeks. If necessary, the fibrous scar tissue that had since formed over the dura could be removed, using the same preparations as when the hole was first drilled. After a craniotomy was no longer usable, it was closed under these same conditions.

RECORDING PROCEDURES

Monkeys were transferred from their cage to the primate chair using the pole and collar technique of Anderson and Houghton (1983) and were then prepared for recording using the procedures described above.

A custom-built stepping motor microdrive transdurally introduced the recording electrode into V1. Once isolated, a cell's CRF was characterized using a modified version of the custom CRF-plotting program originally written by Jack Gallant, Heather Drury, and Ed Connor. The monkey was required to fixate for five seconds while an oriented bar was moved about the visual field under mouse control. Auditory feedback

of cell activity was used to determine the CRF boundaries. A mirror image of the stimulus was presented in the opposite hemifield to prevent horizontal biases towards the CRF location (unless the CRF was within approximately 10 degrees polar angle of the vertical meridian). In this way, the cell's optimal color, orientation, and bar width could be determined. The bar length used in subsequent paradigms was constrained between one and two degrees because of task difficulty considerations.

After characterizing these basic CRF properties, the cell's preferred orientation was determined using a modified version of the orientation discrimination paradigm. Here, attention was always directed to the cell's CRF, and all trials were of the no-surround condition. Furthermore, while the discrimination remained the same from trial to trial, the orientation of the reference stimulus varied from trial to trial (typically over five values). Typically, 20 trials were run for a given test, using four repetitions of five orientations, centered around the preferred orientation estimated in the preliminary test. The orientation tuning was then determined by examining the mean firing rate evoked by each reference stimulus. The reference stimulus was shown for 300 ms; however, responses in V1 typically have a delay in response onset of at least 30 ms (Vogels and Orban, 1990). Thus, the mean response during this period was determined by finding the cell's mean firing rate between 30 ms and 330 ms after stimulus onset. If the peak of the orientation tuning curve was not within the range of tested orientations, this test would be run again until the peak orientation could be determined. If necessary, the value of the peak orientation was estimated by visual interpolation. An example of a cell's orientation tuning curve is shown in figure 4. In this example, the cell's optimal orientation was 90 degrees.

After determining the cell's preferred orientation, its attention-related modulation was assessed using the full orientation discrimination paradigm. The reference and test stimulus orientations were chosen so that they fell to either side of the cell's optimal

orientation. In the above example, a 12 degree orientation discrimination would require the reference stimulus and matching test stimulus to be oriented to 84 degrees and the non-matching test stimulus to be oriented to 96 degrees. Thus, assuming an accurate assessment of the cell's preferred orientation and a symmetric orientation tuning curve (as is typical in V1), match and non-match trials should give the same test stimulus response, all other factors being equal. If the orientation tuning curve was too narrow to allow this strategy, the reference stimulus was chosen to be of the cell's optimal orientation.

All trials were run in blocks by attentional condition, with 12 trials of attending to one location (such as the CRF), 12 trials attending to the other location, and six passive trials. These interleaved blocks were then repeated up to eight times, depending upon the length of time the cell was held.

DATA ANALYSIS

Cells were considered for analysis if there were at least three repetitions of every relevant condition and if the response to the bar-alone condition when attention was directed to the CRF was significantly greater than zero. If the non-match and match responses differed by a factor of two (determined by analyzing the trials where attention was directed to the CRF and the test stimulus was shown with no surround), all trials of all conditions of the lesser of these two were discarded from further analysis.

In testing for attentional effects, responses are typically measured during the test stimulus period. As for the reference stimulus analyses of orientation tuning, the response to the test stimulus was determined by its mean firing rate from 30 ms to 330 ms after test stimulus onset. The pre-cue baseline activity, recorded before the onset of the attentional cue, was then subtracted from this mean firing rate on a trial by trial basis.

These are referred to as the *subtracted responses*. When the original test stimulus responses are used, without baseline subtraction, they are referred to as the *raw responses*.

Almost all statistical comparisons were made with randomization tests (Manly, 1991). The randomization technique was chosen because many of the responses and derived indices used in this study were not normally distributed, as determined by the probability plot correlation coefficient test (Filliben, 1975). Thus, parametric tests that assume normally distributed samples, such as the Student's t-test, the f-test, and the traditional ANOVA, are arguably inappropriate for these data. Randomization tests are a suitable alternative: they can be used for all statistical comparisons in this study, including one-sample tests, two-sample tests, paired comparisons, and ANOVAs; they are more powerful than traditional non-parametric tests; and they produce results that converge on those derived from parametric tests that assume normal distributions when the data are normally distributed, it was considered the most appropriate alternative. The one exception is the chi-squared test, which was used when necessary in its standard normal form. The number of randomizations performed for a given test depended upon its nature: 50,000 permutations were used for ANOVAs, while 100,000 permutations were used for all other tests.

When ANOVAs were performed on mean responses from a population of cells, the ANOVA method depended upon the how the data were collected. If responses to every condition were collected in every cell, a within-cell ANOVA was performed using each condition's mean firing rate. If responses to every condition were not measured in every cell, e.g., one population of cells was treated to one condition while another population was treated to another, an ANOVA was performed on the normalized mean firing rates. These were calculated for every cell by dividing each condition's mean firing rate by the cell's mean firing rate across all conditions. In all figures of ANOVA-

related data, both measures of mean response across all conditions are displayed. In almost all situations that a within-cell ANOVA was performed on the raw mean firing rates, an ANOVA of the normalized mean firing rates gave similar measures of statistical significance.

Gain coefficients

Every stimulus condition, i, has an associated test stimulus mean firing rate, $\bar{t}_i$. In addition to a mean firing rate, every stimulus condition has an associated gain coefficient, α_i, as well. The gain coefficient is the gain by which the cell's CRF must be scaled to best fit a given condition's responses.

To model the cell's CRF, the mean response for each trial's reference stimulus was first plotted as a function of that trial's modal horizontal and vertical eye positions during the reference stimulus period. The modal eye position was used because it gave the most robust estimate of the position of the eyes during the 300 ms reference stimulus period. The reference stimulus period was used because reference stimuli were always shown without a surround, whereas test stimuli were shown under three different surround conditions. Thus, using test stimuli would result in either more response variance (assuming different surrounds gave different responses) or one-third the number of trials (if only one surround condition were used).

These data were then fitted with the sum of two quadratics, one for each eye direction:

$$f(x,y) = \left(\left(a_2x^2 + a_1x + a_0\right) + \left(b_2y^2 + b_1y + b_0\right)\right)$$

The fit was accomplished by finding the a and b coefficients that minimized the sum-squared error between this function and the data, i.e., minimizing

$$\sum_{i=1}^{m}\sum_{j=1}^{n_i}\left(r_{ij}-f(x_{ij},y_{ij})\right)^2$$

over the n_i trials of all m conditions, where i is the condition number and j is the trial number for that condition, and where r_{ij}, x_{ij}, and y_{ij} are each trial's reference stimulus response, modal horizontal eye position, and modal horizontal vertical eye position, respectively. The second-order term for each direction was used only if the resulting quadratic peaked within the range of eye positions and was convex; otherwise, only the linear term was used. Thus, when both second-order terms met these criteria, the CRF was modeled by a two-dimensional convex parabolic surface; when neither second-order term met these criteria, the CRF was modeled by a plane.

After modeling the cell's CRF using the reference stimulus responses, this model was scaled by a gain coefficient, α_i, to fit each condition i's test stimulus response. That is, for a given condition i, the α_i was found that minimized the following function over condition i's n_i trials:

$$\sum_{j=1}^{n_i}\left(t_{ij}-\alpha_i\frac{f(x_{ij},y_{ij})}{\bar{r}}\right)^2$$

The normalization by the mean reference stimulus response, $\bar{r}$, ensures that α_i will assume values of the same order as the original mean firing rates. Attentional analyses that had used cell mean firing rate for each condition, $\bar{t}_i$, could then use the gain coefficients, α_i, as an eye position-independent measure of the cell's responses.

Response onset times

Response onset times were calculated using the method described by Legéndy and Salcman (1985) and extended by Hanes et al. (1995; also see Thompson et al., 1996). Dr. Jeffrey Schall generously supplied the algorithm described in Hanes et al. (1995),

which we then adapted to suit our study. Briefly, we determined the response onset time for each trial independently. This entailed finding the first spike after test stimulus presentation for which the cell's activity deviated significantly ($p<0.05$) from the probability that it was drawn from the poisson distribution

$$P = e^{-rt}\sum_{j=1}^{\infty}\frac{(rT)^{i}}{i!}$$

where r is the mean firing rate for the cell, n is the number of spikes since test stimulus presentation, and T is the length of time since test stimulus presentation. The response onset time for each condition for a given cell was then taken as the median onset time for all trials of that condition. Because r is the mean firing rate for the cell, and because this included multiple epochs of activity throughout one trial – not just the activity evoked by the test stimulus – certain cells were not amenable to this analysis. For the 13 cells in which more than half the trials in one or more conditions did not show significant activation using this technique, each condition's trials were collapsed together before applying the Poisson algorithm (Thompson et al., 1996).

3 Results

212 cells were recorded from the operculum of primary visual cortex; 127 were well isolated, gave significant responses to visual stimulation, and were held long enough to make at least one meaningful statistical comparison. Of these 127 cells, 99 were recorded using standard-contrast stimuli and 28 were recorded using high-contrast stimuli (during the full orientation discrimination paradigm; some cells were recorded under both contrast conditions while assessing orientation tuning). The main analyses of attentional modulation were carried out on the standard-contrast results. While all of these 99 cells were tested for the effects of attentional location (attending-to and attending-away conditions), only 59 were tested for the effects of attentional task, i.e., they include the passive fixation condition, as well. To distinguish between these two populations, the superset of 99 cells is referred to as the AT set (for attending-**a**way and attending-**t**o), while the subset of 59 cells with all three attentional conditions is referred to as the PAT set (for **p**assive, attending-**a**way, and attending-**t**o). The 28 high-contrast cells were recorded in the first monkey, Ronald. Of the 99 cells in the AT set, 14 were recorded from Ronald and 86 were recorded from a second monkey, Scratchy. All 59 cells in the PAT set were recorded in Scratchy. Eye position data was collected only for Scratchy, and only for a subset of these cells. Where eye position analyses are concerned, the PAT set comprises 54 cells and the AT set comprises 64 cells.

EXAMPLE CELL

Effects of attention on mean firing rate

An example of a cell's responses to all three attentional conditions of the full orientation discrimination paradigm is shown in figure 5. Figure 5A shows the rasters for every trial, grouped by surround (none, parallel, and orthogonal) and attentional (passive, away, and to) conditions. Figure 5B shows the mean responses to the test stimulus in each condition, along with the associated standard errors.

While the bar graph in figure 5B more effectively illustrates the effect of attention on test stimulus responses, the rasters in figure 5A show a number of other significant characteristics. The cell demonstrated brisk responses to both the reference and test stimuli, and also a prolonged discharge lasting up to about 500 ms after reference stimulus offset; following the test stimuli, this off-discharge was truncated by termination of data collection once there was a behavioral response, but in any event it was not included in the data analysis period. This cell also demonstrated a slight modulation of activity following the offset of the cue stimulus (period C) in the attending-to conditions without an associated on-response. In the attending-to conditions, the cue (two degree diameter) circumscribed the excitatory region of the CRF, which was 0.86 degrees, and might therefore have encroached upon a weak off-surround region. Alternatively, there may have been a slight attentional modulation of baseline activity, a possibility investigated in more detail in a subsequent section.

The mean evoked responses (period D minus period A) are plotted as histograms in figure 5B. In each attentional condition, the parallel surround suppressed the cell's response relative to both the no surround and orthogonal surround conditions. This

corresponds to an orientation contrast effect (Knierim and Van Essen, 1992), where responses correlate to the perceptual saliency of the stimulus in the CRF.

For each surround condition, the attending-away responses were decreased relative to both the passive response and the attending-to response. An ANOVA showed that surround condition and attentional condition both significantly affected the cell's responses ($p<0.0001$), but attentional condition did not significantly affect surround modulation. Combining across surround conditions, the response when attention was engaged away from the CRF was decreased by 22% compared to passive fixation. When attention was directed to the CRF, responses were returned nearly to the passive fixation levels, increasing by a relative 23%.

Accounting for possible biases in eye position

While responses varied with attentional condition for this cell, it was possible that these changes were not due to attentional modulation, *per se*, but instead were due to small changes in eye position that covaried with attentional condition. For example, suppose that when the animal attended to the left hemifield, he biased his eye position slightly to the left, and when he attended to the right hemifield, he biased his eye position slightly to the right. As a result, the test stimulus might have fallen on different parts of the cell's CRF, as schematized in figure 6A, and thus elicited different responses. In fact, the example cell described in figure 5 did show slight but significant biases in both horizontal and vertical eye positions. The modal value of the horizontal eye position during the reference stimulus period (c.f. Methods) was shifted to the right by 2.2 arc-minutes when attention was directed to the right ($p<0.0001$), and vertical eye position was concomitantly shifted upward by 1.1 arc-minutes ($p<0.01$). However, even in the presence of eye position biases there might well be genuine attentional effect on cell

responsiveness, as schematized in figure 6B. That is, even though the stimulus might have excited different parts of the CRF, this difference in excitation may not account for all of the observed difference in response; this would indicate a change in the cell's overall responsiveness. One way to determine whether this is the case is to transform firing rate to a measure that can account for changes in eye position. This was achieved by modeling the spatial profile of the relevant part of the cell's CRF and using this model to address whether the magnitude of the response profile varied as a function of condition (c.f. Methods).

Figure 7 shows the example cell's reference stimulus responses plotted as a function of each trial's modal reference stimulus horizontal and vertical eye positions. These data were best fit by a plane that is more steeply sloped along the horizontal axis than the vertical axis (see Methods). A planar fit for the central part of the CRF is not surprising since the total range of eye position values (~15 arc-minutes) is a small fraction of the cell's 0.86 degree CRF diameter. The quality of this fit is easier to visualize using an analysis along just the horizontal eye position dimension, as shown in figure 8 (note that with the exception of figure 8 all data analyzed in this study used both horizontal and vertical eye position information in the manner described in the Methods).

Figure 8A shows the same data as figure 7 plotted as a function of horizontal eye position, alone, along with their associated receptive field model. After modeling the cell's CRF using the reference stimulus responses, this model was scaled by a gain coefficient to obtain a least-squares fit to each condition's test stimulus response. These gain coefficients were then used as an eye-independent measure of the cell's responses in lieu of the mean firing rate. Figure 8B shows the fit generated by these gain coefficients for the passive conditions (no surround, parallel surround, and orthogonal surround).

Comparing figure 5B with figure 8C shows that the nature of attention and surround modulation were little affected by taking eye position biases into account. In each attentional condition the parallel surround still suppressed the cell's response relative to both the no surround and the orthogonal surround conditions. Also, for each surround condition, the attending-away responses were still decreased relative to both the passive responses and the attending-to responses. Because only one gain coefficient was used to describe each condition's responses, though, no statistical test was applied to determine whether attention and surround had a significant effect at the single-cell level. Population analyses can be used to determine, statistically, whether the changes in mean firing rate of the type described in figure 5 are robust to considerations of eye position (see below).

POPULATION ANALYSES: PAT SET

Establishing that attention modulates evoked neuronal responses in V1 requires satisfying three criteria: first, that responses vary significantly as a function of attentional condition; second, that these differences are not attributable to biases in eye position; and third, that these differences are not attributable to changes in baseline firing rate. These changes in baseline firing rate could be either of pre-cue activity, which is subtracted from every trial, or of interstimulus activity, which could intrude upon the evoked response. The population analyses were initially restricted to the smaller though more comprehensive PAT set, of which the preceding example cell is a member. After the nature of this modulation has been established, they were then applied to the larger AT set.

Surround modulation

Knierim and Van Essen (1992) reported orientation-specific surround modulation in macaque V1. In that study, cells were placed into surround modulation categories, using as its criterion a response difference of one standard error. The categories that relate to this study include orientation contrast (or "popout," where responses in the parallel surround condition are less than those in either the no surround or the orthogonal surround conditions), uniform orientation (where responses in the orthogonal surround condition are less than those in either the no surround or parallel surround conditions), general suppression (where mean surround response is less than the no surround response and the cells do not belong to either of the two previous categories), facilitation (where mean surround response is greater than the no surround response), and no effect. Figure 9 shows how the PAT cells (n=59) in the present study were categorized: collapsing across attentional conditions, there were 26/59 (44%) orientation contrast cells, no uniform orientation cells, 14/59 (24%) general suppression cells, 6/59 (10%) facilitation cells, and 13/59 (22%) no effect cells.

Responses vary with attentional condition

Figures 10 shows the population analyses for the subtracted responses (raw response minus pre-cue baseline) of all nine conditions of the full orientation discrimination paradigm (PAT set, n=59). Figure 10A shows the mean responses for each condition; figure 10B shows these responses normalized by each cell's mean firing rate, making the modulations across cells easier to compare. Note that the ordinate does not go to zero in either panel A or in panel B, nor in many subsequent illustrations where small differences are being compared. The prominent orientation contrast effect is

immediately apparent, with mean responses being considerably smaller in the parallel surround conditions than in either the no surround conditions or in the orthogonal surround conditions. While the difference due to surround condition is the most pronounced, responses appear to be affected by attentional condition, as well, with smaller responses in the attending-away conditions (open circles) than in either the passive conditions (crosses) or in the attending-to conditions (closed circles). Consistent with these observations, a within-cell ANOVA demonstrated a main effect of surround ($p<0.0001$) and a main effect of attention ($p<0.01$); however, the interaction term did not approach significance. Thus, while cell responsiveness varied with attentional condition, surround modulation did not. Within individual cells, 41/59 (69%) showed significant main effects of surround and 11/59 (19%) showed significant main effects of attention [7/59 (12%) of these cells showed significant main effects of both surround and attention]; in none of the cells was the interaction term statistically significant. Because attention did not significantly affect surround modulation, subsequent analyses of the effects of attentional condition on the subtracted responses were collapsed across surround conditions, except where noted.

To examine the relative effect of attentional condition on cell responses, each cell was normalized by its response to a common condition, passive fixation (figure 10C). Compared to passive fixation, responses were decreased by 7% when attention was engaged away from the CRF ($p<0.01$). This decrease was relieved when attention was directed to the CRF (by a relative 15%, $p<0.01$; inset).

In figures 11 and 12, these effects are examined in more detail at the single-cell level by making separate comparisons of the effects of attentional task and of attentional location. Even though the mean responses shown were collapsed across surround conditions, the statistical significance of the main effect of attention for each cell was determined by an ANOVA that did not ignore surround condition.

Figure 11 illustrates the effect of engaging in an attentionally demanding task for the subtracted responses. In figure 11A, each cell's mean responses for the passive conditions and the attending-away conditions are shown as a pair of points connected by a line. The responses are plotted on a log scale, and significant main effects of attention between these two conditions are shown as filled circles. 10/59 (17%) cells showed a significantly decreased response in the attending-away condition compared to the passive condition, while only 2/59 (3%) showed significantly greater activity in the attending-away condition. Figure 11B shows the distribution of the pair-wise differences between the passive and attending-away responses for each cell. This reveals a significant decrease in the attending-away condition ($p<0.01$). Figure 11C shows the fractional differences for each cell's attending-away mean response relative to its passive mean response. The attending-away responses showed a median 5% decrease relative to the passive responses ($p<0.01$), compared to the 7% mean decrease in mean response shown in figure 10C.

Figure 12 illustrates the effect of moving the locus of attention on the subtracted responses. 11/59 (19%) cells showed a significantly increased response when attention was directed to the cell's CRF, while only 1/59 (2%) showed significant decrease. For the population, taking pair-wise differences between the attending-away and attending-to responses revealed a significant increase in the attending-to condition ($p<0.001$). Normalized by the attending-away condition, responses in the attending-to condition showed a median increase of 5% ($p<0.01$), compared to the 15% mean increase shown in figure 10C (inset). The discrepancy between these median and mean increases was due to a small number of cells with large increases (figure 12C).

Eye positions were biased by attentional condition

Figure 13 illustrates the mean eye position biases for all cells with eye position data (n=64). When attention was directed from the left hemifield to the right hemifield, horizontal eye position shifted in the same direction by a small but statistically significant 1.2 arc minutes on average. This shift was significant for the eye position data acquired for 31/64 (48%) cells, with only 1/64 (2%) instances of a significant shift in the opposite direction. Vertical bias was negligible over the population (0.2'), and it was statistically significant for the data of only 9/64 (14%) cells.

Response differences are not attributable to biases in eye position

Figure 14 directly compares attentional modulations as measured with mean firing rates (closed diamonds) to attentional modulations as measured with gain coefficients (open diamonds). Responses are collapsed across surround conditions. There was no significant effect of response type on attentional modulation, indicating that eye position biases did not account for the attentional differences in mean firing rate. The only effect of using gain coefficients instead of mean firing rate was a small but insignificant attenuation of task-related suppression; location-related modulation remained unchanged.

Figure 15 shows the mean gain coefficients for all nine conditions, without collapsing across surround conditions. Similar to the analysis of the mean subtracted responses in figure 10, figure 15A shows the mean gain coefficients for each condition; figure 15B shows these gain coefficients normalized by each cell's mean gain coefficient across conditions. These figures show that the effects as measured with gain coefficients are similar to the effects in figure 10, which were measured with the

subtracted responses. A within-cell ANOVA of these gain coefficient data demonstrated a main effect of surround ($p<0.0001$) and a main effect of attention ($p<0.05$) but not a significant interaction between the two. Again, because attentional condition did not significantly affect surround modulation, subsequent analyses of attention's effects on the gain coefficients collapse responses across surround conditions.

When each cell's responses were normalized by its passive condition (figure 15C), engaging in an attentionally demanding task (away from the CRF) significantly decreased responses by 5% ($p<0.05$). This was relieved when attention was directed to the CRF (by a relative 6%, $p<0.001$; inset).

Figure 16A shows the task-related effects at the single-cell level; statistical analyses were not done on individual cells because each cell had only one gain coefficient value for each condition. In figure 16B, the pair-wise differences show a significant decrease in the attending-away gain coefficients ($p<0.01$). The fractional differences, shown in figure 16C, show a median suppression of 5% ($p<0.05$) in the attending-away condition, consistent with the mean suppression of 5% shown in figure 15C.

Similarly, figure 17A shows the effect of moving the locus of attention on individual cells' gain coefficients. Pair-wise differences demonstrated a significant increase in the gain coefficients of the attending-to condition ($p<0.001$). The fractional differences, shown in figure 17C, show a median facilitation of 3% in the attending-to condition. As with the subtracted responses, this median facilitation is less than the 6% mean facilitation in figure 15C. Judging from the distribution of fractional differences in 17C, this, too, appears to be due to a small number of large facilitations.

Response differences are not attributable to changes in baseline

Pre-cue baseline

The preceding analyses were based upon the test stimulus firing rate (period G in figures 1 and 2) relative to the baseline firing rate before the cue (period A). If this pre-cue baseline changed with attention, though, differences in activity during the test stimulus period might have reflected a change in the amount of baseline subtracted rather than in responsiveness to visual stimulation.

Figure 18 shows the effect of attention on pre-cue baseline. Figures 18A and 18B illustrate the effect of attentional task, and figures 18C and 18D illustrate the effect of attentional location. The single-cell response pairs in figure 18A show that 4/59 (7%) cells had significantly increased pre-cue baseline when attention was engaged (away from the CRF) relative to passive fixation (figure 18A). This is not different from what would be expected by chance, and attentional task did not have a significant effect on pre-cue baseline over the population, either (figure 18B). Similarly, 5/59 (8%) cells showed a significant increase in pre-cue baseline when attention was then moved to the CRF, while only 1/59 (2%) showed a significant decrease (figure 18C). This increase was very small across the population (0.36 Hz), but it appeared to be statistically significant ($p<0.05$; figure 18D). However, a within-cell ANOVA across all three conditions indicated no significant modulation of pre-cue activity by attention.

Given that there was little or no effect of the attentional condition on the pre-cue baseline, whether or not this baseline was subtracted from test stimulus responses should have little effect on the aforementioned modulation. To determine if this were, in fact, the case, responses to all three attentional conditions, collapsed across surround conditions, were compared when both subtracting and not subtracting pre-cue baseline

(that is, comparing the subtracted and raw responses). As expected, raw responses (total firing rate) had significantly elevated firing rates relative to the subtracted responses ($p<0.0001$, figure 19A); however, attentional modulation remained unaffected (figure 19B).

This was supported by a within-cell ANOVA across all nine conditions using the raw responses, without collapsing across surround conditions. There was, as before, a significant effect of attention ($p<0.01$) and of surround ($p<0.0001$), but no significant effect of attention on surround modulation (figures 20A and 20B). Within individual cells, 43/59 (73%) showed significant effects of surround and 12/59 (20%) showed significant effects of attention [8/59 (14%) of these cells showed significant main effects of both surround and attention]; as with the subtracted responses, none of the cells had a statistically significant interaction between the two. Similarly, when each cell's raw responses were normalized by its raw passive condition (figure 20C), engaging in an attentionally demanding task (away from the CRF) significantly decreased responses by 6% ($p<0.01$). This was relieved when attention was directed to the CRF (by a relative 11%, $p<0.001$; inset).

Figure 21 illustrates the effect of engaging in an attentionally demanding task for the raw responses. 11/59 (19%) cells showed a significantly decreased response in the attending-away condition compared to the passive condition, while only 2/59 (3%) showed significantly greater activity in the attending-away condition. For the population, pair-wise differences revealed a significant decrease in the attending-away condition ($p<0.01$). Fractional differences show a median decrease of 5% in the attending away condition ($p<0.05$), consistent with the 6% mean decrease in figure 20C.

Figure 22 illustrates the effect of moving the locus of attention for the raw responses. 11/59 (19%) cells showed a significantly increased response when attention

was directed to the CRF, while only 1/59 (2%) showed significant decrease. For the population, pair-wise differences revealed a significant increase in the attending-to condition ($p<0.001$). Fractional differences show a median increase of 5% when attention was directed to the CRF ($p<0.01$). As before, because of a small number of cells showing large individual facilitations, this is about half the mean facilitation shown in figure 20C (inset).

Interstimulus baseline

The above analyses show that subtracting the pre-cue baseline did not have a significant effect on measures of attentional modulation. It remains possible, though, that attention could alter the amount of activity during the interstimulus period directly preceding the test stimulus (period E2); in turn, this change in interstimulus baseline might continue into the test stimulus period, and differences in activity during the test stimulus period may reflect a tonic change in cell baseline, regardless of visual stimulation (Desimone and Duncan, 1995).

To measure the effect of attention on interstimulus baseline, the cells' firing rates during the last 300 ms before helper ring and test stimulus presentations were compared across all three attentional conditions. A within-cell ANOVA demonstrated no significant effect of attention on interstimulus activity. Figure 23 shows comparisons of the interstimulus activity for both task-related (passive versus attending-away) and location-related (attending-away versus attending-to) conditions. When attention was engaged, away from the CRF, 4/59 (7%) cells showed a significant increase in activity, and 1/59 (2%) cell showed a significant decrease in activity. These numbers are not significantly different from what would be expected by chance, and the population difference between these two conditions was not significantly different from zero,

When attention was moved to the CRF, 3/59 (5%) cells showed a significant increase in activity, and 2/59 (3%) cells showed a significant decrease in activity. These numbers, too, are not significantly different from chance, and the population difference between the two conditions were not significantly different from zero. These data illustrate that interstimulus baseline does not vary with attention in V1.

Attention did not affect surround categorizations

Figure 24 shows the surround categorizations for all three attentional conditions in the PAT set. As would be expected from the above results, a chi-squared test showed no significant effect of attention on surround categorization.

POPULATION ANALYSES: AT SET

Surround modulation

Figure 25 shows how the AT cells (n=99) in the present study were categorized: collapsing across attentional conditions, there were 33/99 (33.3%) orientation contrast cells, 2/99 (2%) uniform orientation cells, 27/99 (27.3%) general suppression cells, 9/99 (9.1%) facilitation cells, and 20/99 (28.3%) no effect cells. A chi-squared test showed no significant difference between this distribution and that seen in the PAT set.

Response modulation by attentional location

Figure 26 shows the mean responses for all six conditions of the AT set (n=99). These include the three surround conditions attention directed away from the CRF and for

attention directed to the CRF. These values are shown for all three response measures: subtracted responses (figure 26A), gain coefficients (figure 26B), and raw responses (figure 26C). For all three response measures, a within-cell ANOVA demonstrated a main effect of surround ($p<0.0001$) and a main effect of attention ($p<0.01$ for the gain coefficients, $p<0.001$ for the other two). Under no conditions, though, was there a significant effect of attention on surround modulation.

Figure 27 illustrates in individual AT cells the effect of moving the locus of attention for the subtracted responses. 20/99 (20%) cells showed a significantly increased response when attention was directed to the cell's CRF, while only 3/99 (3%) showed significant decrease. For the population, pair-wise differences revealed a significant increase in the attending-to condition ($p<0.001$). Fractional differences showed a median increase of 7% in the attending-to condition ($p<0.001$) and a mean increase of 18% ($p<0.001$).

A similar result is obtained by analyzing the gain coefficients of the AT set (figure 28), where pair-wise differences demonstrated a significant increase in the attending-to condition ($p<0.001$). Fractional differences showed a median increase of 6% in the attending-to condition ($p<0.001$) and a mean increase of 18% ($p<0.001$).

Figure 29 illustrates the effect of moving the locus of attention for the raw responses of the AT set. 19/99 (19%) cells showed a significantly increased response when attention was directed to the CRF, while only 3/99 (3%) showed significant decrease. For the population, pair-wise differences revealed a significant increase in the attending-to condition ($p<0.001$). Fractional differences showed a median increase of 5% in the attending-to condition ($p<0.001$) and a mean increase of 16% ($p<0.001$).

The magnitude of these facilitations are similar to those seen in the PAT set; however, the significance levels are markedly higher. This is probably due to the increased sample size (99 cells versus 59 cells). Also, as with the PAT set, the mean

facilitations were markedly higher than the median facilitations because of a small number of cells with large attending-related changes in activity.

Neither pre-cue baseline (figure 30) nor interstimulus baseline (figure 31) was significantly changed between the two attentional conditions. 8/99 (9%) cells show a significant increase in pre-cue baseline when attention is directed to the CRF, and 3/99 (3%) cells show a significant decrease; 6/99 (6%) cells show a significant increase in interstimulus baseline when attention is directed to the CRF, and 2/99 (2%) cells show a significant decrease. Thus, confirming the results from the PAT set, responses in V1 are significantly facilitated when the locus of attention is brought to bear on a cell's CRF, and this facilitation can not be attributed to biases in eye position or changes in baseline activity. Also similar to the PAT set, attentional location had no significant effect on surround categorization (figure 32).

COMPARISON OF EFFECTS BETWEEN MONKEYS

As mentioned before, while the PAT set was drawn exclusively from Scratchy, the AT set was drawn from both monkeys (14 cells from Ronald, 85 cells from Scratchy).

Figures 33A and 33B show the mean responses for the attending-away and attending-to conditions for both monkeys. An ANOVA demonstrated no significant difference in attentional modulation between the two monkeys. Figures 33C and 33D show the mean responses for the three surround conditions for both monkeys. An ANOVA demonstrated a small but significant difference between the surround modulations. In Scratchy, as in the AT set when taken as a whole, both surround conditions suppressed responses relative to the no surround condition, though the parallel surround responses were more suppressed than the orthogonal surround

responses. In Ronald, though, these surround conditions suppressed responses equally relative to the no surround conditions.

These two sub-populations of the AT set were then examined to determine if the attentional effects differ significantly between the two monkeys. Figures 34A and 34B show the mean responses for all six conditions (the three surround conditions under both location-related attentional conditions) for Ronald. Unlike the entire AT set, a within-cell ANOVA revealed a significant main effect of surround ($p<0.001$) but not a significant main effect of attention; however, an ANOVA based upon the normalized responses did reveal a significant main effect of attention ($p<0.01$). The difference between these two results may be due to the small number of relevant cells recorded in Ronald. Neither analysis showed a significant effect of attention on surround modulation. For individual cells, 8/14 (57%) showed significant modulation by surround condition and 4/14 (29%) showed significant modulation by attention (3/13 (23%) showed both); only 1/14 (7%) cells showed a significant interaction between the two. Similarly, figures 34C and 34D show the mean responses for all six conditions for Scratchy. These, too, demonstrated a significant attentional effect on overall responsiveness ($p<0.0001$) but not on surround modulation. 50/85 (59%) cells showed a significant modulation by surround condition and 19/85 (22%) showed a significant modulation by attention [10/85 (11%) of these cells showed significant main effects of both surround and attention]; only 2/85 (2%) showed a significant interaction between the two.

TASK DIFFICULTY

To test whether task difficulty affected responses, we separated the task into relatively easy and difficult discriminations. Discriminations of 20 degrees were considered easy

(n=38, for the PAT set, n=59 for the AT set), while those of less than 20 degrees (median = 12 degrees) were considered difficult (n=24 for the PAT set, n=43 for the AT set). Note that each set comprised more cells than in the analyses above; this is because three cells (in both the PAT set and the AT set) were tested under both task difficulties (only the most difficult task condition tested in a given cell were used for the previous analyses).

Examining first the PAT set, an ANOVA indicated that task difficulty had no significant effect on either attentional modulation (figures 35A and 35B) or surround modulation (figures 35C and 35D). In fact, the magnitude of attentional modulation was slightly (though not significantly) smaller in the difficult task than in the easy task. This was also clear when examining the AT set: neither attentional modulation (figures 36A and 36B) nor surround modulation (figures 36C and 36D) was significantly affected by task difficulty.

TIME COURSE OF EFFECTS

We analyzed the time course of responses to ascertain whether attentional modulation was evident from the onset of neural responses or only after a delay. This also provides a means to compare the time course of modulations caused by attentional task with the time course of modulations caused by attentional location.

Figure 37A shows the population peristimulus time histograms (PSTHs) for all three attentional conditions of the PAT set. The population PSTH was derived by averaging together each cell's mean PSTH, where each trial is aligned to test stimulus onset and each cell is normalized by its overall mean test stimulus response. While the responses shown in this and the following figure were combined across surround conditions, statistics of onset times were calculated on the no-surround condition alone,

so that possible (though unlikely) differences due to surround modulation would not weaken whatever effect might be present. A within-cell ANOVA demonstrated that no-surround test stimulus response onset times were unaffected by attention. Response onset times were 53.5±3.7 ms for the passive condition, 53.9±3.4 ms for the attending-away condition, and 54.4±3.3 ms for the attending-to condition. An analysis of the AT set (figure 37B) revealed onset times of 49.1±2.5 ms for the attention-away condition and 48.7±2.7 ms for the attending-to condition. Similar to the PAT set, a paired test indicated that these distributions were not significantly different from one another. In all cases, the binned PSTHs achieved their half-maximal responses by 40 ms after stimulus onset.

The PSTHs in figure 37 are relatively noisy because they were constructed by constraining the data to 10 ms bins. Nonetheless, it is apparent that differences among curves are not pronounced until well after the onset of responses. This variability can be reduced by convolving each cell's PSTHs with a Gaussian (σ = 10 ms) before averaging them together. Figures 38A (PAT set) and 38C (AT set) show the result of this smoothing and allow for a more detailed investigation of each condition's time course.

The time course of location-related attentional facilitation can be examined by comparing the attending-away time course with the attending-to time course. Clearest in the AT set (figures 38C and 38D), the attending-away and attending-to responses diverged about 70-80 ms after test stimulus onset, well after the 30-50 ms response onset time. The difference between the attending-to and attending-away responses achieved near-maximal amounts by 90 ms, a level it sustained, for the most part, throughout the test stimulus period. While there appeared to be a mild effect in the opposite direction during the helper ring presentation, this was not significant.

The time course of the effect of engaging in an attentionally demanding task was largely similar to the location-related time course, except in sign (figures 38A and 38B).

Attending-away responses were clearly decreased relative to the passive responses by about 80 ms, quickly peaking by 100 ms and maintaining that level, within one standard error, throughout the rest of the response period. The attending-away response was slightly though visibly decreased relative to the passive response as early as 30-40 ms after stimulus onset; however, as noted before, there was no significant difference in their onset times.

CONTRAST

In initial recordings, stimuli were presented at high contrast, which left pronounced positive after-images to human observers. These were discontinued and were not used in attentional analyses; however, they did provide the opportunity to examine possible neural correlates of positive after-images that have been described psychophysically (Helmholtz, 1924).

An example of this contrast effect is shown in figure 39. Under standard-contrast conditions, the response to the test stimulus ceased relatively quickly, and the cell was quiescent during most of the one second interval between the reference stimulus display and the helper ring display (period E), when nothing but the fixation point was shown on the screen. Under high-contrast conditions, though, the firing rate was high throughout this period.

To examine the interstimulus period across cells, activity during this period was taken as the mean of its final 300 ms (period E2), and it was compared to the activity during the pre-cue period (period A). The AT set was used for standard-contrast activity, and only the attending-away conditions were analyzed (one condition had to be chosen to perform within-cell analyses). As a population, cells tested under high-contrast conditions demonstrated significant interstimulus period activation ($p<0.01$,

figure 40D). 14/28 (50%) of these cells reflected this significant activation while 3/28 (11%) showed a significant suppression (figure 40C). In comparison, stimuli of standard-contrast did not induce a comparable activation (figures 40A and 40B). In fact, 21/99 (21%) cells showed a significant suppression during the late interstimulus period, while only 2/99 (2%) showed a significant activation.

Nelson (1991) reported that, under his recording conditions, responses to a stimulus in V1 were typically unaffected by stimuli that precede it by more than 600 ms (only 8/79 cells showed suppression by stimuli preceding it by more than 600 ms). This relationship, though, is dependent upon stimulus contrast. To determine whether standard- and high-contrast stimuli differentially affect how paired stimuli interact, reference stimulus activity was compared to test stimulus activity. Only those trials where the reference and test stimuli were identical were used, i.e., match conditions with no surround stimulation; as before, analyses were restricted to the attending-away condition. Under standard-contrast conditions, the cell population showed no significant difference between reference and test stimulus activation (figure 41A; though individually, 9/99 (9%) cells showed a significant suppression of test stimulus activation and 4/99 (4%) cells showed a significant activation). Under high-contrast conditions, test stimulus responses were suppressed relative to the reference stimulus responses ($p<0.05$, figure 41B; this was reflected in 2/28 (7%) cells).

Because high-contrast stimuli so dramatically affect responsiveness, the present attentional analyses were performed upon standard-contrast responses alone. However, when these analyses were repeated on the high-contrast conditions, the results were not significantly different from those seen in the standard-contrast conditions.

4 Discussion

The results of this study demonstrate that neuronal responses in V1 can be modulated both by attentional task and by the location of spatial attention. This modulation could not be attributed to systematic biases in eye position, and it was mediated through the stimulus driven responses without affecting baseline activity. The facilitation seen as a function of attentional location may have been apparent only because engaging in an attentionally demanding task elicited an initial suppression. Furthermore, these effects may be mediated through similar mechanisms, a hypothesis that is supported by the activation time courses and that helps explain the present results in the context of previous V1 attentional studies. These attentional modulations did not interact with surround modulations, though further explorations of attention's interaction with V1 surround modulations may be warranted. High contrast stimuli caused extended interstimulus period activity and paired-pulse suppression, perhaps corresponding to their associated positive after-images.

ATTENTIONAL MODULATION IN V1

Effect of attentional location

The results of the present study confirm the suggestion by Motter (1993), that the location of attention can have significant effects on V1 responses. He reported 24/96 (25%) cells showing a significant response increase when attention was directed to the CRF and 10/96 (10%) cells showing a significant response decrease. In the present

study, the ratio of cells showing significant facilitation versus significant suppression was notably higher (20:3 in the AT set, 11:1 in the PAT set). More importantly, the present study indicates that the changes in responses with attentional condition are not attributable to eye position biases, a potentially critical confound in Motter's results.

Small biases in eye position did exist in the present experiments. After compensating for their effects, though, all comparisons that were statistically significant using mean firing rates remained significant using the post-compensated gain coefficients; however, the magnitude of attentional modulation was affected by the analysis method. Task-dependent suppression was somewhat attenuated when the data were analyzed using the gain coefficients, as was the location-dependent facilitation. These differences represent the upper bound of eye position contributions to condition-related changes, since there may be an incidental covariance between the two.

In both the present study and Motter (1993), V1 responses are significantly affected by the location of attention; however, a number of other studies have failed to find evidence of this modulation. This difference in results can be accounted for by differences in behavioral task.

In Wurtz and Mohler (1976), V1 responses did not depend upon whether the stimulus in the CRF dimmed or the stimulus outside the CRF dimmed; however, the monkey was rewarded for releasing the response bar when either stimulus dimmed, regardless of its spatial location. As such, the task was essentially a spatially non-specific detection task, since the non-dimming stimulus did not have to be ignored to perform the task correctly. In addition, trials were blocked by which stimulus would be dimmed, making its detection even easier.

While Luck et al. (1997) showed attentional modulation in V4 and V2 using a shape detection task, they did not see attentional modulation in V1. Only one distracter stimulus was displayed at any given time, though, which may have made the task too

easy to elicit V1 modulation. Similarly, Moran and Desimone (1985) had monkeys perform a same-different task with only one simultaneously presented distracter, and they did not elicit V1 modulation. Unfortunately, it is not clear what discrimination Moran and Desimone (1985) had their monkeys perform. In one of the study's examples, the monkeys performed an easy, 90 degree orientation discrimination; however, the text indicates, without further detail, that other forms of discrimination were used as well.

The tasks that did either suggest or demonstrate attentional modulation in V1 typically involved a difficult discrimination. Motter's (1993) task involved an orientation discrimination in the presence of multiple distracters. Gandhi et al. (1998), who demonstrated attentional effects in humans, made their motion discrimination difficult enough to maintain only 78% correct performance. Similarly, Worden and Schneider (1996) saw attentional modulation in human V1 only when the discriminandum was presented with a field of distracters, and this effect was augmented when the distracters were similar in form to the target.

The attentional modulation described in the present study is consistent with these results. The task was a difficult orientation discrimination (never greater than 20 degrees, often 12 degrees or less) in the presence of full-field distracters. While these distracters were not displayed on one-third of the trials, surround condition was randomized – the monkey could not tailor his attentional effort to surround condition, but rather could expect that these distracters were likely to appear on any given trial.

Perhaps the most striking example of task dependence, the ERP experiments that did not show V1 modulation were, uniformly, sequential presentation tasks, i.e., only one stimulus was displayed on the screen at any given time (Mangun et al., 1993; Gomez Gonzalez et al., 1994; Heinze et al., 1994; Clark and Hillyard, 1996). Simultaneous presentation of two or more stimuli has been shown to be important for

eliciting marked attentional modulation in V4 (Luck et al., 1997). If the demands of a sequential task are too low to require strong modulation in V4, they are unlikely to require modulation as early as V1.

Effect of attentional task

Relative to passive fixation, responses in the present study were suppressed when the monkey engaged in an attentionally demanding task and attention was not directed to the cell's receptive field. This is in contrast with Wurtz and Mohler (1976) and Boch (1986), where engaging in a more demanding task facilitated responses to receptive field stimuli.

The facilitation seen by Wurtz and Mohler (1976) and Boch (1986) are likely due to concomitant increases in arousal. In the present study, this facilitation may have been absent because the level of arousal was unlikely to have changed during the passive fixation trials. These were interleaved as blocks of six trials within blocks of 24 trials where attention was actively engaged, leaving little time for gross changes in the animal's overall alertness. This may be similar to the V4 responses in Mountcastle et al. (1987), where responses were no different during trials of an active fixation dimming task than between them.

That there is a task-related suppression, instead of simply no change in response, may be a way of slightly but significantly increasing the cell's dynamic range when attention is engaged. The suppression in the present study was around 7%, far smaller than the changes in dynamic range seen in other cells, e.g., photoreceptors, or even in V1 cells when analyzed for contrast gain control (Ohzawa et al., 1985; Heeger, 1992). Thus, it remains to be seen whether this change is functionally significant; however, even modest response differences at the single-cell level can have significant

implications if consistent across a large population of cells (Georgopoulos et al., 1986; Gochin et al., 1994), an idea obviously relevant to neuroimaging studies. For example, Corbetta et al. (1991), using PET, saw an increase in V1 blood flow when selective attention was engaged; however, it remains undetermined whether this reflects an arousal-related facilitation, as seen in Wurtz and Mohler (1976) and Boch (1986), or whether it reflects an active suppression, as seen in the present study.

A task-related suppression similar to that seen in the present study was reported in V4 by Spitzer et al. (1988). Single-unit responses in area V4 were evoked by oriented stimuli displayed to the cell's CRF while the animal performed either a very easy or a difficult orientation discrimination outside the CRF. Responses demonstrated a median suppression of 7% when the monkey was engaged in a difficult task relative to when he was engaged in an easy task. Because of the relative task difficulties in their study, these conditions are analogous to the present study's attending-away and passive conditions, respectively, and as such the similarity between the Spitzer et al. (1988) result and the results of the present study are striking. The task-related suppression seen by Spitzer et al. (1988) may also represent a small increase in the cells' dynamic range, since when attention was then directed to the cell's CRF, response facilitation was notably larger in the difficult task than in the easy task.

This small increase in dynamic range may also explain why Haenny and Schiller (1988), contrary to their stated conclusions, reported evidence suggestive of attentional modulation in V1 with a relatively easy task. Responses to a cell's preferred grating were facilitated when the monkey attended to the preferred grating's orientation, but not when the monkey attended to the orthogonal orientation. Before this facilitation, though, responses were suppressed by repeated presentations of this preferred stimulus. This apparent attentional modulation disappeared when the facilitated response was compared with the original non-habituated response. The relationship between

habituation and attentional modulation was even more striking in V4, where the two were statistically correlated (though in V4, attention facilitated activity beyond the original non-habituated responses). Haenny and Schiller draw a distinction between "dishabituatory effects and true modulation." The results from the present study suggest that habituation in their study may be what allows the "true modulation" to be revealed.

An alternative explanation for this suppression is provided by Rees et al. (1997b), who used fMRI to demonstrate a similar relationship between attentional tasks and V1 responsiveness. Subjects performed either an easy or difficult linguistic task at the center of gaze while moving dots were shown in the periphery. Similar to the present study, V1 responses to the moving dots were greater during the easy task, which was not very attentionally demanding, than during the harder, more attentionally demanding task. In Rees et al. (1997b), though, the decrease in V1 responses to the moving dots during the difficult linguistic task may not be strictly a means of increasing peripheral V1's dynamic range; rather, it may reflect a difference in the amount of attention devoted to the peripheral stimuli. Rees et al. (1997b) suggest that when involved in an easy task at the fovea, one's "leftover" attentional resources automatically settle on non-task related stimuli, facilitating the associated responses.

This was further illustrated by Rees et al. (1997b) using the waterfall effect. When one views coherently moving stimuli for a period of time, a static display will appear to be moving in the opposite direction (Wohlgemuth, 1911). The cortical signal generating this effect can be imaged using fMRI (Tootell, 1995), and the strength of this illusion is affected by how much attention is devoted to an unrelated attentional task (Chaudhuri, 1990). Rees et al. (1997b) have shown that when attention is actively engaged by a difficult linguistic task at the center of gaze there is a decrease in the motion aftereffect signal as early as V1. It remains possible, then, that in the passive

task of the present study, attention is partially directed to the stimulus in the CRF, facilitating responses relative to when attention is actively engaged away from the CRF.

If the increased passive response were due to attentional spill-over, it should be evenly between the attending-away and attending-to magnitudes, as attention would be evenly split between the two locations. Contrary to this hypothesis, though, the magnitude of the passive responses is indistinguishable from the magnitude of responses when attention is directed to the cell's CRF. This would suggest that the task-related modulation reflects a veridical suppression. That the two modulations' time courses are not significantly distinguishable from one another indicates that the location-related facilitation may be acting to directly relieve this suppression.

Surround effects

Responses in this study were significantly modulated by surround condition, and this modulation depended upon the orientation of the surround. This is consistent with the orientation-dependent surround modulation described by Knierim and Van Essen (1992). Though the tasks and stimuli used in these studies were different from one another, the fraction of cells showing the various surround effects were very similar.

Of particular interest to the present study were the orientation contrast cells, which are primarily suppressed when the CRF stimulus was part of a homogeneous texture. Knierim and Van Essen (1992) suggested that these cells may be involved in mediating the pop-out effect, where perceptually salient stimuli automatically draw attention to their location (Treisman and Gelade, 1980).

While orientation specific surround modulations in V1 may be involved in drawing attention, they are not, themselves, significantly affected by its presence or locus in the present study. Previously reported preliminary results (Press et al., 1994)

described a significant effect of attention on surround modulation; however, this inference depended upon a method of selecting cell classes that biased the resulting analyses by a regression to the mean. The present study uses all available cells of a given population in all analyses, thereby avoiding this confound.

Task difficulty

As described above, task difficulty seems to be the single most important determining factor for seeing attentional modulation in V1. However, within the context of the task used in the present study, differences in task difficulty appears not to affect V1 responses differentially. This is in apparent contrast to higher cortical areas, such as V4 (Spitzer et al., 1988) and IT (Spitzer and Richmond, 1991).

Spitzer et al. (1988) recorded responses in V4 using an orientation discrimination paradigm similar to the one used in the present study. They found that difficult discriminations (22.5 degrees) facilitated V4 responses relative to easy discriminations (90 degrees). In the present study, difficult discriminations (less than 20 degrees) elicited statistically indistinguishable V1 responses from easy discriminations (20 degrees). One possible explanation for this difference is that the hard and easy designations are not comparable between the two studies. The easy task in the present study is more difficult than the hard task in Spitzer et al. (1988). Thus, the attentional modulation may be maximal for even a 20 degree discrimination. While this may be true within V1, an eight degree discrimination and a 12-16 degree discrimination will elicit distinguishable levels of attentional effort in humans, as measured by differences in stimulus discriminability (Urbach and Spitzer, 1995).

An alternative and perhaps more likely explanation relates to the method of training and recording used in the present experiment. Because of the number of

conditions and repetitions required in the present study, easy conditions and difficult conditions were seldom both tested on a given single cell. Furthermore, most difficult-discrimination cells were recorded after the monkey had extensive training on the orientation discrimination task, while easy-discrimination cells were typically recorded earlier in the animal's experience with the task. Thus, the "difficult" discrimination trials and "easy" discrimination trials may have represented similar task difficulties when the data were collected. In conjunction with the manifold less controlled variables relating to the monkeys motivation and state of mind (such as level of frustration and level of hydration), these factors render the lack of modulation with task difficulty difficult to interpret.

EFFECTS ON BASELINE ACTIVITY

The analyses described in the present study distinguish between two means by which responsiveness in V1 could be affected by attention: response modulation and baseline modulation. The results indicate that attentional modulation in V1 is effected by changing stimulus-evoked responses without changing baseline activity.

When attention is directed to the CRF, pre-cue baseline is not significantly changed relative to when it is directed to the opposite hemifield. Attentional task has a similar lack of effect on pre-cue baseline, eliciting no significant difference between passive fixation and engaging attention away from the cell's CRF.

In contrast, Luck et al. (1997) demonstrated significantly different response modulations depending upon whether baseline activity was subtracted from the response period. This suggested that what response modulation they seemed to see was, in fact, due to modulation of the baseline activity. In the present study, though, subtracting pre-cue baseline did not significantly affect attentional analyses of stimulus-evoked

responses. In addition, attention had no effect on the interstimulus period activity, which preceded the test stimulus response and was most analogous to the baseline period subtracted by Luck et al. (1997).

The results of the present study suggest that if biased competition plays a role in visual attention, it is not evident at the level of V1. Rees et al. (1997a) showed that while inferotemporal cortex demonstrated both response and baseline modulations, only dorsolateral frontal cortex (area 8) demonstrated attentional modulation without a significant activity-response relationship. This indicated a bias signal that was fedback from prefrontal cortex to earlier visual cortex. In contrast, the present study indicates only stimulus-related modulations within V1, suggesting that the extent of this fedback bias signal is limited. The inability of Luck et al. (1997) to see response-related modulations, on the other hand, suggests that processing related certain tasks can be performed using only shifts in baseline activity, without the modulations of visual responses seen in this and a number of other studies outlined above.

The response time courses also demonstrate that, in V1, attention modulates the stimulus-evoked responses and not the baseline activity. Significant attention-related differences are not seen until about 80 ms after test stimulus onset. This is over 30 ms after response onset, indicating that attention does not exert an influence on cell activity until well after it has begun responding to a stimulus.

Another question addressed by the time course information is whether the speed of processing, at the level of V1, is affected by attention. One of the posited effects of spatial attention is to accelerate visual processing near the attentional locus (Sternberg and Knoll, 1973; Maylor, 1985; Stelmach and Herdman, 1991). A recent, striking example was described by Hikosaka et al. (1993a, 1993b, 1993c). Using an illusion first discovered by Kanizsa (1951), they found that an abrupt-onset line segment does not appear abruptly if spatial attention is first oriented near its location; rather, it seems to

grow away from the attended location. Thus, if a line segment were displayed directly to the right of the locus of attention, it would appear to grow away from that location, to the right.

If this effect were due to a difference in processing time at the level of V1, it should be reflected as a difference in latencies for stimuli presented at different distances from the attentional locus. In the present study, though, response latencies were indistinguishable across attentional conditions. This would seem to suggest that if processing proximal to the attended location were accelerated, it is not due to changes at or before V1.

A likely location for this accelerated processing to be effected is visual area MT. The line-motion illusion depends upon the magnocellular system (Steinman et al., 1997), which constitutes the predominant input to MT. In addition, apparent motion can be used to null the attention-induced effect (Miyauchi et al., 1992). This apparent motion is induced by displaying the line as growing in some direction with a given velocity instead of as a single sudden-onset stimulus. The results of the present study are consistent, then, with Newsome et al. (1986), who demonstrated that MT, but not V1, is able to represent high-velocity apparent motion.

THE SOURCE OF ATTENTIONAL MODULATION

The results of the present study show that attention significantly modulates responses in V1; however, while the modulations are significant, the magnitudes are relatively small. Selective attention must decrease the amount of information available to the visual system by one or two orders of magnitude (Van Essen et al., 1991). This, along with the substantial physiological evidence for larger modulations throughout the ventral

stream, support a multistage model of attention, where visual processing throughout the ventral stream is modulated, in parallel, by some attentional control.

The most likely location of this attentional control is within the pulvinar (c.f. Introduction). The pulvinar has extensive connections with the entire ventral stream, from V1 through IT (Benevento and Rezak, 1976; Ogren and Hendrickson, 1977; Rezak and Benevento, 1979), as well as reciprocal connectivity with area 7a in parietal cortex (Baleydier and Mauguiere, 1977; Baleydier and Morel, 1992). Responses in both 7a and its reciprocal target in the pulvinar, Pdm, are modulated by covert detection tasks (Bushnell et al., 1981; Goldberg and Bruce, 1985, Petersen et al., 1985; Steinmetz et al., 1994; Robinson et al., 1995). And the inferior pulvinar, which along with the lateral pulvinar projects to V1, receives substantial projections from the superior colliculus, a structure that may be important for exogenously shifting spatial attention (Robinson and Kertzman, 1995).

There are a number of issues that remain to be resolved before this model can be accepted, though. First, while lesions of the inferior pulvinar significantly interfere with pattern discrimination (Chalupa et al., 1976), responses within the inferior pulvinar have not been shown to be modulated by attention (Petersen et al., 1985). The apparent absence of attentional modulation in the pulvinar may reflect the task used to probe it, a dimming detection task; nevertheless, such modulation must be demonstrated before the pulvinar's role in spatial attention can be accepted.

Another caveat to the pulvinar's role in visual attention is how the various nuclei interact with one another. Both the inferior and lateral pulvinars, which each contain a retinotopic representation of the visual field, project to the entire ventral stream. It is Pdm, though, that reciprocally connects with parietal cortex and whose responses have been shown to be modulated by spatial attention. Pdm lays outside either of these retinotopic maps, and the connectivity between different regions of the pulvinar are

notably sparse. One way in which different regions of the pulvinar could interact is through the overlying reticular nucleus. All projections into and out of the pulvinar pass through the reticular nucleus and make collateral connections. Inhibitory cells in the reticular nucleus, in turn, project into the pulvinar. Because the pulvinar's innervation of the reticular nucleus is diffuse, the reticular nucleus provides a means by which different nuclei of the pulvinar can influence one another. Again, physiological evidence of such interactions is needed before the pulvinar's role in mediating visual attention can be determined.

PROBING FOR ATTENTION IN V1

The magnitude of attentional effects reported in the present study are relatively small, on the order of 5%-15%. The question remains whether this modulation is typical of V1 processing or whether larger modulations could be evoked with different tasks.

One hypothesis developed in the preceding discussion, for example, is that the 15% facilitation seen when attention is directed to a cell's CRF is apparent only because engaging in an attentionally demanding task first suppressed the cell's responsiveness. Without this suppression, the attending-away response might have been maximal, leaving no room to demonstrate a location-related facilitation. The attentional modulation seen by Haenny and Schiller (1988) seems to support this hypothesis, as the facilitation they saw in V1 seemed to be dependent upon the cell's responses being habituated by repeated stimulus presentations. In the present study, the "standard contrast" stimuli were, for the most part, of relatively high contrast. An experiment that might elicit larger facilitations in V1, then, would be to use low contrast stimuli. Characterizing V1 attentional modulations at a number of different contrasts would provide a direct test of this hypothesis.

Another means to reveal larger attentional modulations in V1 might be to use a motion discrimination task. V1 is the principal source of input to area MT, which processes stimulus motion, and preliminary fMRI experiments using motion discrimination show V1 modulations greater than 20% (Ghandi et al., 1998).

Finally, another experiment that might reveal large modulations in V1 is one that examines the interaction between figure-ground processing in V1 and selective attention. In contrast to the oriented-bar stimuli used in the present study, Lamme (1995) and Zipser et al. (1996) described responses to textured stimuli in V1 that appear to be directly related to figure-ground segregation. Lamme (1995) presented dense textured arrays of oriented lines or moving dots that had one region contrasting in motion or orientation from the background. Responses in V1 were facilitated when the cell's CRF was within the figure but not when it was within the ground. Similarly, Zipser et al. (1996) used dense oriented line textures to the same effect, defining the figure region by one of a number of cues, including disparity, color, luminance, and orientation. Almost three quarters of all cells were significantly affected by whether the CRF was within the figure region, and one sixth of these modulations were cue-independent. These figure-ground modulations typically developed between 30 and 40 ms after response onset; the example shown in Lamme (1995) had a latency of almost 100 ms.

The results of Lamme and colleagues suggest that V1 interacts with higher visual cortices to mediate figure-ground segregation. This is supported by these modulations' disappearing under anesthesia (Lamme et al., 1998). These stimuli, then, would be excellent candidates for further investigating the role of V1 in mediating visual attention, examining the physiological interaction between selective attention and figure-ground segregation.

CONTRAST

In the present study, high-contrast stimuli resulted in after-discharges more consistently than the lower, standard contrast stimuli. This was evident as late as 700-1000 ms after stimulus offset. Duysens et al. (1985) reported shorter after-discharges than those seen in the present study (102-221 ms median duration, depending upon stimulus orientation). This may be due to their using an anesthetized preparation, while the monkeys used in the present study were awake and alert. Alternatively, this difference may, in part, be due to their method of measuring response duration; the figures illustrating response time courses in Toyama et al. (1977) and Duysens et al. (1985) appear similar to those seen here.

High contrast also temporarily decreases subsequent contrast sensitivity (Georgeson and Georgeson, 1987). Of particular relevance to the present study, Nelson (1991) demonstrated that displaying an oriented bar at a cell's receptive field suppressed responses to subsequent bars of the same orientation. This suppression was contrast dependent and, in a small number of cells, lasted over one second. The results in the present study bear this out. Responses to a second stimulus of the same orientation presented one second after the reference stimulus were significantly suppressed when using high contrast stimuli, but not when using low contrast stimuli. Interestingly, a smaller percentage of individual cells showed this suppression in the high-contrast condition, though the population effects were notably larger.

CONCLUDING REMARKS

Many previous studies have failed to show modulation of V1 responses by spatial attention. One exception is Motter (1993), though he neither reported the magnitude of these modulations nor controlled for possible critical confounds caused by biases in eye position. The present study provides evidence that spatial attention significantly modulates V1 activity and that this modulation can not be attributed to covariant biases in eye position. Visual processing at this earliest stage of cortical processing is affected by behavioral state; however, the functional significance of these effects remains to be determined.

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Figure 1. The orientation discrimination paradigm used to direct attention and elicit responses in primary visual cortex (V1). This was only performed after the classical receptive field (CRF, dotted circle) had been mapped while the animal passively fixated. **A**. The animal began every trial by fixating a small fixation point and depressing the response lever. **B**. A cue, shown for 200 ms, indicated that attention was to be directed to the cell's CRF. It could also be shown in the opposite hemifield or not be shown at all (for passive trials). **C**. The cue disappeared and nothing was shown for one second. **D**. Reference stimuli were then shown for 300 ms at both possible attention locations (at the CRF and in the opposite hemifield). **E**. These were removed and nothing was shown for one second; this is referred to as the interstimulus period. Then, **F**. helper rings were shown at both possible attention locations for 200 ms, followed immediately by **G**. test stimuli for 300 ms at both locations. These were shown either alone (like the reference stimuli), surrounded by parallel oriented bars, or, as in this example, surrounded by orthogonally oriented bars. The orientation of each test stimulus was either the same as the reference stimuli or rotated by the amount of discrimination (which varied between 6 degrees and 20 degrees). After the test stimuli were removed, **H**. the monkey had to release the response lever within 700 ms if the reference and test stimuli *at the cued location* were different orientations. Otherwise, the lever had to be held down for one full second.

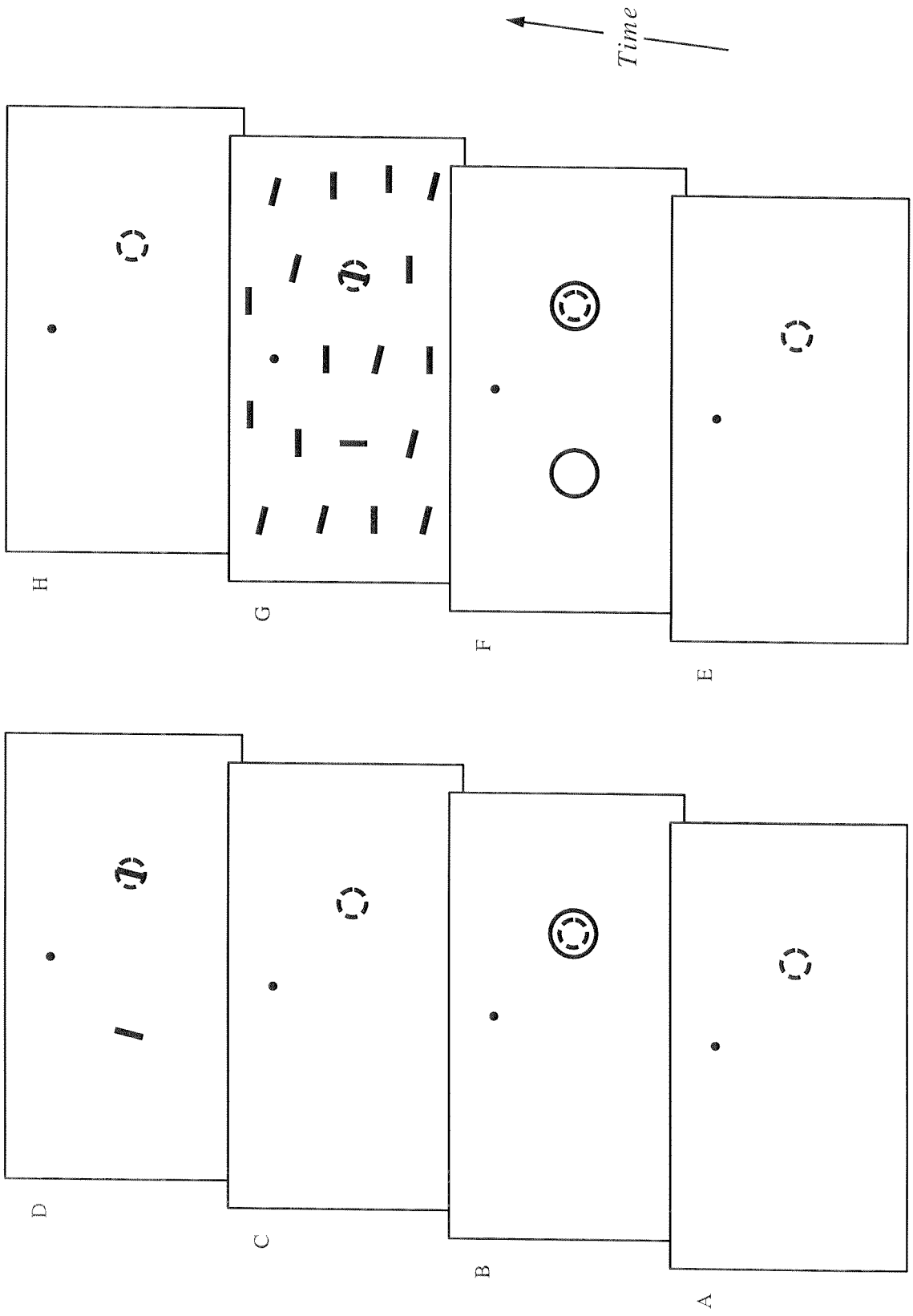

Time
A
B
C
D
E
F
G
H

Figure 2. The time course of the behavioral paradigm. Eye position was measured, and often recorded, throughout each trial. The monkey had to fixate throughout each trial within a 40 arc-minute window about the fixation point. This was substantially larger than a typical V1 receptive field. Most analyses in this study drew from responses during the test stimulus period, indicated by the gray swath. The one second interstimulus period is divided into two sub-periods for some analyses: the first 700 ms, period E1, and the last 300 ms, period E2.

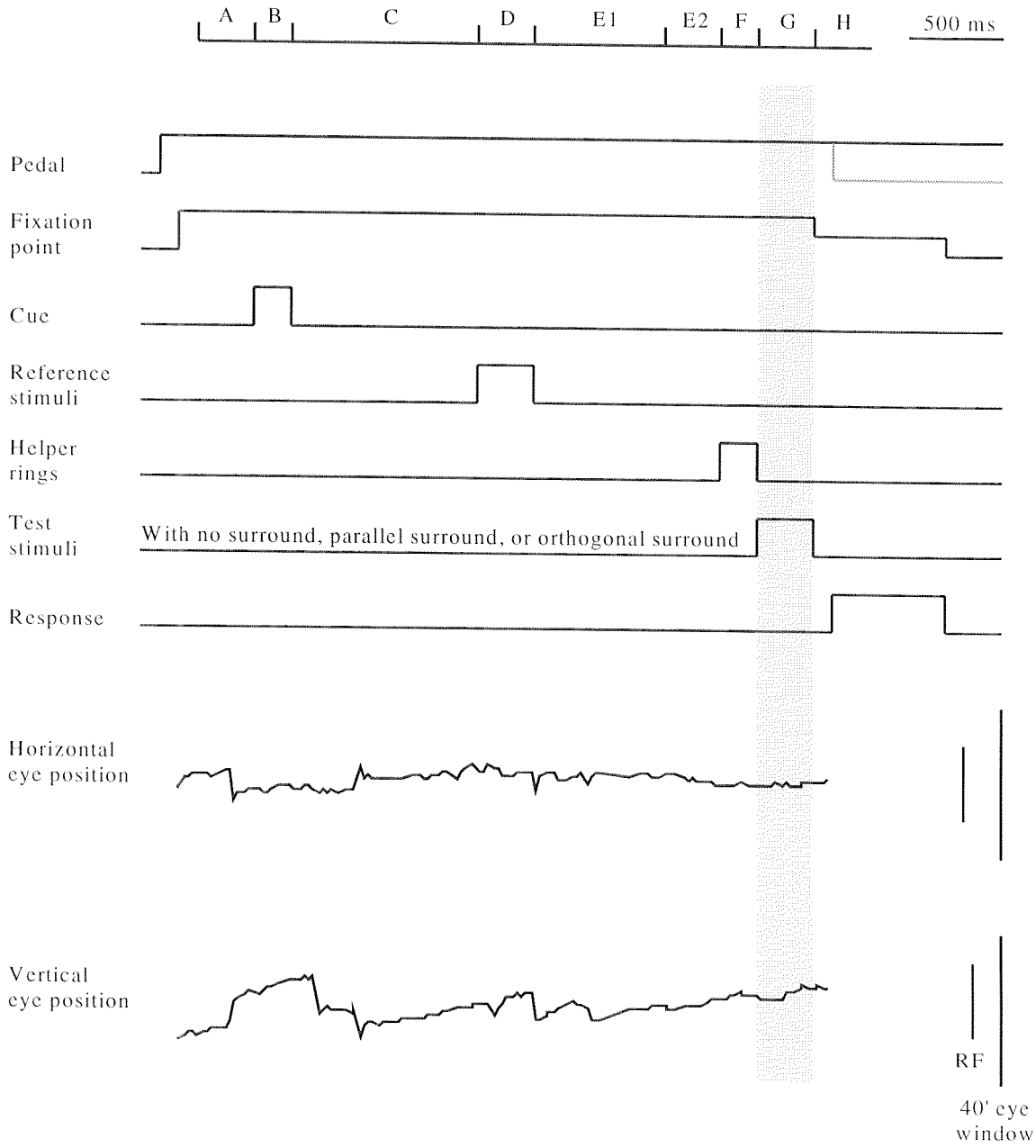
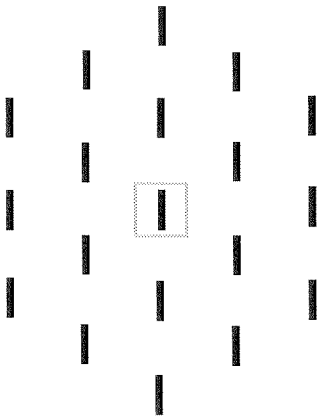

A
B
C
D
E1
E2
F
G
H
500 ms
Pedal
Fixation point
Cue
Reference stimuli
Helper rings
Test stimuli
With no surround, parallel surround, or orthogonal surround
Response
Horizontal eye position
Vertical eye position
RF
40' eye window

Figure 3. The test stimulus shown at the CRF can be shown either alone, surrounded by parallel bars, or surrounded by orthogonal bars. The spacing of this hexagonal array ranged from 1 to 2.6 degrees (median = 1.9 degrees). Though not shown in this figure, half of the surround bars, chosen at random every trial, were rotated by the amount of the discrimination. Thus, the relationship between the test stimulus and the surround stimuli could not be used to perform the discrimination task; attention had to be directed to the cued location.

No surround

Parallel surround



Orthogonal surround

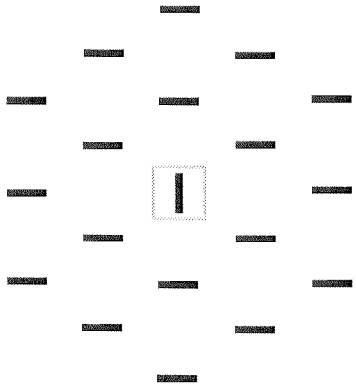


Figure 4. After isolating a cell, its orientation tuning was assessed. The peak response for this cell was elicited by a vertical bar (90 degrees). The stimulus orientations during the main discrimination task were chosen to fall on either side of this point. Thus, if the discrimination were 12 degrees, the orientation of the reference stimulus and the matching test stimulus would be 84 degrees, while the orientation of the nonmatching test stimulus would be 96 degrees.

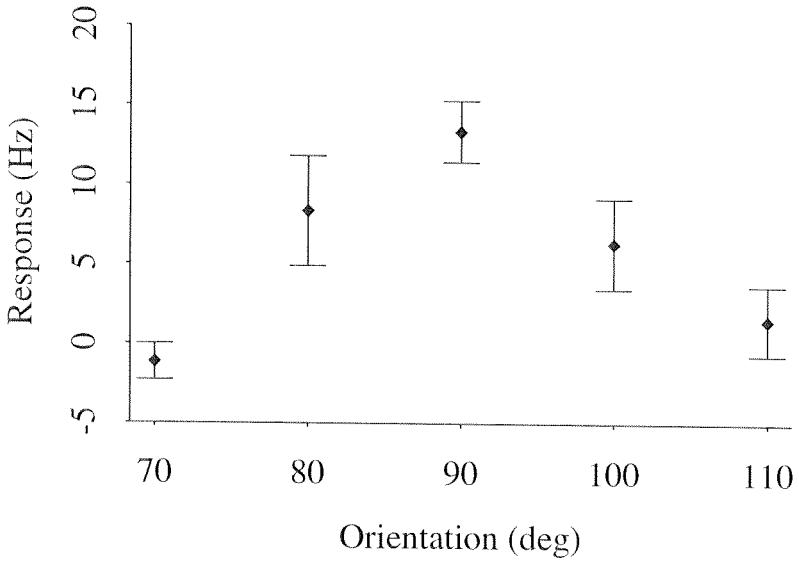
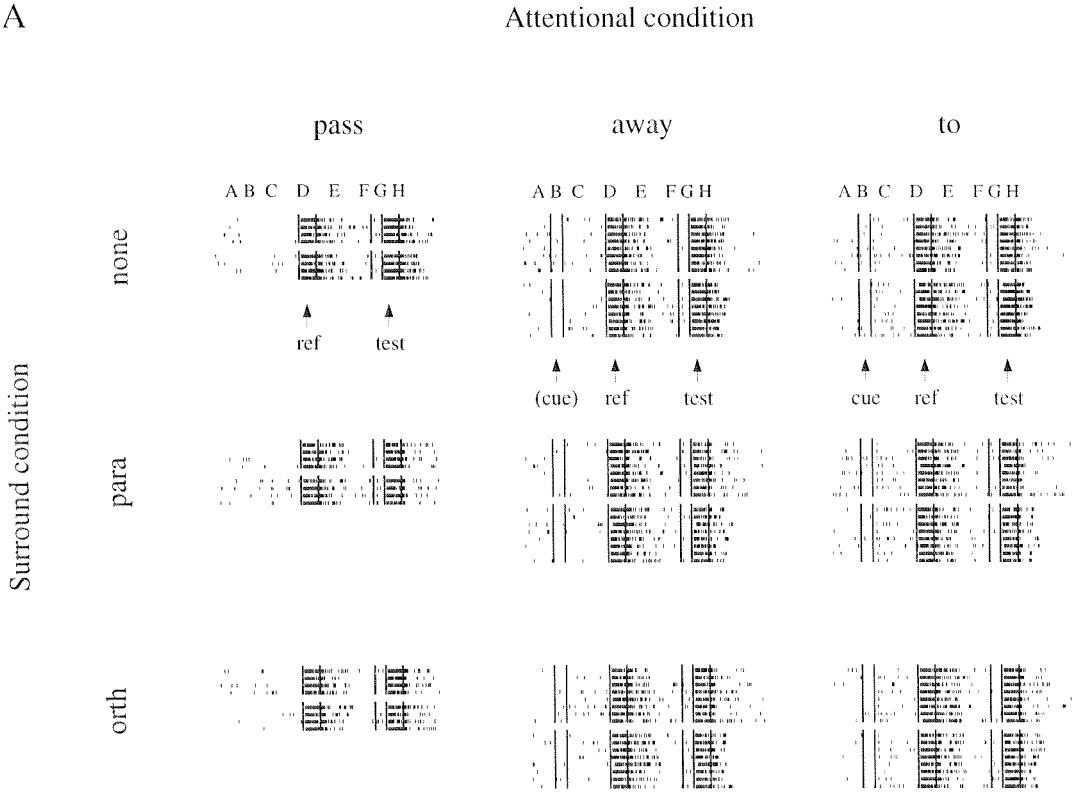

Response (Hz)
-5
0
5
10
15
20
70
80
90
100
110
Orientation (deg)

Figure 5. An example of a cell's responses during the orientation discrimination task using standard-contrast stimuli. **A**. Rasters under all nine combinations of attention and surround conditions. Each condition is grouped into match trials (shown first) and non-match trials (shown second, following a small vertical space). Every spike is shown as a small vertical tick. The connected vertical bars represent stimulus onsets and offsets; there are seven such events (five for the passive condition, where there is no cue): cue onset, cue offset, reference stimulus onset, reference stimulus offset, helper ring onset, helper ring offset and test stimulus onset (these are simultaneous, and thus constitute one event), and test stimulus offset. Note that the cue shown in the attending-away condition is displayed in the hemifield contralateral to the CRF. The epoch A-H, as defined in figures 1 and 2, are shown at the top of each column. **B**. Mean responses for each condition, with standard error bars. For each attentional condition, the parallel surround response (striped bar) was suppressed relative to either the no surround (unfilled bar) or orthogonal surround (filled bar) responses. For each surround condition, the attending-away response was decreased relative to both the passive and attending-to responses.

Cell 04.49.03

A



B

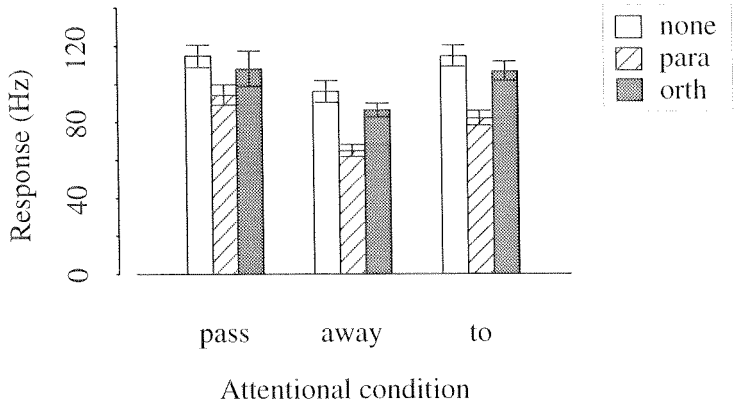
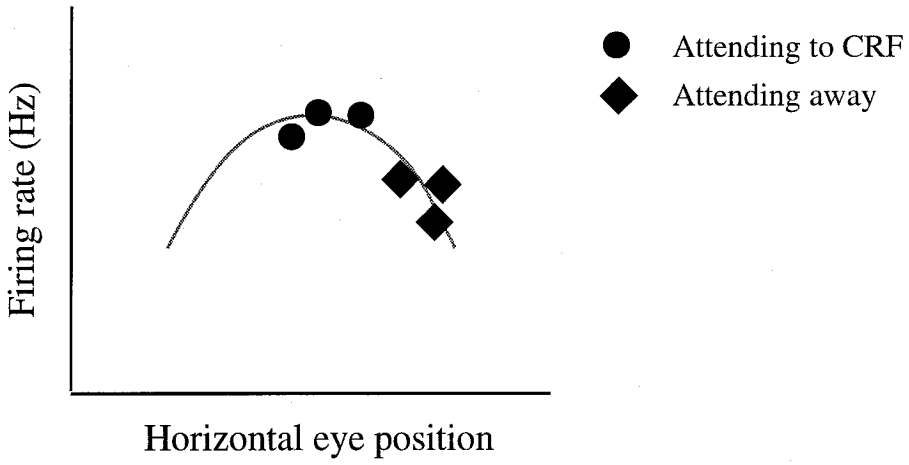


Figure 6. Possible effects of eye position biases. **A**. If the monkey biased his eye position towards the attended location, the test stimulus might stimulate different parts of the cell's receptive field. As a result, the differences seen between attentional conditions might not reflect a veridical attentional modulation of cell responsiveness. **B**. On the other hand, it remains possible the difference in responsiveness reflected an attentional modulation, even in the presence of an eye position bias.

A If mean difference is due to eye position



B If mean difference is due to attention

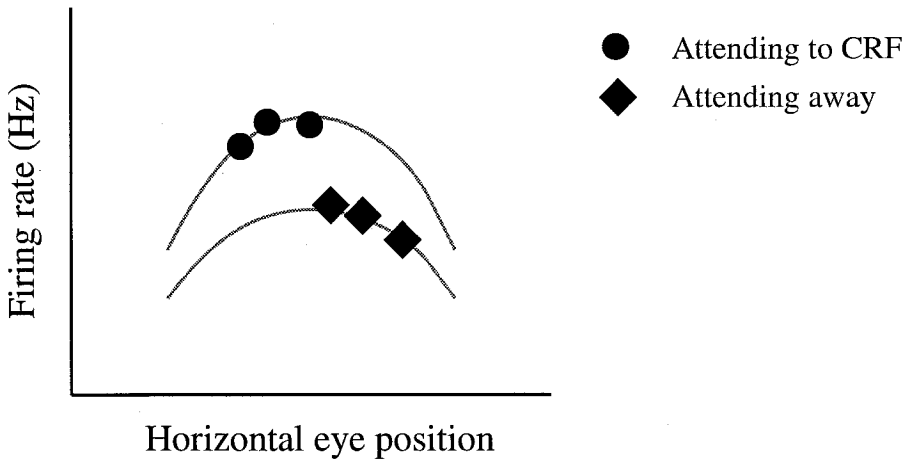


Figure 7. To model a cell's CRF, the reference stimulus responses were plotted as a function of horizontal and vertical eye position. These were then fit by the sum of two quadratics, one along each eye direction. The second-order term for each direction was used only if the quadratic was convex and peaked within the range of eye positions given by the data. In this example, these criteria were not met in either direction and the data were modeled by a plane.

Cell 04.49.03

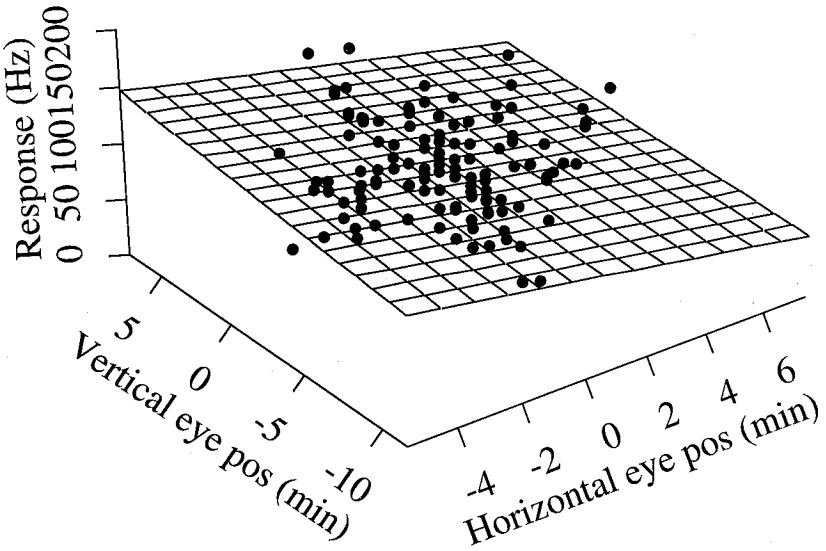
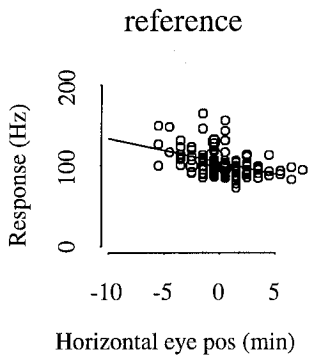

Response (Hz)
0 50 100150200
5 0 -5 -10
Vertical eye pos (min)
-4 -2 0 2 4 6
Horizontal eye pos (min)

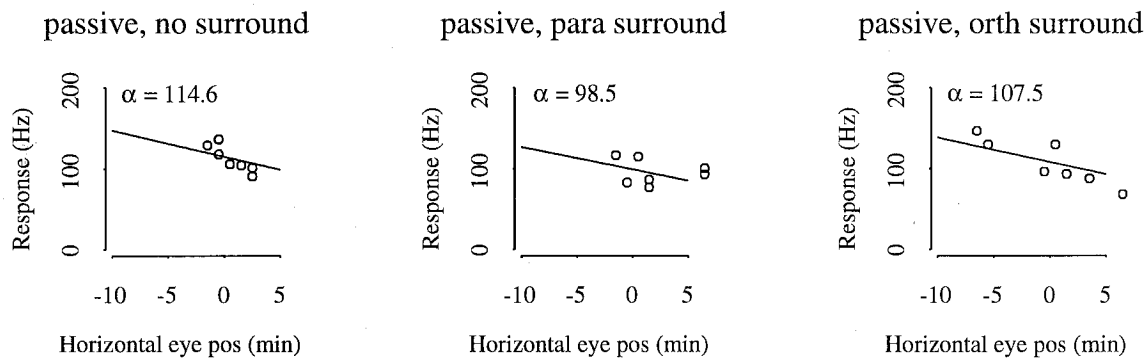
Figure 8. An example of using the CRF shape to determine surround and attention response modulation. Only horizontal eye position is illustrated in this figure, since the three-dimensional fit was more difficult to visualize. **A.** As described in the previous figure, the CRF was modeled by fitting a quadratic to the reference stimulus responses. **B.** This quadratic was then scaled by a gain coefficient to find the best fit in all available conditions. Thus, for a given cell each condition has associated with it a single value, given by α. The passive responses are illustrated in this figure. **C.** Each condition's gain coefficient can then be used instead of its mean firing rate. The results for this example are qualitatively similar to those determined by mean firing rate (figure 5B).

Cell 04.49.03

A



B



C

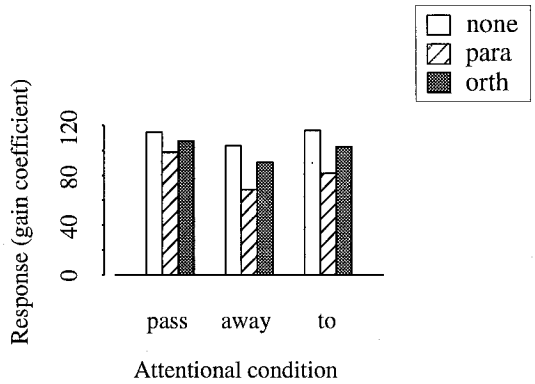


Figure 9. Cells of the PAT set were categorized by surround modulations (Knierim and Van Essen, 1992), collapsing across attentional conditions. Of the 59 cells in the PAT set, there were 26 orientation contrast, 14 general suppression, 6 facilitation, no uniform orientation, and 13 no effect cells.

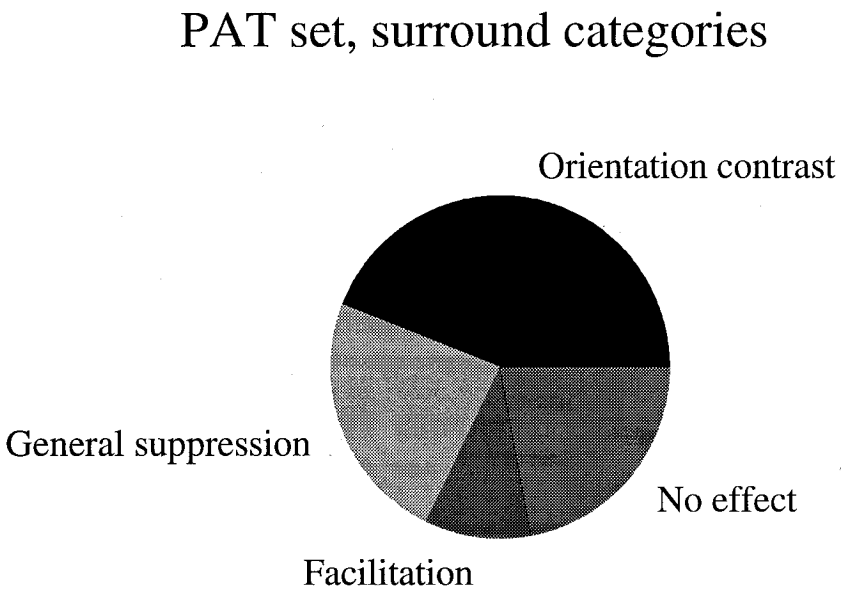

PAT set, surround categories
Orientation contrast
General suppression
No effect
Facilitation

Figure 10. PAT set pre-cue baseline-subtracted responses in the full orientation discrimination paradigm (n=59) for all three surround conditions (none, parallel, and orthogonal) and all three attentional conditions (passive [Xs], attending-away [open circles], and attending-to [closed circles]). **A**. Mean responses across cells. The ordinate does not go to zero in this or in many subsequent illustrations where small differences are being compared. A within-cell ANOVA demonstrated a significant effect of surround ($p<0.0001$) and a significant effect of attention ($p<0.01$), but no significant interaction between the two. **B**. Means and standard errors of the normalized responses. As in the single-cell example, for each attentional condition the parallel surround responses were suppressed relative to either the no surround or orthogonal surround responses; for each surround condition the attending-away responses were decreased relative to both the passive and attending-to responses. **C**. To compare across attentional conditions, each cell's responses were normalized by its passive fixation response, after collapsing across surround conditions. Compared to passive fixation, engaging attention away from the CRF caused a 7% decrease in responsiveness ($p<0.01$). This decrease was relieved when attention was directed to the cell's CRF. This relief reflected a 15% increase in responsiveness relative to the attending-away condition ($p<0.01$, inset).

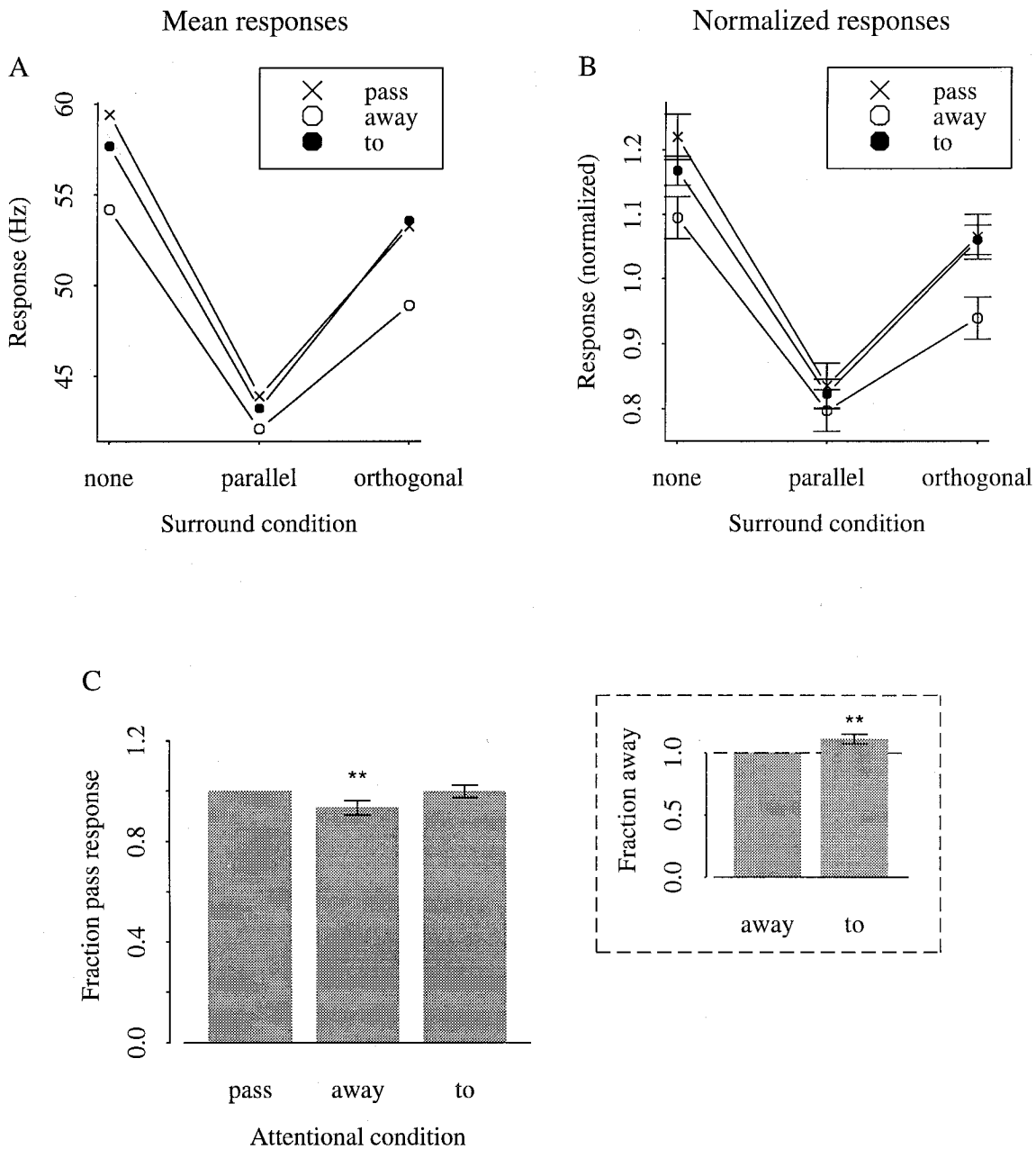

PAT set, subtracted responses
(raw response minus pre-cue baseline)
Mean responses
Normalized responses
A
B
pass
away
to
Response (Hz)
45
50
55
60
Response (normalized)
0.8
0.9
1.0
1.1
1.2
none
parallel
orthogonal
Surround condition
C
Fraction pass response
0.0
0.4
0.8
1.2
**
pass
away
to
Attentional condition
Fraction away
0.0
0.5
1.0
away
to

Figure 11. Effect of attentional task on PAT set subtracted responses (n=59) was assessed by comparing passive and attending-away conditions (collapsed across surround conditions). **A**. Mean response of each cell to passive fixation and attending-away conditions. Each cell's responses to these two conditions are shown as a pair of points and an interconnecting line. Filled circles indicate a significant difference between the two attentional conditions for that cell. Ten cells showed significantly decreased responses when attention was engaged relative to passive fixation, while only two showed a significant increase. **B**. A histogram of pair-wise differences across cells. Cells with significant differences between the two conditions (same cells as in panel A) are shown as filled squares. A comparison of the pair-wise differences revealed a significant decrease across the population when attention was engaged, relative to passive fixation ($p<0.01$). **C**. A histogram of the normalized differences (normalized by the passive condition). Responses in the attending-away condition were decreased relative to the passive condition by a median of 5% ($p<0.01$), consistent with the mean 7% decrease in figure 10C.

Effects of attentional task

PAT set, subtracted responses

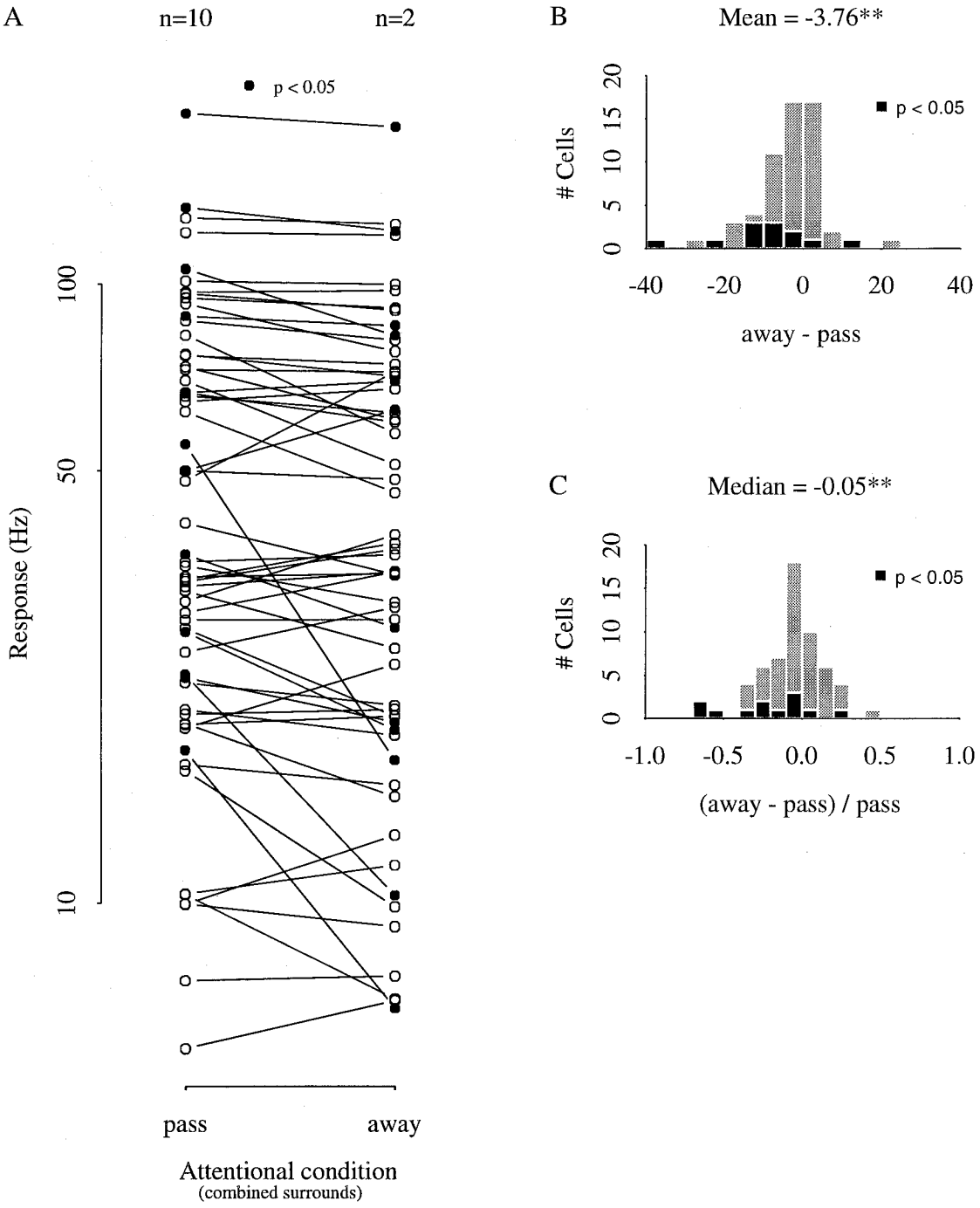


Figure 12. Effect of attentional location on PAT set subtracted responses (n=59) was assessed by comparing attending-away and attending-to conditions (collapsed across surround conditions). **A.** Mean response of each cell to attending-away and attending-to conditions. Filled circles indicate a significant difference between the two attentional conditions. 11 cells showed significantly increased responses when attention was directed to the CRF, while only one showed a significant decrease. **B.** A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. Responses across the population were significantly increased when attention was directed to the CRF ($p<0.01$). **C.** A histogram of the normalized differences (normalized by the attending-away condition). Responses in the attending-to condition were increased relative to the attending-away condition by a median of 5% ($p<0.01$), compared to the mean 15% increase in figure 10C.

Effects of attentional location

PAT set, subtracted responses

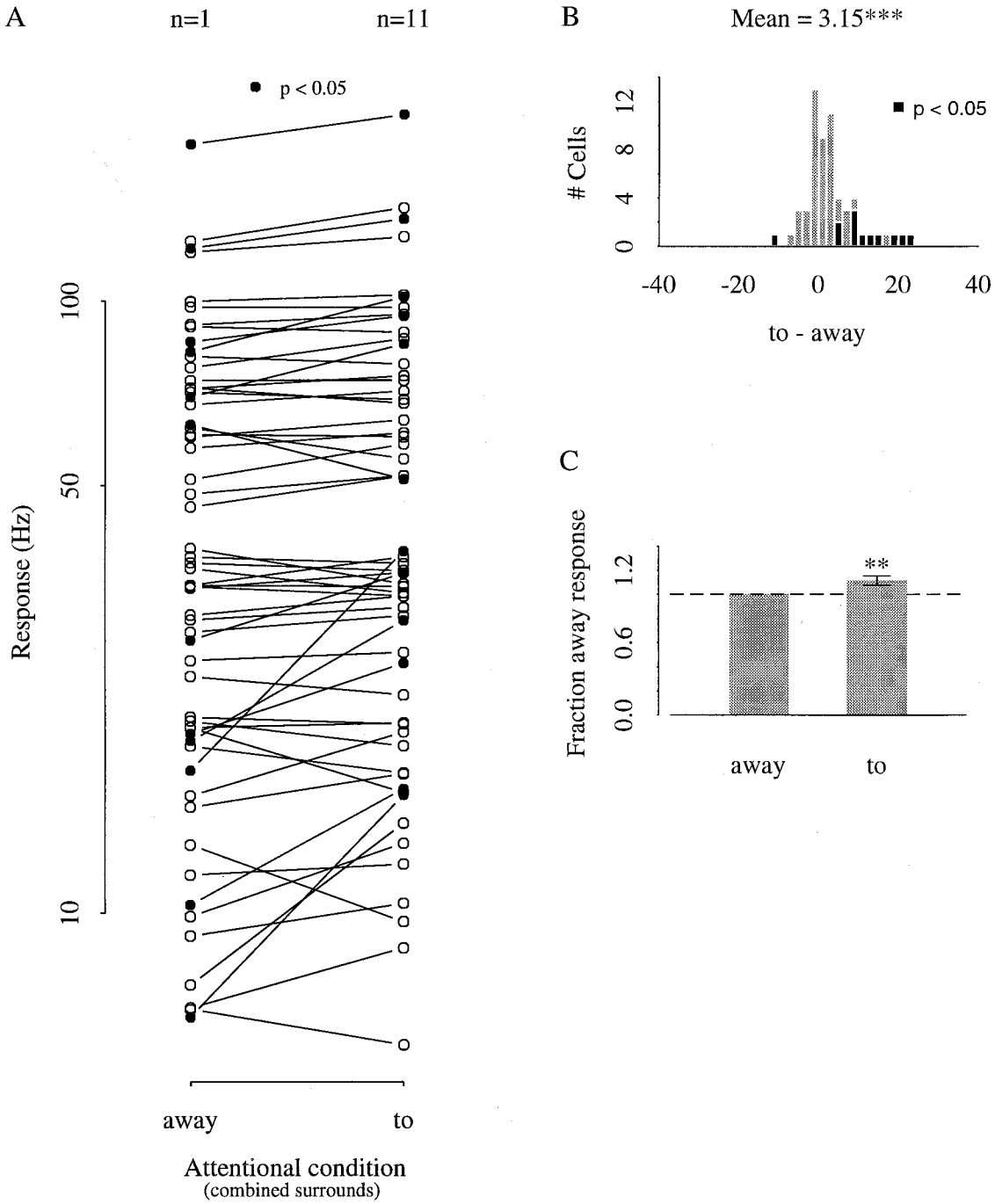
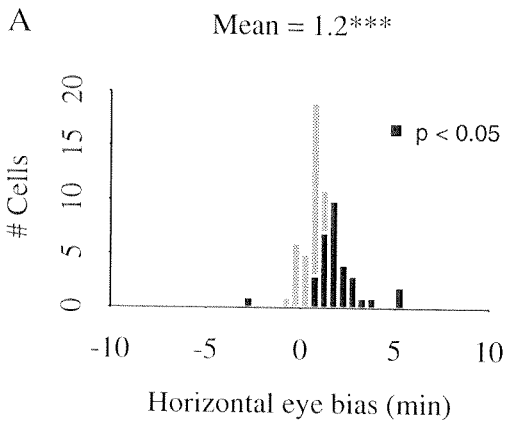


Figure 13. Eye position varied as a function of attended location (AT set, n=99). For each cell, mean eye position when attending to the left was subtracted from the mean eye position when attending to the right. Every trial's eye position was taken as its modal value during the test stimulus period. Cells with significant differences are indicated by filled squares. **A**. When attention was directed to the right, horizontal eye position was biased to the right, on average, by 1.2′ ($p<0.001$). This was significant in 31 cells. One cell showed a significant bias in the opposite direction. **B**. When attention was directed to the left, vertical eye position was not significantly biased (0.2′ upwards). Seven cells showed a significant upwards bias and two cells showed a significant downwards bias.


A
Mean = 1.2***
# Cells
0 5 10 15 20
p < 0.05
-10 -5 0 5 10
Horizontal eye bias (min)

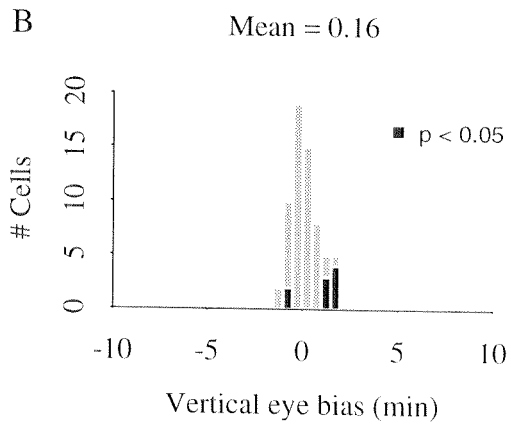

B
Mean = 0.16
# Cells
0 5 10 15 20
p < 0.05
-10 -5 0 5 10
Vertical eye bias (min)

Figure 14. PAT set activity as measured by gain coefficients (n=54, open diamonds) was compared directly with PAT set activity as measured by the pre-cue baseline-subtracted responses (n=59, filled diamonds), collapsing across surround conditions. Gain coefficients showed a slightly decreased effect of attention. This difference did not approach statistical significance. **A**. Mean activities across cells. **B**. Means and associated standard errors of activity after within-cell normalization.

Gain coefficients vs. subtracted responses

PAT set (collapsed across surround conditions)

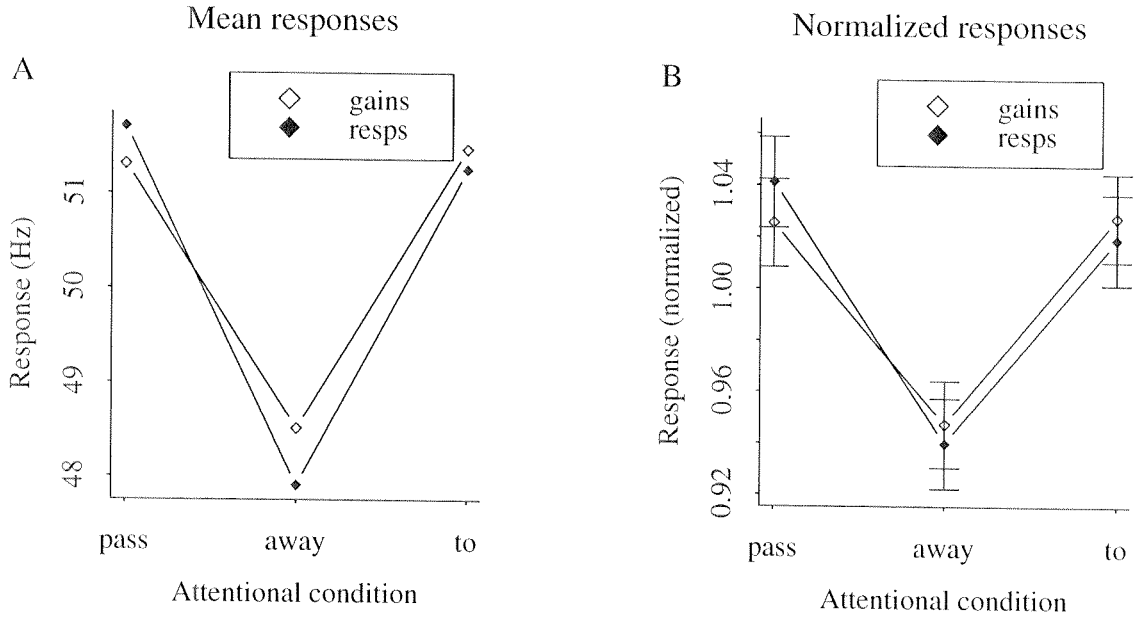


Figure 15. PAT set gain coefficients (n=54) for all nine conditions in the full orientation discrimination paradigm. **A.** Mean gain coefficients across all cells. A within-cell ANOVA shows a significant effect of surround ($p<0.0001$) and a significant effect of attention ($p<0.05$), but no significant interaction between the two. **B.** Means and standard errors of the normalized gain coefficients. **C.** Compared to passive fixation, engaging attention away from the CRF caused a 5% suppression ($p<0.05$). This suppression was relieved when attention was directed to the cell's CRF. This relief reflected a 6% increase in responsiveness relative to the attending-away condition ($p<0.001$, inset).

PAT set, gain coefficients

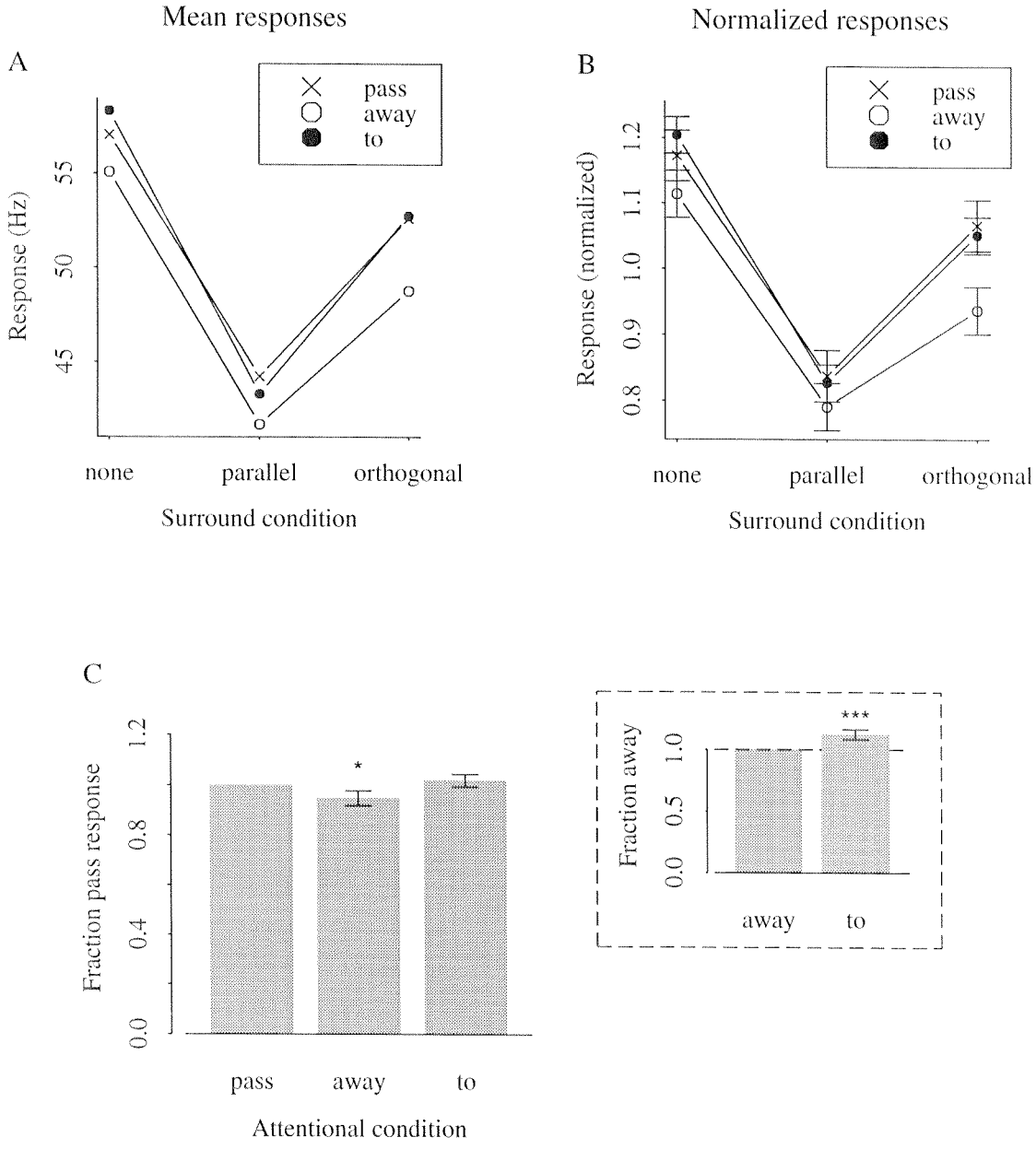


Figure 16. Effect of attentional task on PAT set gain coefficients (n=54, collapsed across surround conditions). **A**. Gain coefficient of each cell to passive fixation and attending-away conditions. **B**. A histogram of pair-wise differences across cells. Gain coefficients across the population were significantly decreased when attention was engaged, relative to passive fixation ($p<0.05$). **C**. A histogram of the normalized differences (normalized by the passive condition). Gain coefficients in the attending-away condition were decreased relative to the passive condition by a median of 5% ($p<0.01$), consistent with the mean 5% decrease in figure 15C.

Effects of attentional task

PAT set, gain coefficients

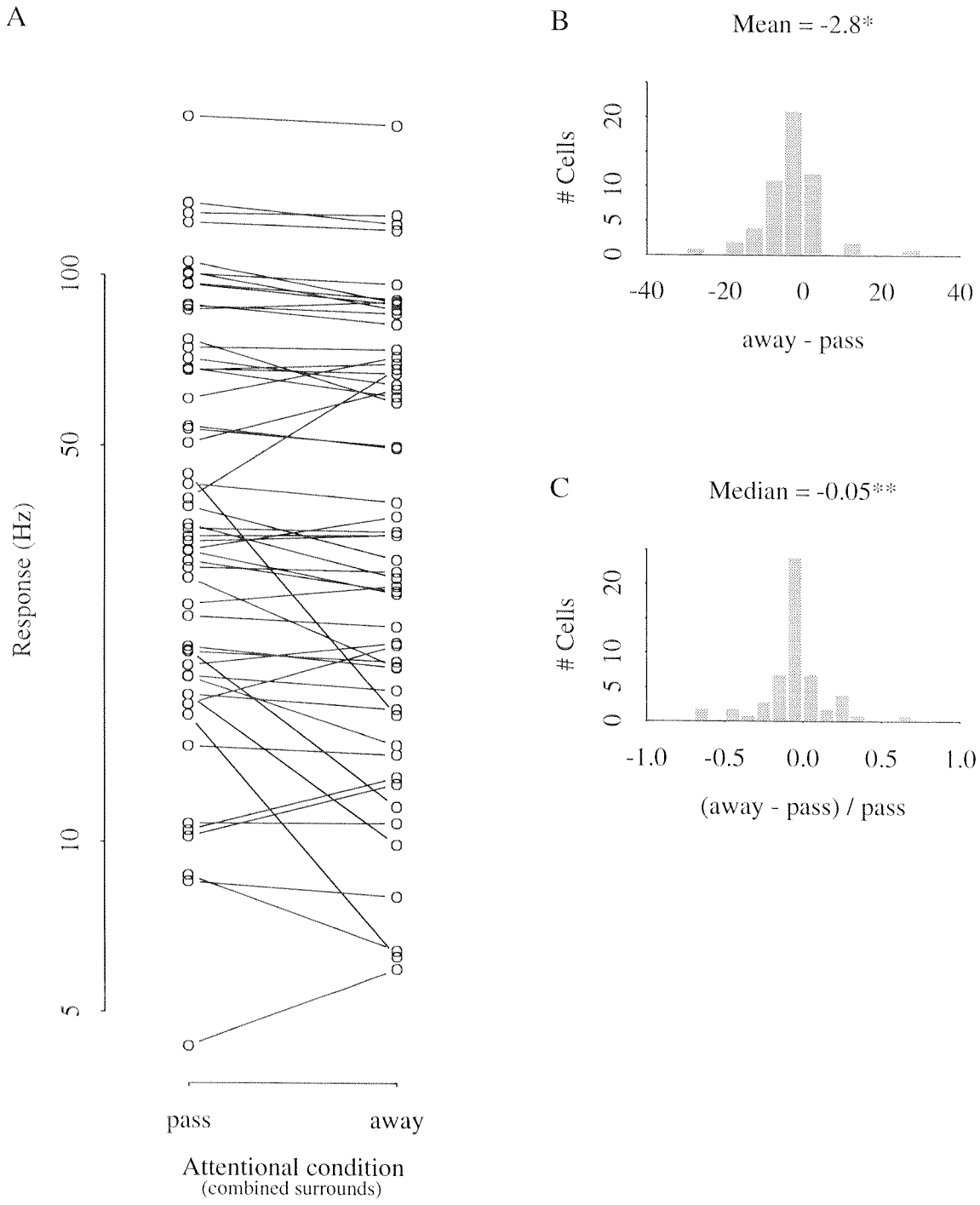


Figure 17. Effect of attentional location on PAT set gain coefficients (n=54, collapsed across surround conditions). **A**. Gain coefficient of each cell to attending-away and attending-to conditions. **B**. A histogram of pair-wise differences across cells. Gain coefficients across the population were significantly increased when attention was directed to the CRF ($p<0.001$). **C**. A histogram of the normalized differences (normalized by the attending-away condition). Gain coefficients in the attending-to condition were increased relative to the attending-away condition by a median of 3% ($p<0.05$), compared to the mean 6% increase in figure 15C.

Effects of attentional location

PAT set, gain coefficients

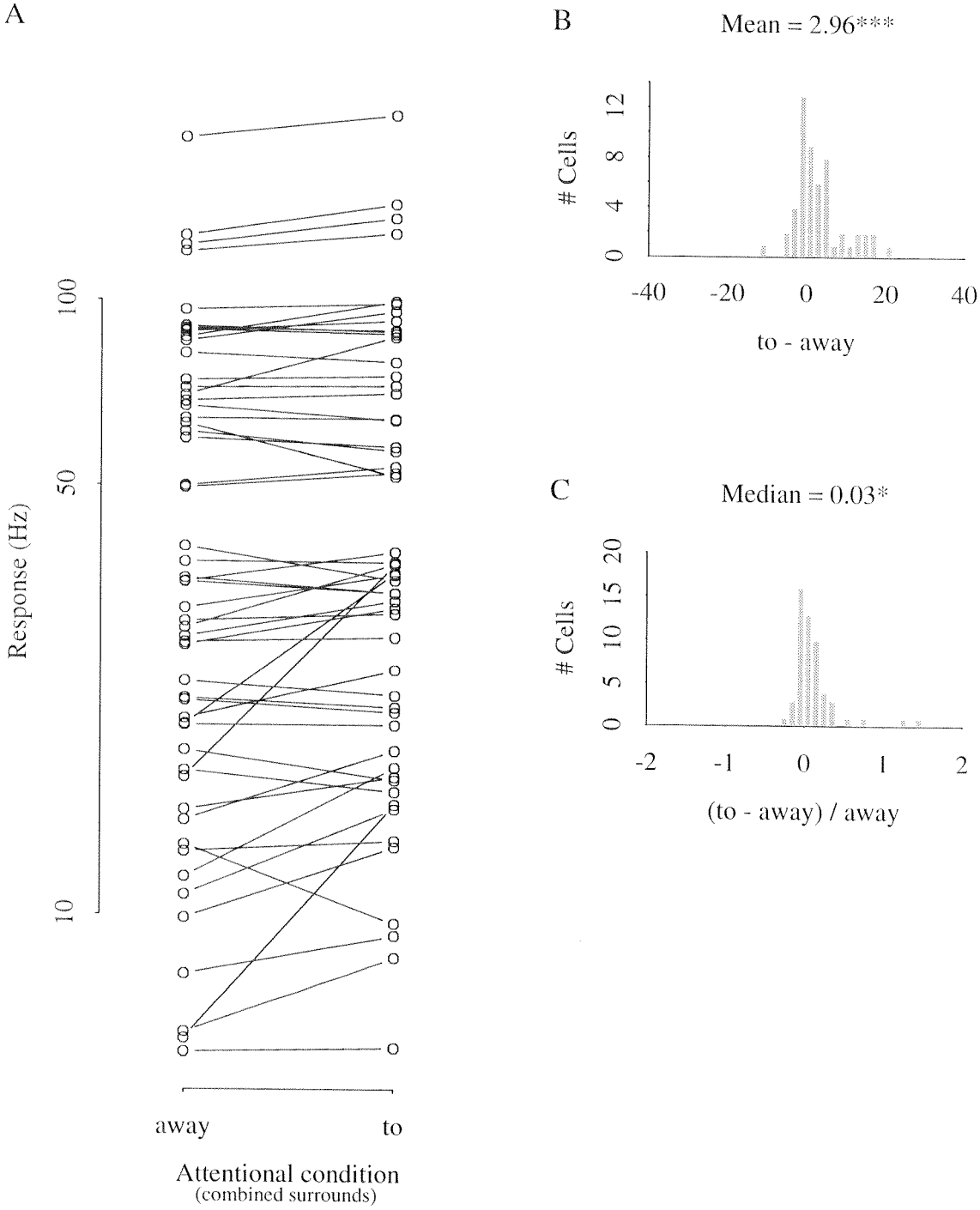


Figure 18. Effect of attention on PAT set pre-cue baseline activity (period A in figures 1 and 2), collapsed across surround condition (n=59). **A**. Mean pre-cue baseline activity for each cell to passive and attending-away conditions. Filled circles indicate a significant difference between the two conditions. Engaging attention away from the cell's CRF significantly increased pre-cue baseline activity in four cells relative to passive fixation. **B**. A histogram of pair-wise differences across cells. As a population, the pair-wise differences between passive and attending-away pre-cue baselines showed no significant effect of attentional task. **C**. Mean pre-cue baseline activity for each cell to attending-away and attending-to conditions. Directing attention to the cell's CRF from the opposite hemifield significantly increased pre-cue baseline activity in five cells and decreased it in one. **D**. As a population, the pair-wise differences demonstrated a significant increase in pre-cue baseline activity when attention was directed to the cell's CRF ($p<0.05$). An ANOVA across all three attentional conditions, though, revealed no significant effect of attention on pre-cue baseline activity ($p>0.1$).

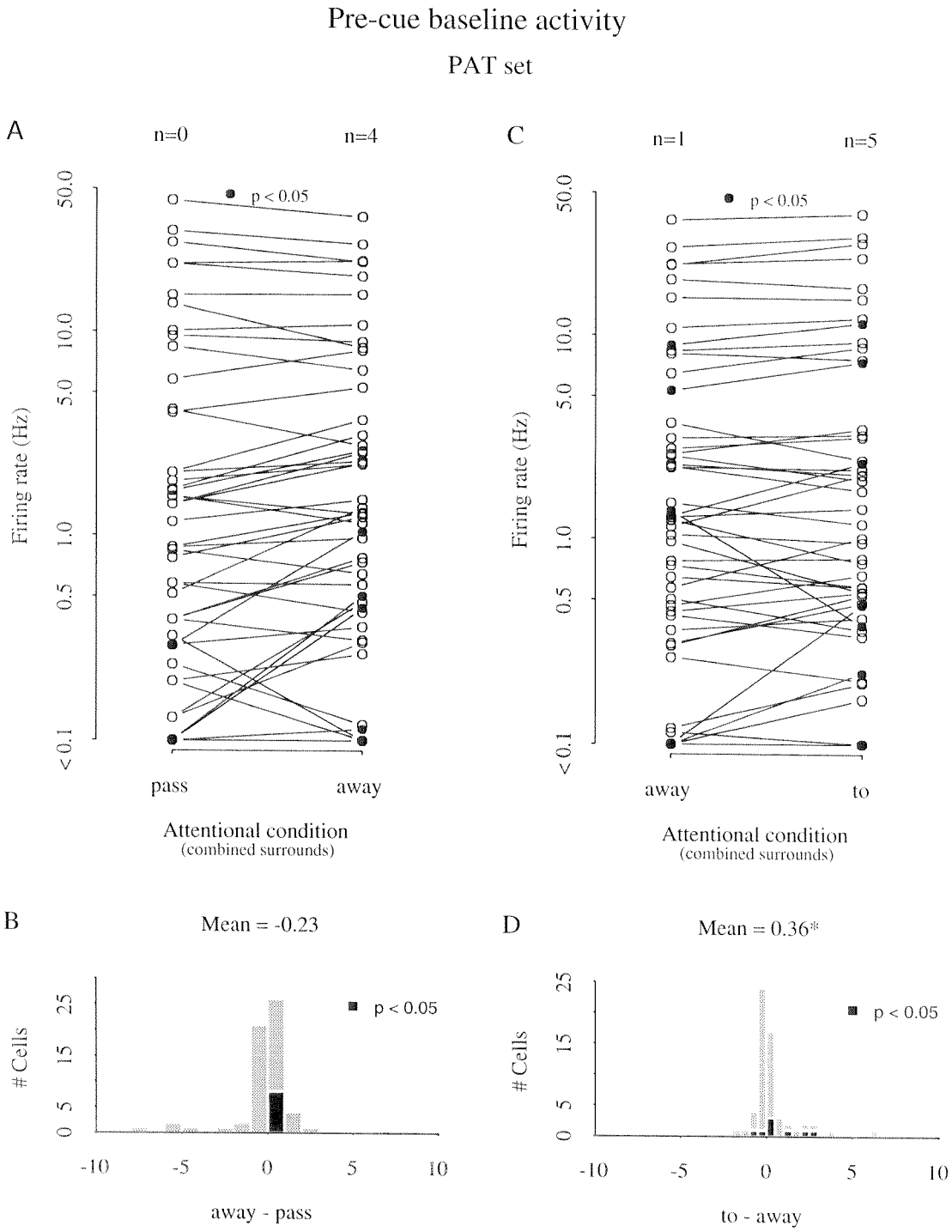

Pre-cue baseline activity
PAT set
A
n=0
n=4
p < 0.05
Firing rate (Hz)
50.0
10.0
5.0
1.0
0.5
< 0.1
pass
away
Attentional condition
(combined surrounds)
C
n=1
n=5
p < 0.05
Firing rate (Hz)
50.0
10.0
5.0
1.0
0.5
< 0.1
away
to
Attentional condition
(combined surrounds)
B
Mean = -0.23
p < 0.05
Cells
0
5
15
25
-10
-5
0
5
10
away - pass
D
Mean = 0.36*
p < 0.05
Cells
0
5
15
25
-10
-5
0
5
10
to - away

Figure 19. Raw responses (open diamonds) were compared directly with the pre-cue baseline-subtracted responses (filled diamonds), collapsing across surround conditions (PAT set, n=59). **A**. Mean activities across cells. The mean subtracted responses were higher than the subtracted responses, as would be expected. **B**. Means and associated standard errors of activity after within-cell normalization. Subtracting pre-cue baseline had no significant effect on attentional modulation.

Raw responses vs. subtracted responses

PAT set

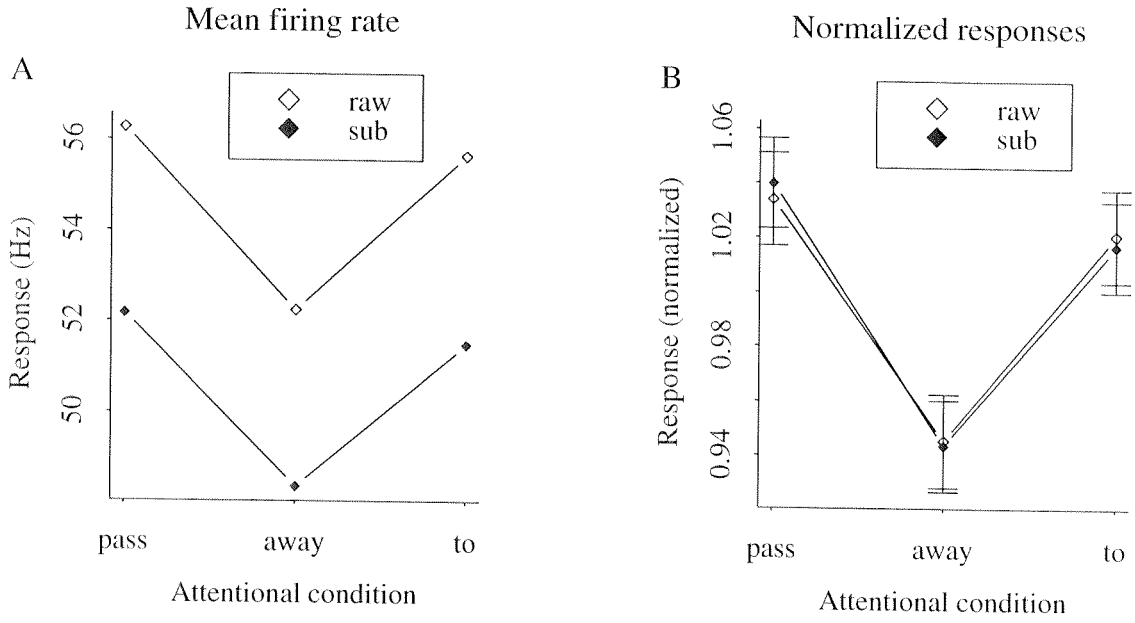


Figure 20. PAT set raw responses (n=59) for all nine conditions in the full orientation discrimination paradigm. **A**. Mean raw responses across all cells. A within-cell ANOVA shows a significant effect of surround ($p<0.0001$) and a significant effect of attention ($p<0.01$), but no significant interaction between the two. **B**. Means and standard errors of the normalized raw responses. **C**. Compared to passive fixation, engaging attention away from the CRF caused a 6% suppression ($p<0.01$). This suppression was relieved when attention was directed to the cell's CRF. This relief reflected an 11% increase in responsiveness relative to the attending-away condition ($p<0.001$, inset).

PAT set, raw responses

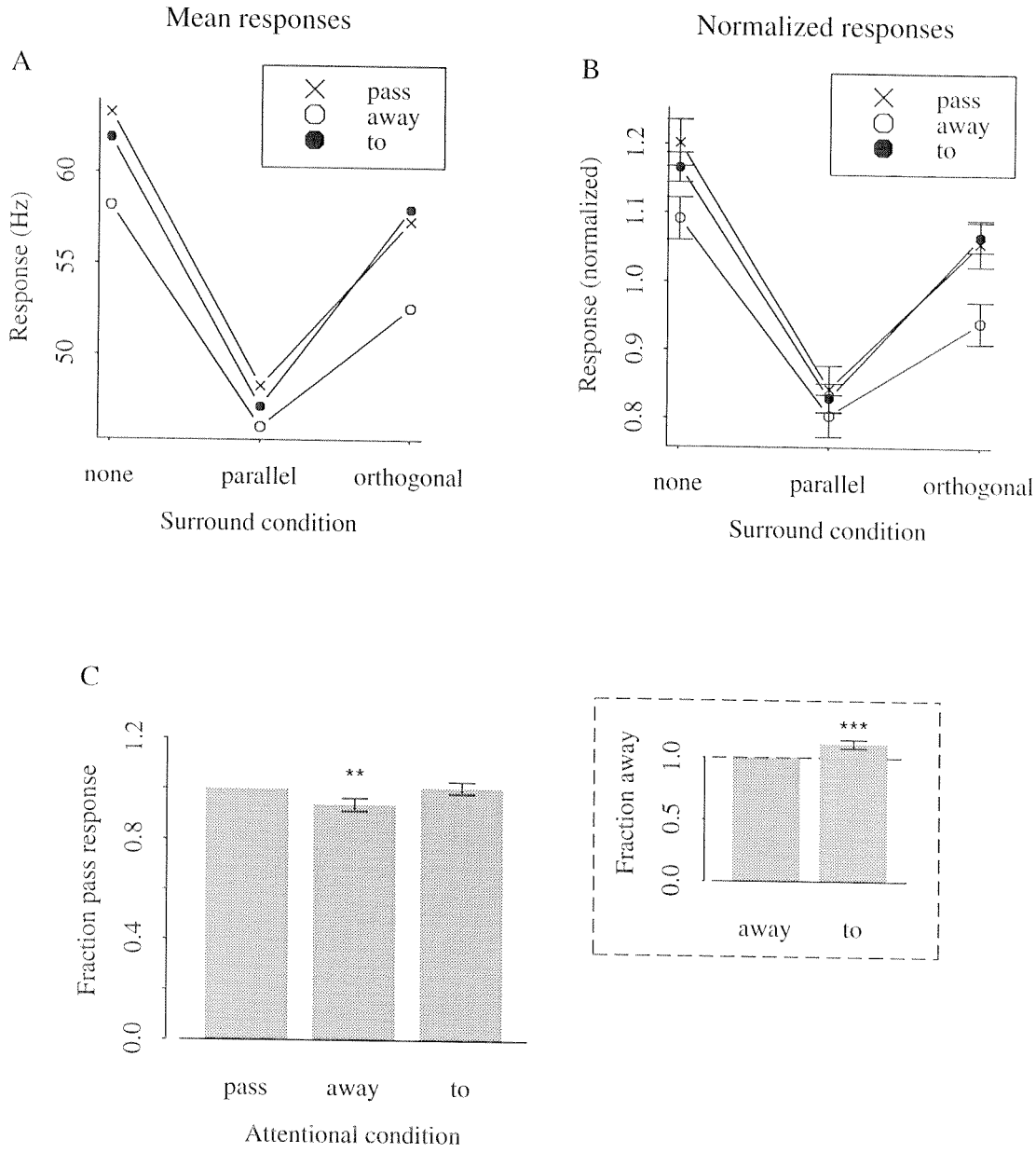


Figure 21. Effect of attentional task on PAT set raw responses (n=59, collapsed across surround conditions). **A.** Mean response of each cell to passive fixation and attending-away conditions. Filled circles indicate a significant difference between the two attentional conditions for that cell. 11 cells showed significantly decreased responses when attention was engaged relative to passive fixation, while only one showed a significant increase. **B.** A histogram of pair-wise differences across cells. Cells with significant differences between the two conditions are shown as filled squares. A comparison of the pair-wise differences revealed a significant decrease across the population when attention was engaged, relative to passive fixation ($p<0.01$). **C.** A histogram of the normalized differences (normalized by the passive condition). Responses in the attending-away condition were decreased relative to the passive condition by a median of 5% ($p<0.05$), consistent with the mean 6% decrease in figure 10C.

Effects of attentional task

PAT set, raw responses

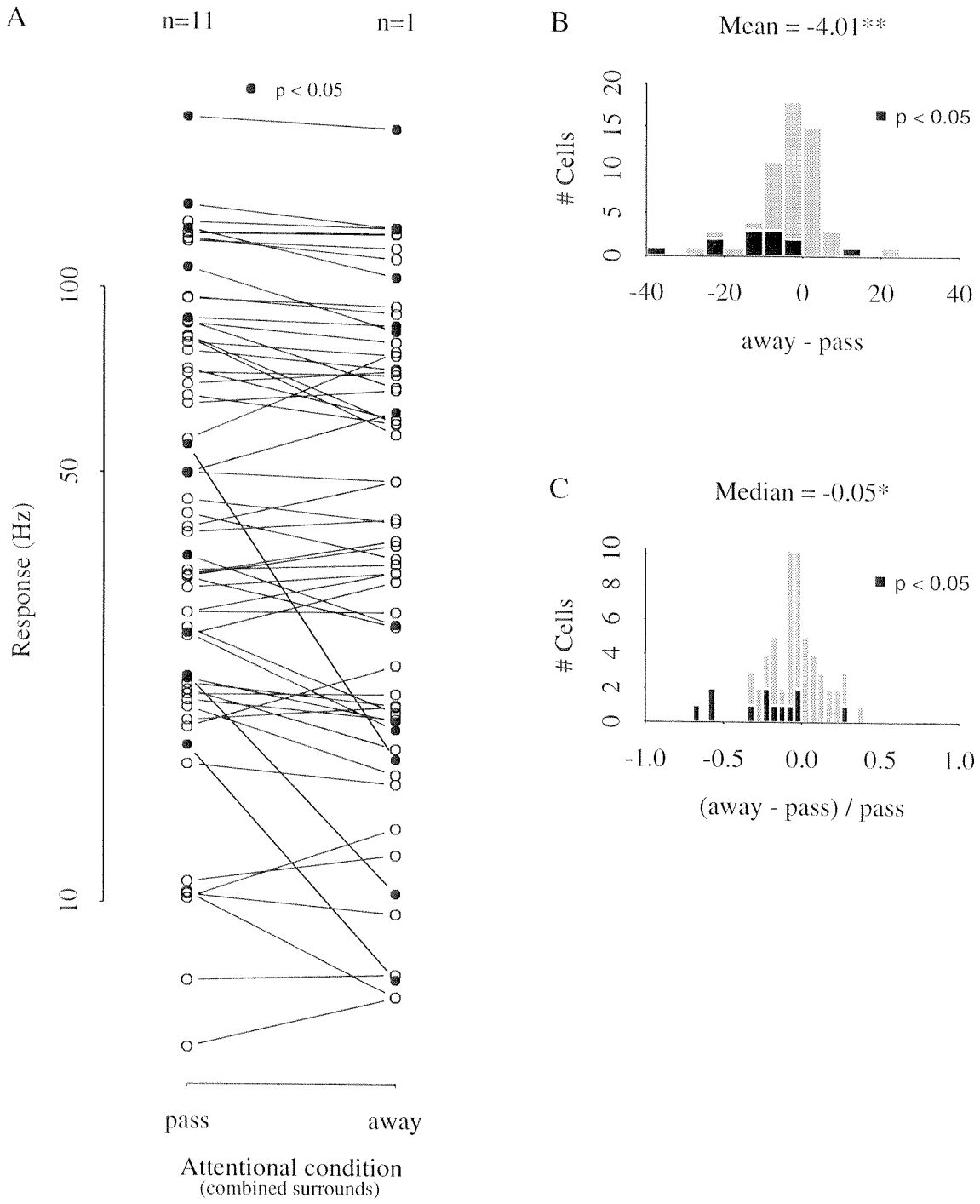


Figure 22. Effect of attentional location on PAT set raw responses (n=59, collapsed across surround conditions). **A**. Mean response of each cell to attending-away and attending-to conditions. Filled circles indicate a significant difference between the two attentional conditions. 11 cells showed significantly increased responses when attention was directed to the CRF, while only one showed a significant decrease. **B**. A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. Responses across the population were significantly increased when attention was directed to the CRF ($p<0.001$). **C**. A histogram of the normalized differences (normalized by the attending-away condition). Responses in the attending-to condition were increased relative to the attending-away condition by a median of 5% ($p<0.001$), compared to the mean 11% increase in figure 20C.

Effects of attentional location

PAT set, raw responses

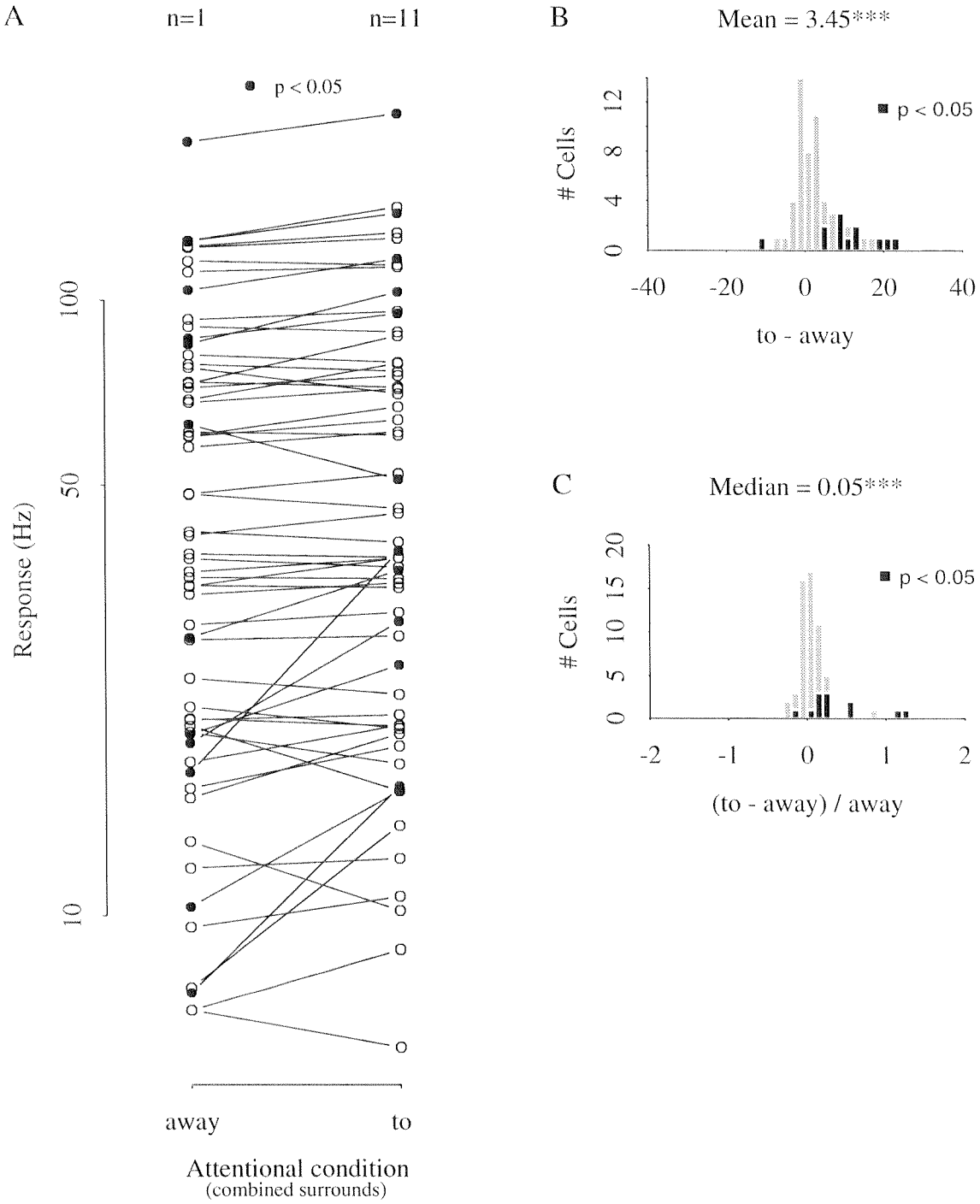


Figure 23. Effect of attention on PAT set interstimulus baseline activity (period E2 in figures 1 and 2), collapsed across surround condition (n=59). **A**. Mean interstimulus baseline activity for each cell to passive and attending-away conditions. Filled circles indicate a significant difference between the two conditions. Engaging attention away from the cell's CRF significantly increased interstimulus baseline activity in four cells relative to passive fixation and decreased it in one. **B**. A histogram of pair-wise differences across cells. As a population, the pair-wise differences between passive and attending-away interstimulus baselines showed no significant effect of attentional task. **C**. Mean interstimulus baseline activity for each cell to attending-away and attending-to conditions. Directing attention to the cell's CRF from the opposite hemifield significantly increased interstimulus baseline activity in three cells and decreased it in two. **D**. As a population, the pair-wise differences between attending-away and attending-to interstimulus baselines showed no significant effect of attention on interstimulus baseline activity.

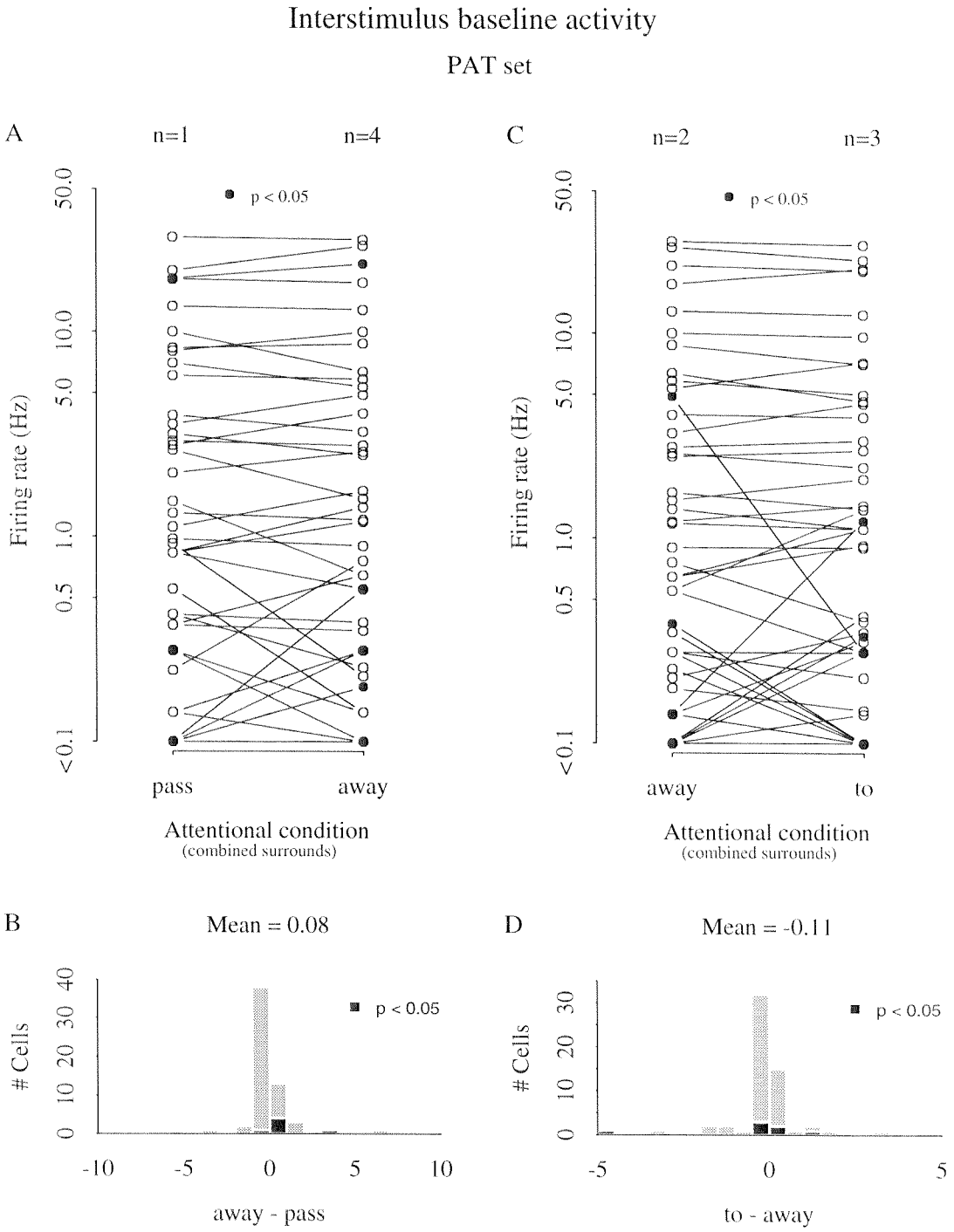

Interstimulus baseline activity
PAT set
A
n=1
n=4
p < 0.05
Firing rate (Hz)
50.0
10.0
5.0
1.0
0.5
<0.1
pass
away
Attentional condition
(combined surrounds)
C
n=2
n=3
p < 0.05
away
to
Attentional condition
(combined surrounds)
B
Mean = 0.08
# Cells
p < 0.05
away - pass
D
Mean = -0.11
# Cells
p < 0.05
to - away

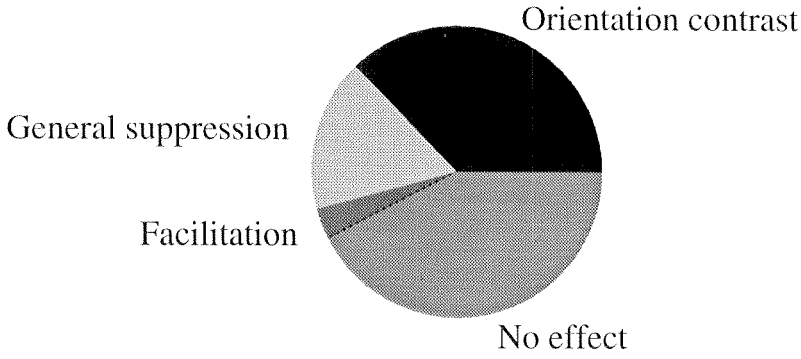
Figure 24. Effect of attention on PAT set surround categorizations (n=59). **A.** During passive fixation, there were 22 orientation contrast cells, 10 general suppression cells, 2 facilitation cells, and 25 no effect cells. **B.** When attention was directed away from the CRF, there were 23 orientation contrast cells, 14 general suppression cells, 2 facilitation cells, 1 uniform orientation cell, and 25 no effect cells. **C.** When attention was directed to the CRF, there were 27 orientation contrast cells, 13 general suppression cells, 5 facilitation cells, and 14 no effect cells. These distributions were not significantly different from one another by a chi-squared test.

Effect of attention on surround categorizatio

PAT set

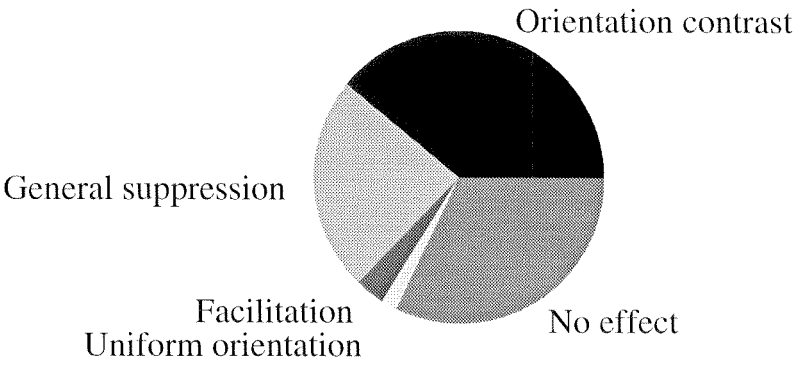
A

pass



B

away



C

to

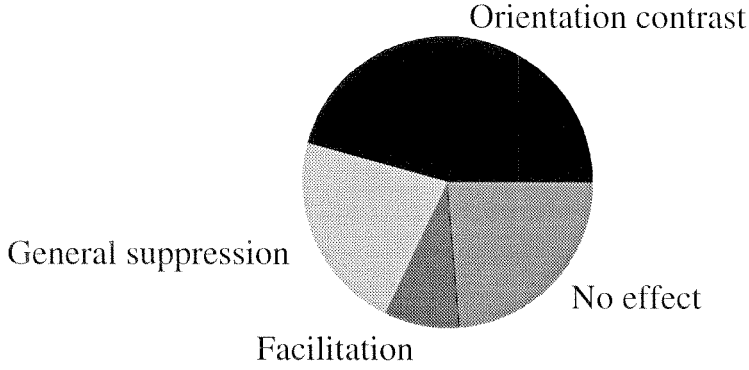


Figure 25. Cells of the AT set were categorized by surround modulations, collapsing across attentional conditions. Of the 99 cells in the PAT set, there were 33 orientation contrast, 27 general suppression, 9 facilitation, 2 uniform orientation, and 28 no effect cells. This distribution was not significantly different from that seen in the PAT set (figure 9) by a chi-squared test.

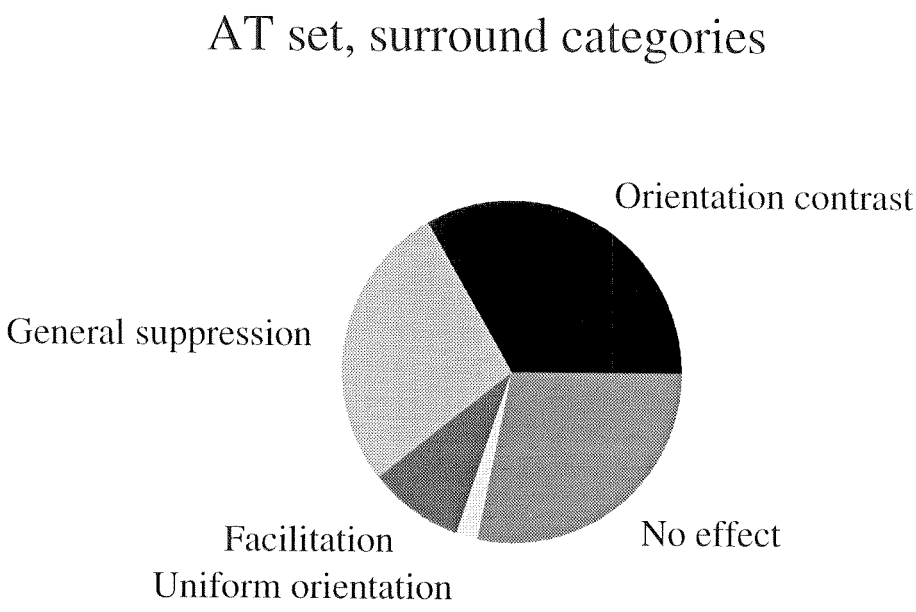

AT set, surround categories
Orientation contrast
General suppression
Facilitation
Uniform orientation
No effect

Figure 26. AT set responses (n=99) for all three surround conditions (none, parallel, and orthogonal) and both attentional conditions (attending-away [open circles] and attending-to [closed circles]). Subtracted responses (panels **A** and **B**), gain coefficients (panels **C** and **D**), and raw responses (panels **E** and **F**) are shown. The left-hand column (panels **A**, **C**, and **E**) shows the mean responses across cells. The right-hand column (panels **B**, **D**, and **F**) shows the means and standard errors of the normalized responses. For all three response measures, a within-cell ANOVA demonstrated a main effect of surround ($p<0.0001$) and a main effect of attention ($p<0.01$ for the gain coefficients, $p<0.001$ for the other two). Under no conditions was there a significant effect of attention on surround modulation.

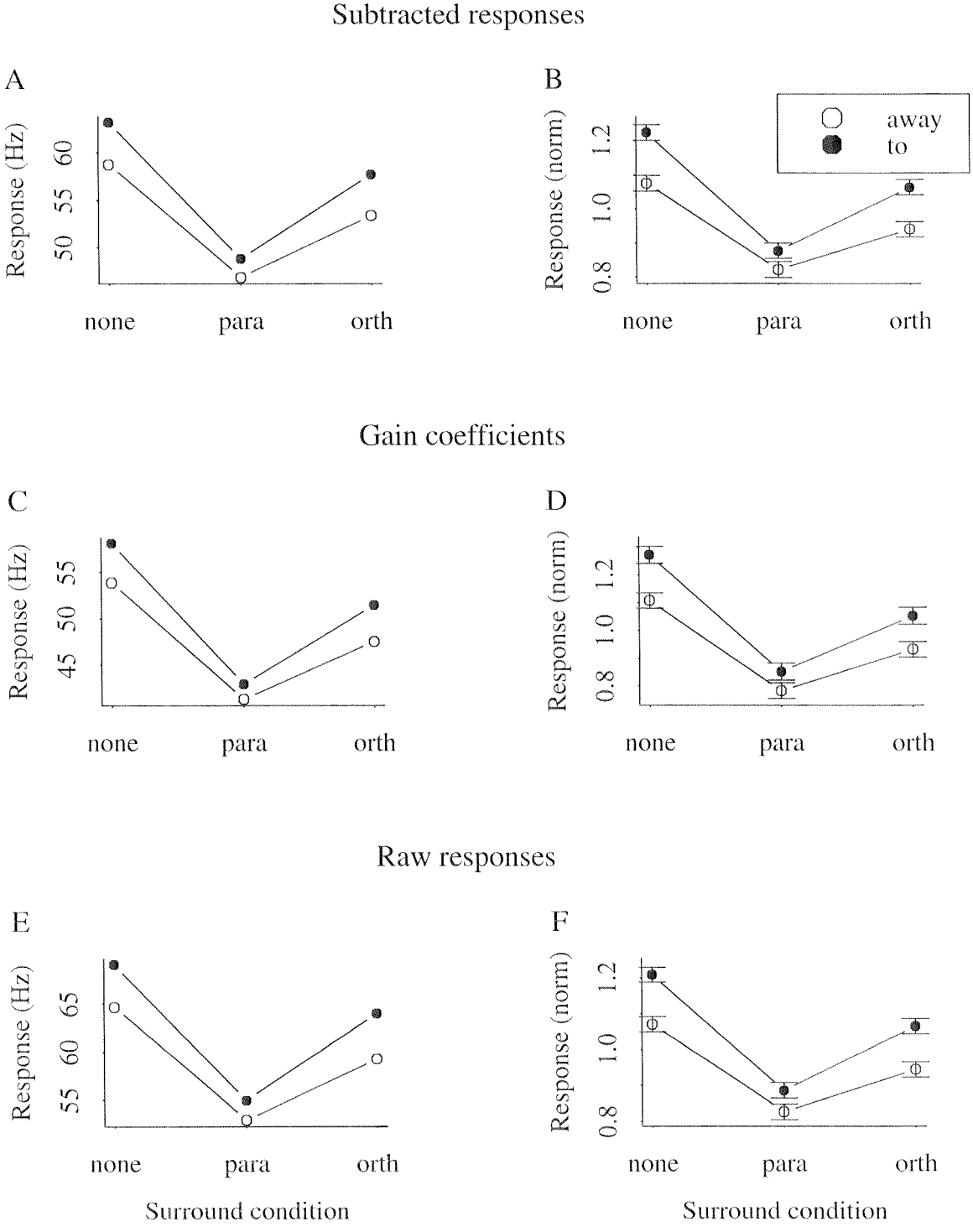

Subtracted responses
A
Response (Hz)
50 55 60
none
para
orth
B
Response (norm)
0.8 1.0 1.2
away
to
none
para
orth
Gain coefficients
C
Response (Hz)
45 50 55
none
para
orth
D
Response (norm)
0.8 1.0 1.2
none
para
orth
Raw responses
E
Response (Hz)
55 60 65
none
para
orth
Surround condition
F
Response (norm)
0.8 1.0 1.2
none
para
orth
Surround condition

Figure 27. Effect of attentional location on AT set subtracted responses (n=99, collapsed across surround conditions). **A.** Mean response of each cell to attending-away and attending-to conditions. Filled circles indicate a significant difference between the two attentional conditions. 20 cells showed significantly increased responses when attention was directed to the CRF, while only three showed a significant decrease. **B.** A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. Responses across the population were significantly increased when attention was directed to the CRF ($p<0.001$). **C.** A histogram of the normalized differences (normalized by the attending-away condition). Responses in the attending-to condition were increased relative to the attending-away condition by a mean of 16% ($p<0.001$) and a median of 7% ($p<0.001$).

Effects of attentional location

AT set, subtracted responses

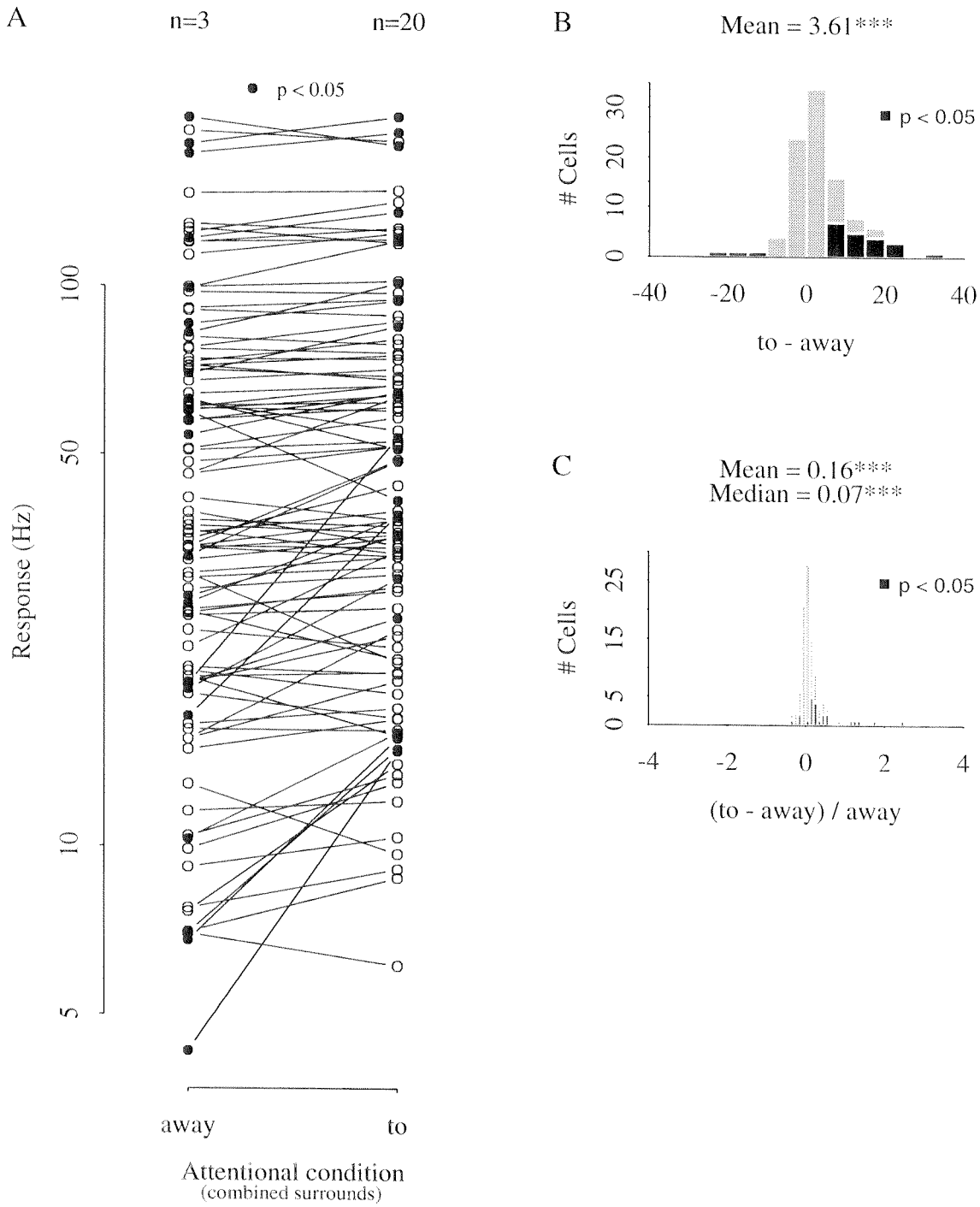


Figure 28. Effect of attentional location on AT set gain coefficients (n=64, collapsed across surround conditions). **A**. Gain coefficient of each cell to attending-away and attending-to conditions. **B**. A histogram of pair-wise differences across cells. Gain coefficients across the population were significantly increased when attention was directed to the CRF ($p<0.001$). **C**. A histogram of the normalized differences (normalized by the attending-away condition). Gain coefficients in the attending-to condition were increased relative to the attending-away condition by a mean of 18% ($p<0.001$) and a median of 6% ($p<0.001$).

Effects of attentional location

AT set, gain coefficients

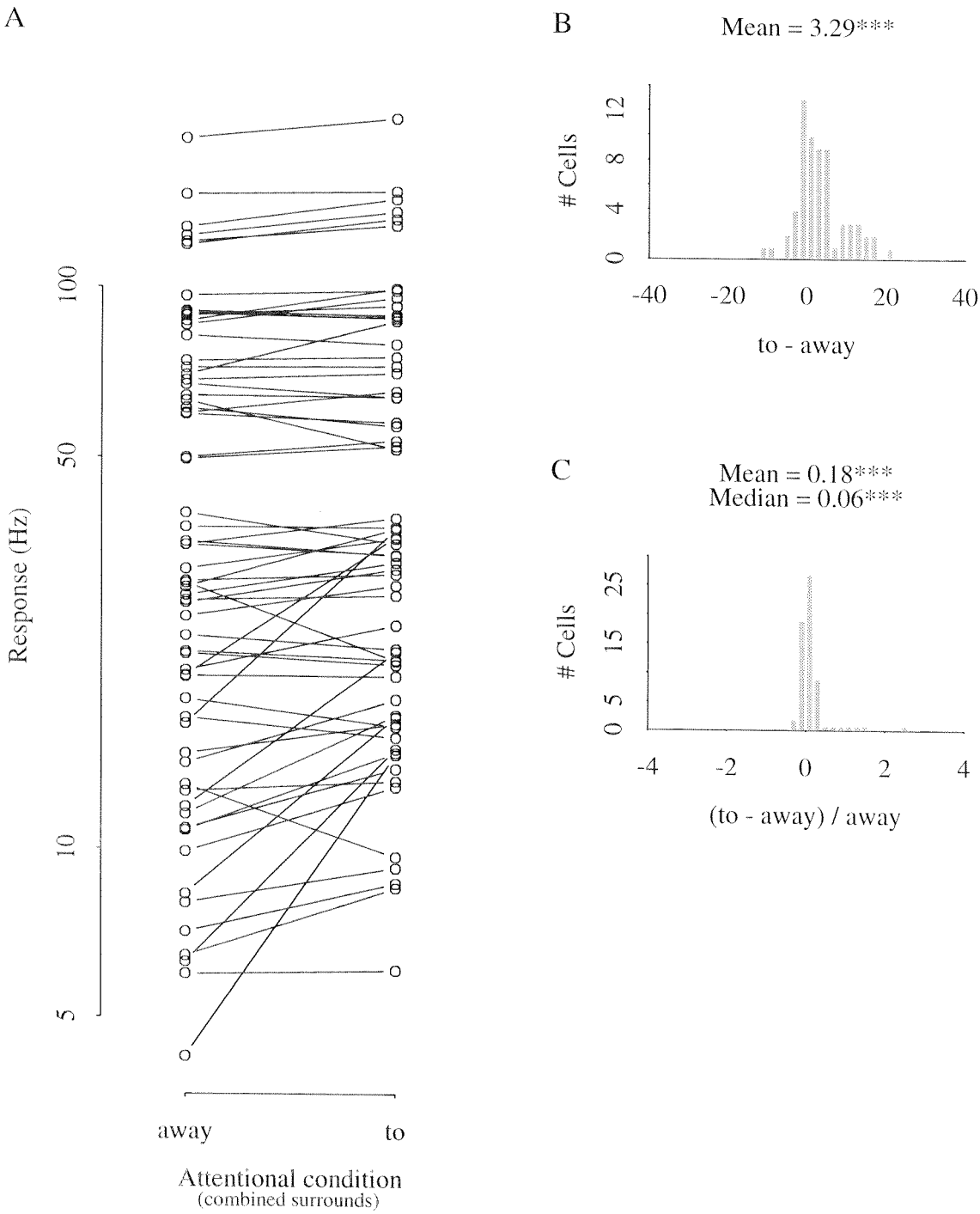


Figure 29. Effect of attentional location on AT set raw responses (n=99, collapsed across surround conditions). **A**. Mean response of each cell to attending-away and attending-to conditions. Filled circles indicate a significant difference between the two attentional conditions. 19 cells showed significantly increased responses when attention was directed to the CRF, while only three showed a significant decrease. **B**. A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. Responses across the population were significantly increased when attention was directed to the CRF ($p<0.001$). **C**. A histogram of the normalized differences (normalized by the attending-away condition). Responses in the attending-to condition were increased relative to the attending-away condition by a mean of 17% ($p<0.001$) and a median of 5% ($p<0.001$).

Effects of attentional location

AT set, raw responses

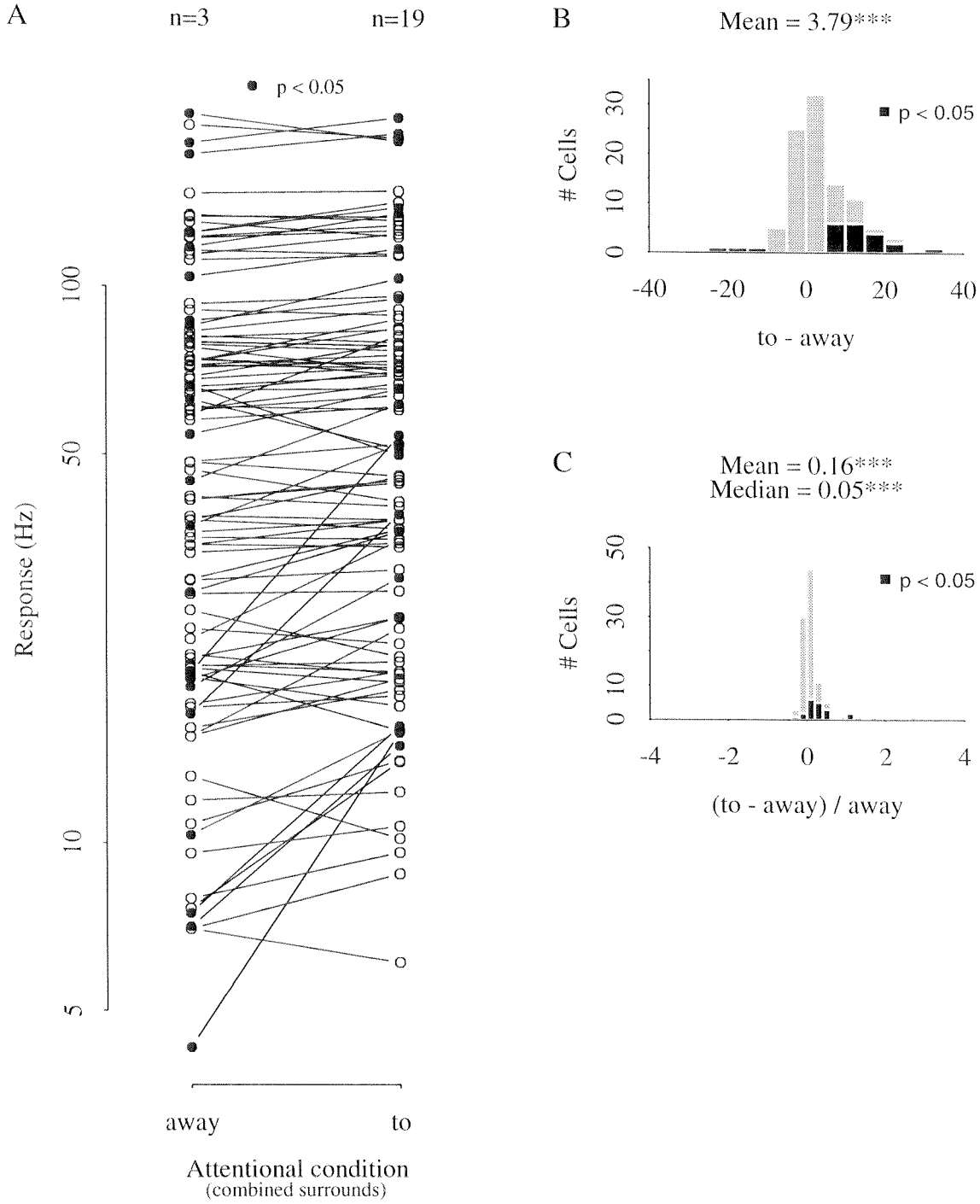


Figure 30. Effect of attentional location on AT set pre-cue baseline activity (period A in figures 1 and 2), collapsed across surround condition (n=99). **A**. Mean pre-cue baseline activity for each cell to attending-away and attending-to conditions. Filled circles indicate a significant difference between the two conditions. Directing attention to the cell's CRF from the opposite hemifield significantly increased pre-cue baseline activity in eight cells and decreased it in three. **B**. A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. As a population, the pair-wise differences between attending-away and attending-to pre-cue baselines showed no significant effect of attention on pre-cue baseline activity.

Pre-cue baseline activity

AT set

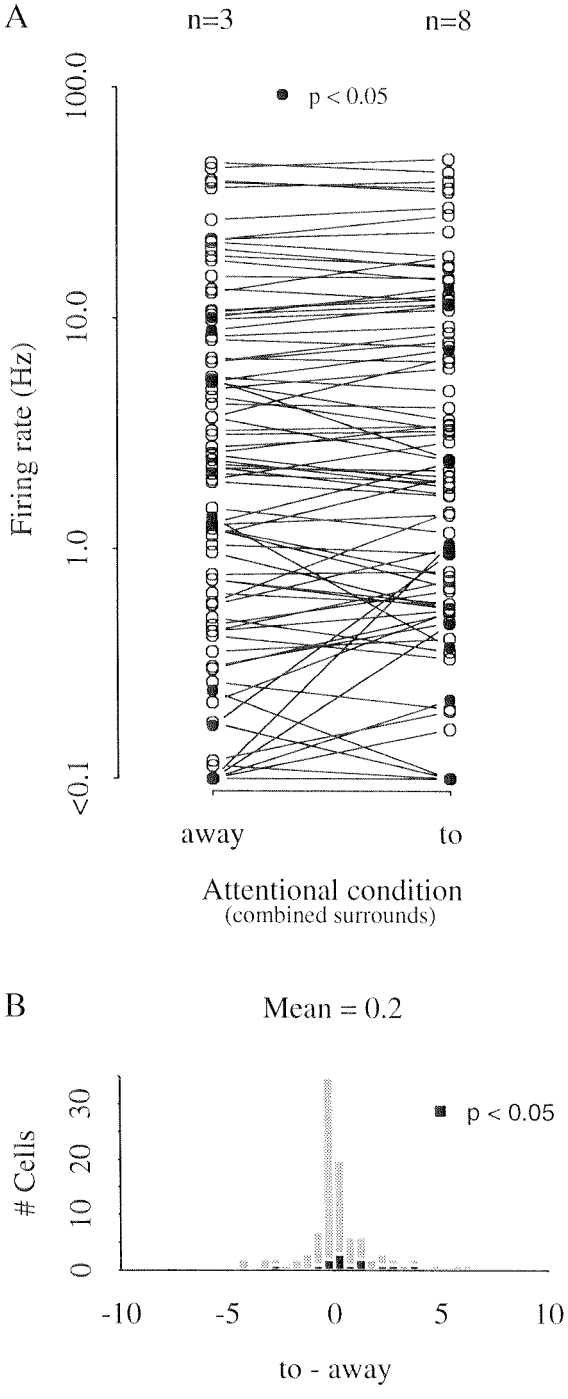
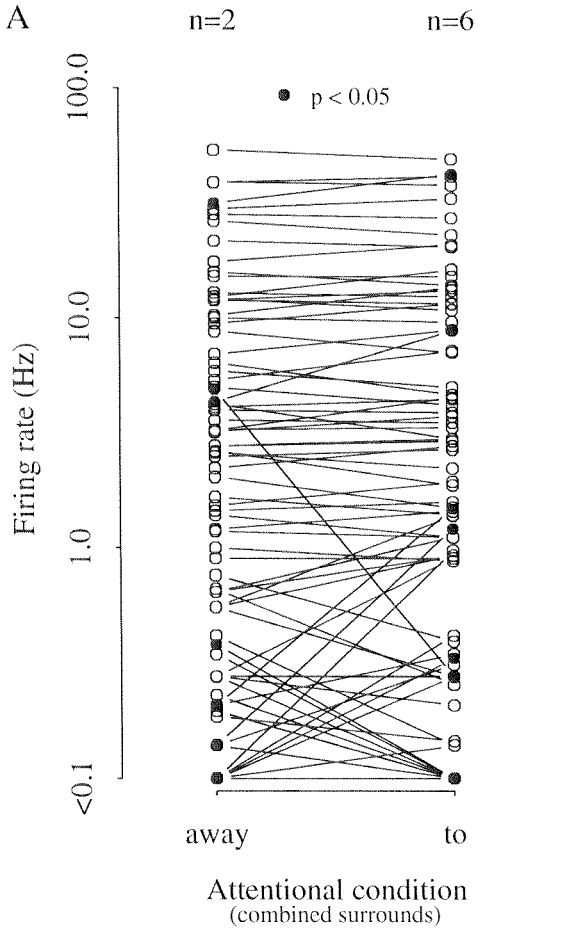


Figure 31. Effect of attention on AT set interstimulus baseline activity (period E2 in figures 1 and 2), collapsed across surround condition (n=99). **A**. Mean interstimulus baseline activity for each cell to attending-away and attending-to conditions. Filled circles indicate a significant difference between the two conditions. Directing attention to the cell's CRF from the opposite hemifield significantly increased interstimulus baseline activity in three cells and decreased it in two. **B**. A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. As a population, the pair-wise differences between attending-away and attending-to interstimulus baselines showed no significant effect of attention on interstimulus baseline activity.

Interstimulus baseline activity

AT set



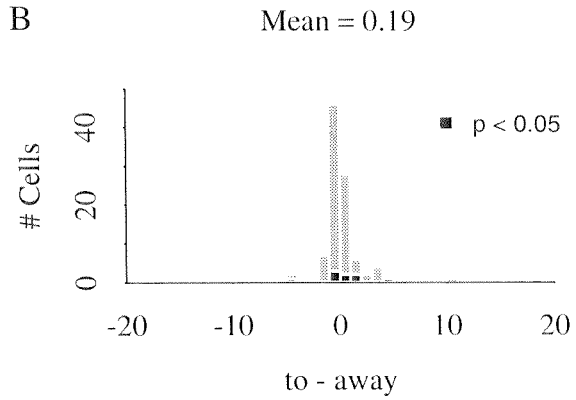
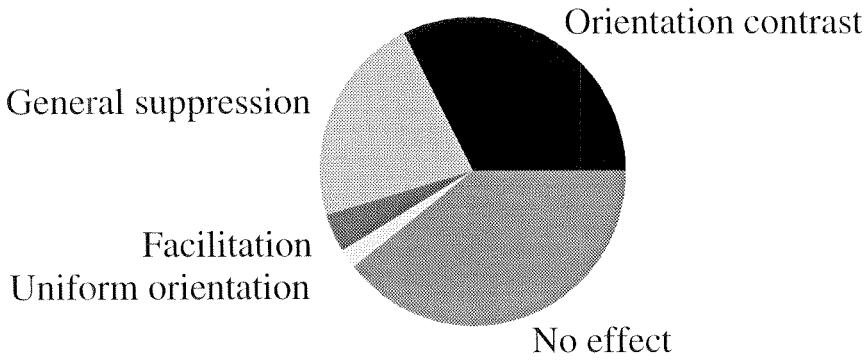


Figure 32. Effect of attention on AT set surround categorizations (n=99). **A**. When attention was directed away from the CRF, there were 32 orientation contrast cells, 22 general suppression cells, 4 facilitation cells, 2 uniform orientation cell, and 39 no effect cells. **B**. When attention was directed to the CRF, there were 38 orientation contrast cells, 26 general suppression cells, 5 facilitation cells, and 30 no effect cells. These distributions were not significantly different from one another by a chi-squared test.

AT set

A away



B to

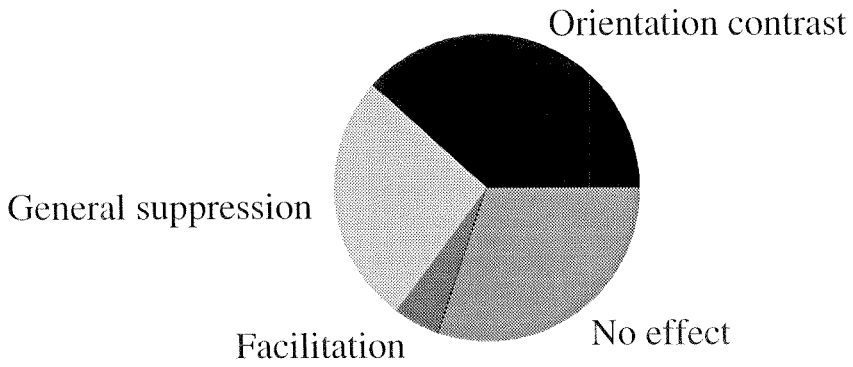


Figure 33. Responses measured in the first monkey, Ronald (n=14, open diamonds), were compared directly with responses measured in the second monkey, Scratchy (n=85, filled diamonds). Differences in both attentional modulation (panels **A** and **B**) and surround modulation (**C** and **D**) are shown. Responses are collapsed across the unanalyzed treatment, i.e., across surround conditions for attention and across attention conditions for surround. The left-hand column (panels **A** and **C**) shows the mean responses across cells. The right-hand column (panels **B** and **D**) shows the means and standard errors of the normalized responses. Using the normalized responses, an ANOVA demonstrated no significant effect of monkey on attentional modulation; however, there was a significant effect of monkey on surround modulation ($p<0.05$).

Ronald vs. Scratchy

AT set

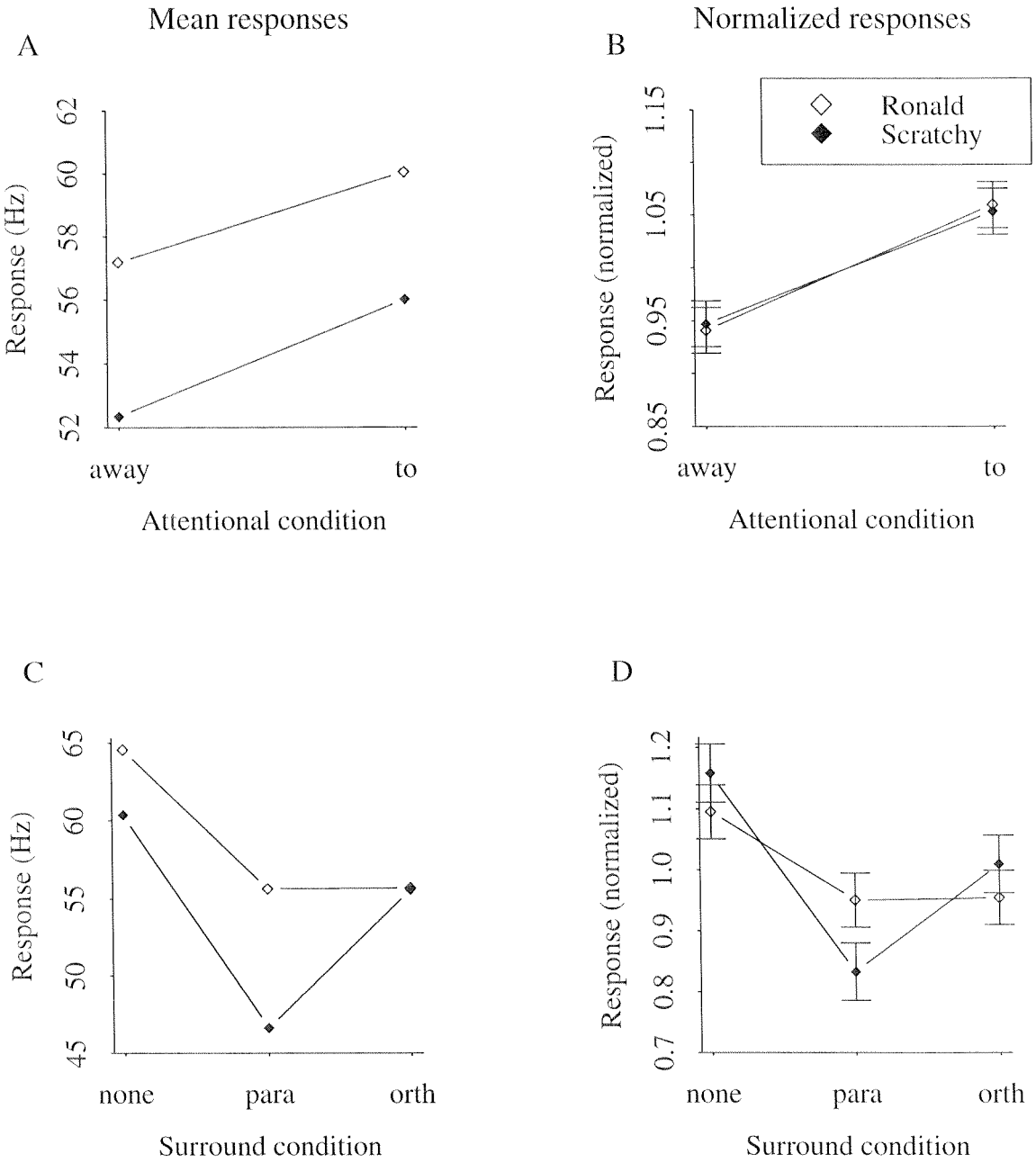
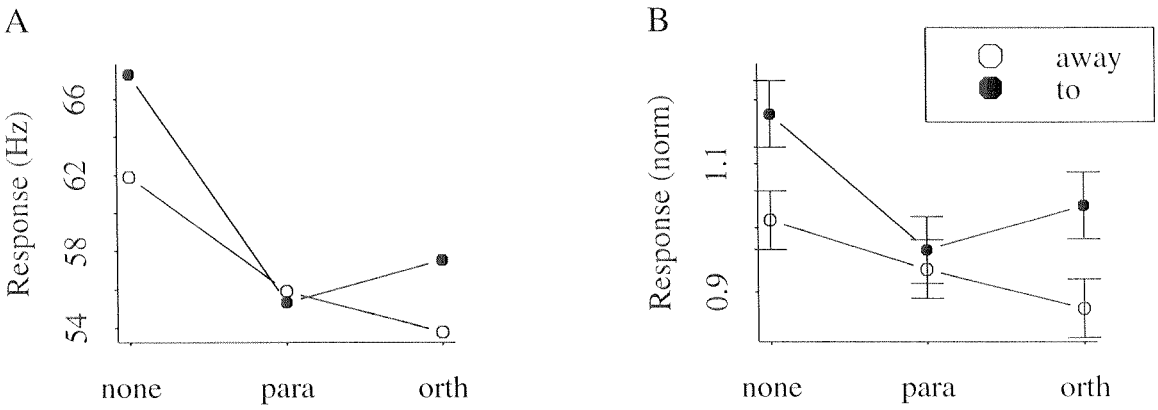


Figure 34. AT set responses for all six conditions, analyzed separately for each monkey. Ronald's responses (n=14) are shown in panels **A** and **B**; Scratchy's responses (n=85) are shown in panels **C** and **D**. The left-hand column (panels **A** and **C**) shows the mean responses across cells. The right-hand column (panels **B** and **D**) shows the means and standard errors of the normalized responses. For Ronald, a within-cell ANOVA demonstrated a main effect of surround ($p<0.001$), but not a main effect of attention; however, an ANOVA using the normalized responses did show a significant main effect of attention ($p<0.01$). The difference between these two may be due to the small number of cells recorded. Neither analysis showed a significant effect of attention on surround modulations. For Scratchy, a within-cell ANOVA demonstrated a significant main effect of surround ($p<0.0001$) and a significant main effect of attention ($p<0.001$), but no interaction between the two.

AT set (by monkey)

Ronald



Scratchy

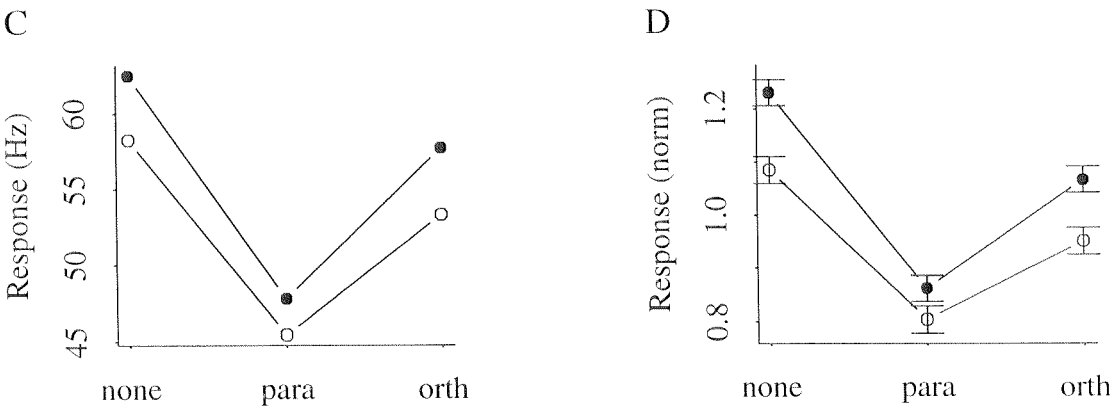


Figure 35. PAT set responses measured using an "easy" task (discrimination=20 degrees, n=38, open diamonds), were compared directly with responses measured using a "hard" task (discrimination<20 degrees, n=24, filled diamonds). Differences in both attentional modulation (panels **A** and **B**) and surround modulation (**C** and **D**) are shown. Responses are collapsed across the unanalyzed treatment. The left-hand column (panels **A** and **C**) shows the mean responses across cells. The right-hand column (panels **B** and **D**) shows the means and standard errors of the normalized responses. Using the normalized responses, an ANOVA demonstrated no significant effect of apparent task difficult on either attentional modulation or surround modulation.

Easy vs. hard

PAT set

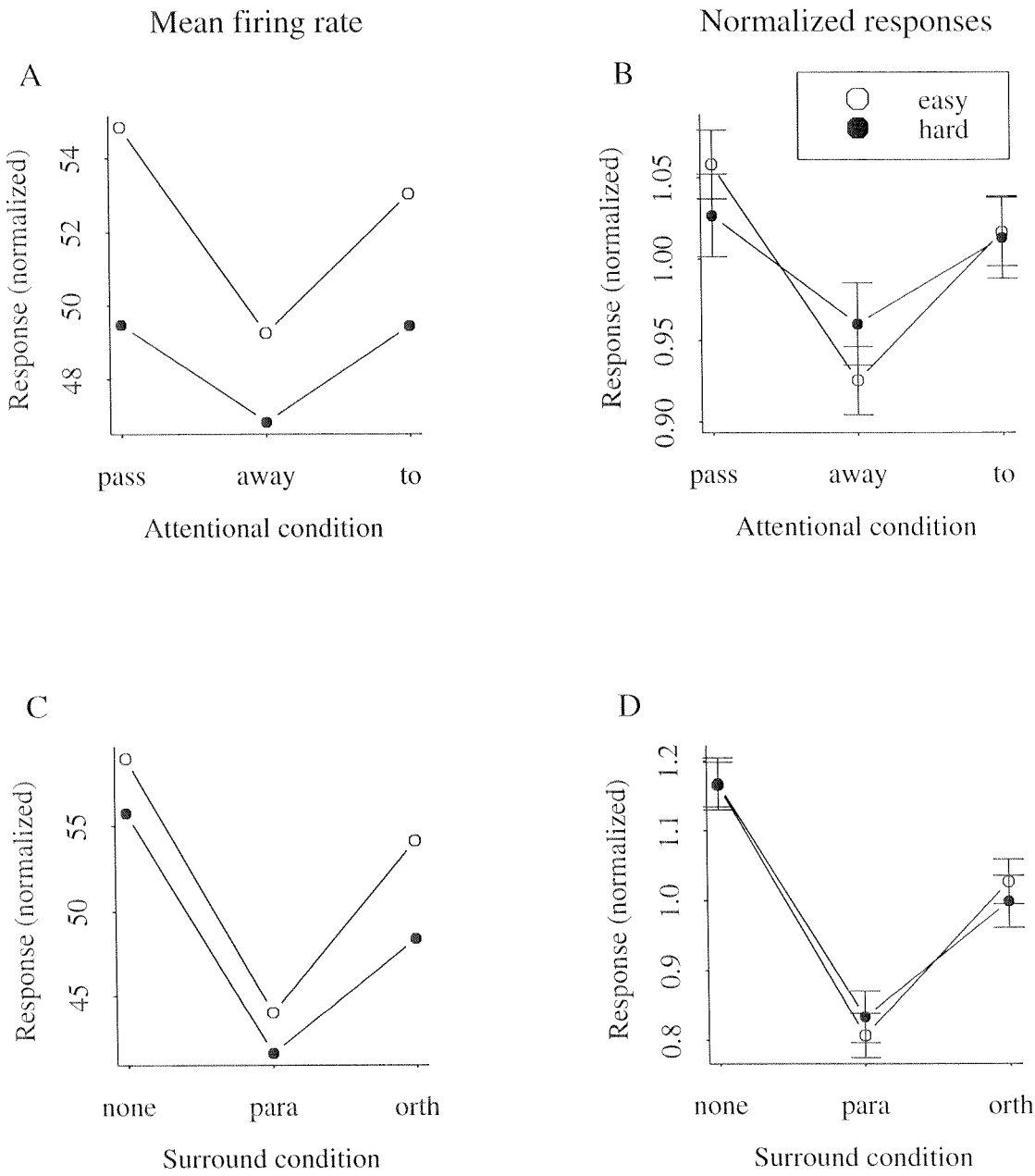


Figure 36. AT set responses measured using an easy task (discrimination=20 degrees, n=59, open diamonds), were compared directly with responses measured using a hard task (discrimination<20 degrees, n=43, filled diamonds). Differences in both attentional modulation (panels **A** and **B**) and surround modulation (**C** and **D**) are shown. Responses are collapsed across the unanalyzed treatment. The left-hand column (panels **A** and **C**) shows the mean responses across cells. The right-hand column (panels **B** and **D**) shows the means and standard errors of the normalized responses. Using the normalized responses, an ANOVA showed the same results as in the PAT set: no significant effect of apparent task difficult on either attentional modulation or surround modulation.

Easy vs. hard

AT set

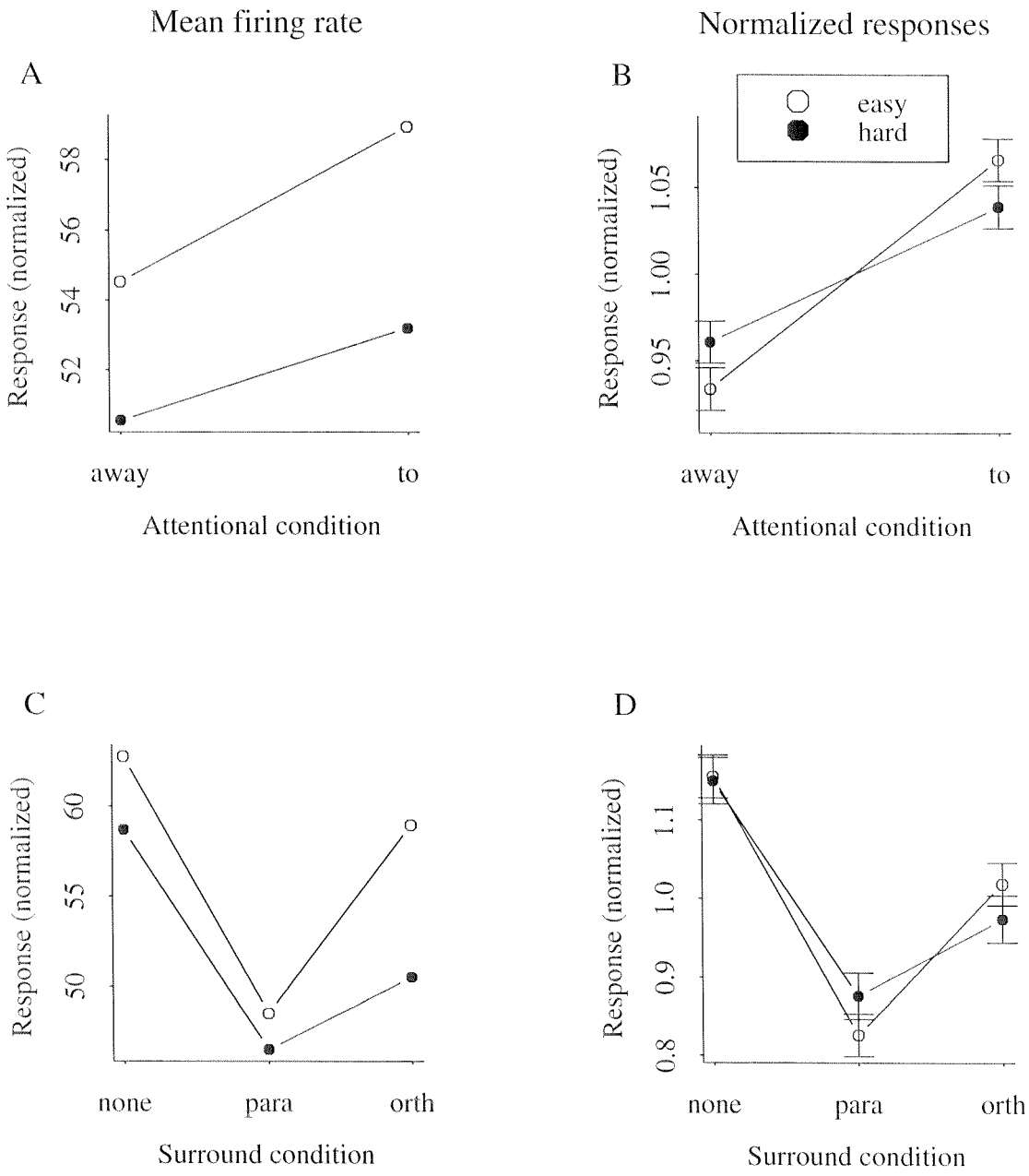
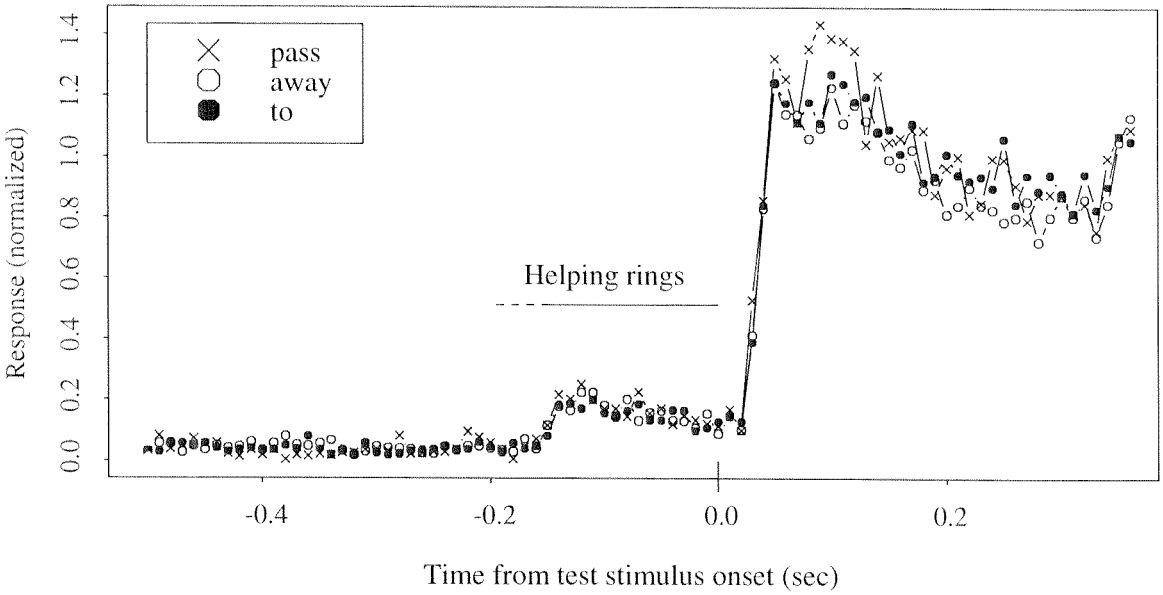


Figure 37. Time courses of activation for the no-surround conditions of both the PAT set (n=59, panel **A**) and the AT set (n=99, panel **B**). There is a mild response preceding the test stimulus onset; this corresponds to the helper-ring presentation, which sometimes elicited a small response. The helper rings were typically shown 200 ms before test stimulus onset, though early recordings sometimes had slightly briefer helper ring displays (the dashed line illustrates this variability). Response onset times did not vary significantly with attentional condition in either set.

Raw responses

A

PAT set



B

AT set

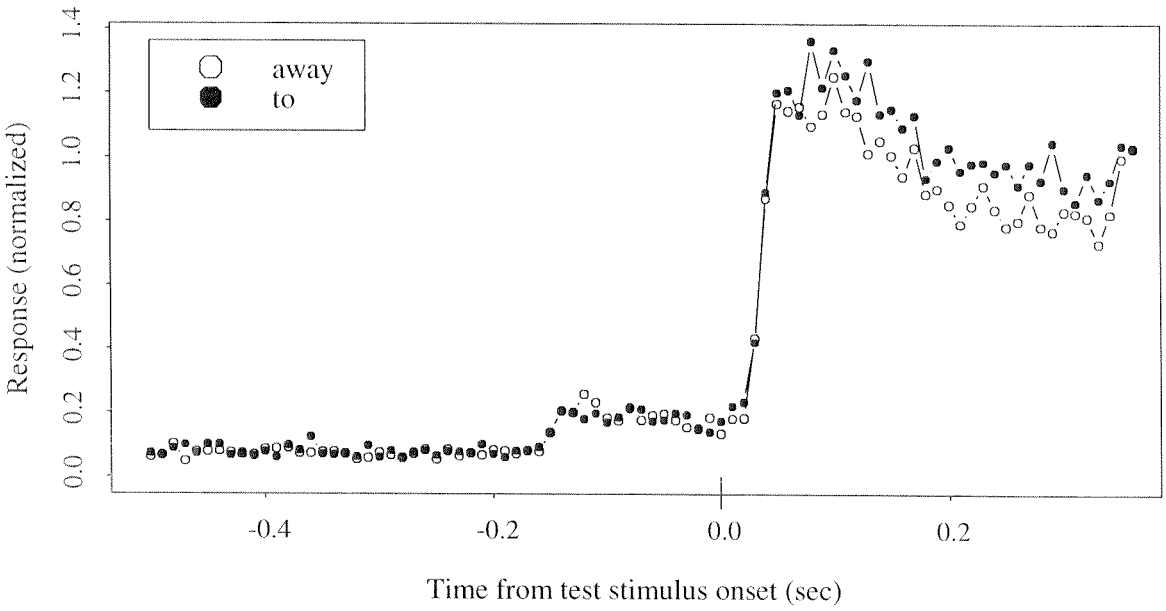


Figure 38. Smoothed time courses for both the PAT set (n=59, panels **A** and **B**) and the AT set (n=99, panels **C** and **D**). The time course themselves are shown in panels **A** and **C**, while the differences between these time courses are shown in panels **B** and **D**. Smoothing was performed using a Gaussian filter (σ=10 ms) on each cell's mean PSTH for each condition, before averaging them together to form the final time courses. The time courses for attentional task (passive vs. attention away) are not significantly different from the time courses for attentional location (attending away vs. attending to). In all cases, though, response modulation does not appear to be notable until about 80 ms after test stimulus onset (time zero), well after the 30-50 ms after stimulus onset that responses are apparent.

Smoothed response time courses

Collapsed across surround conditions

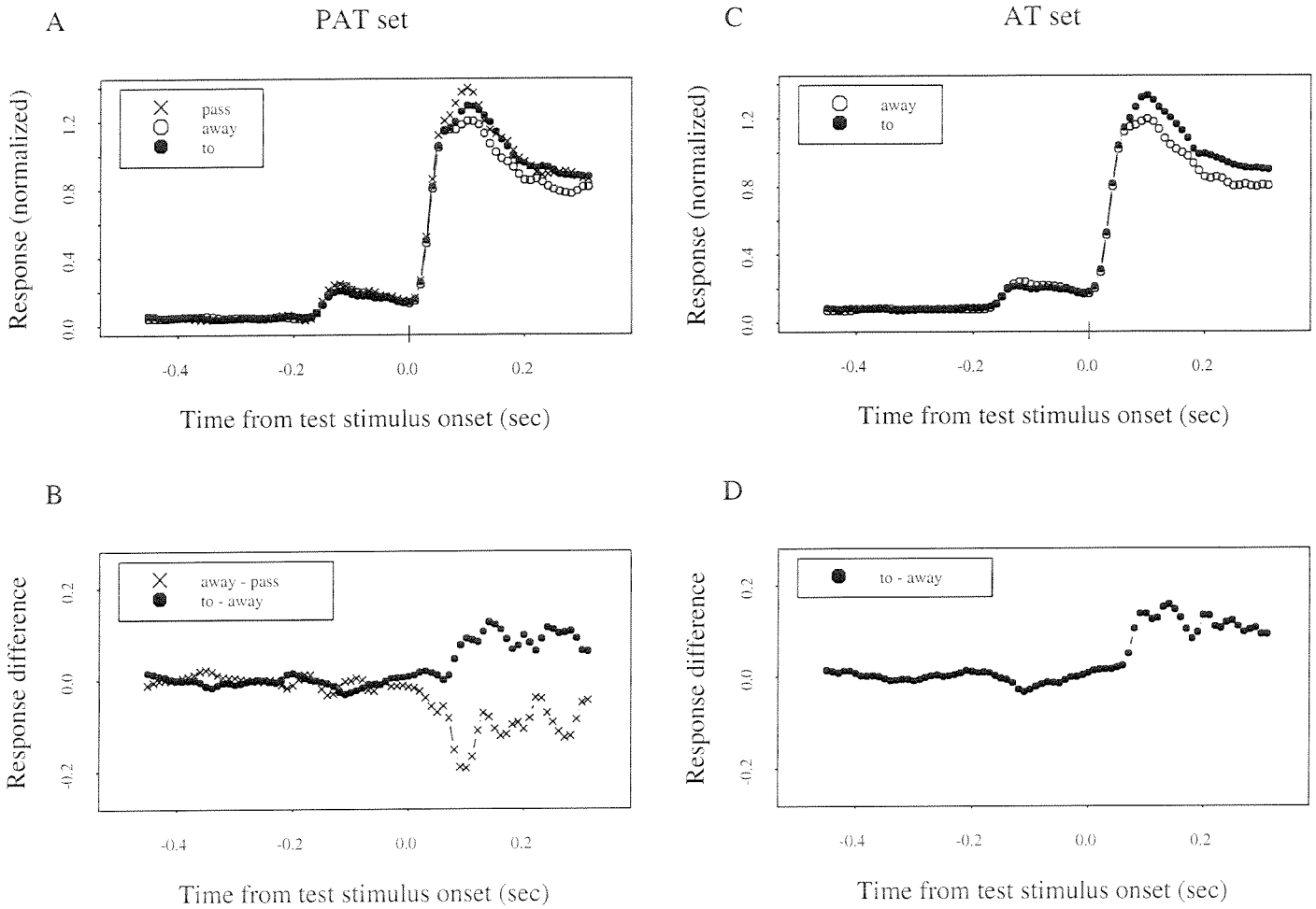
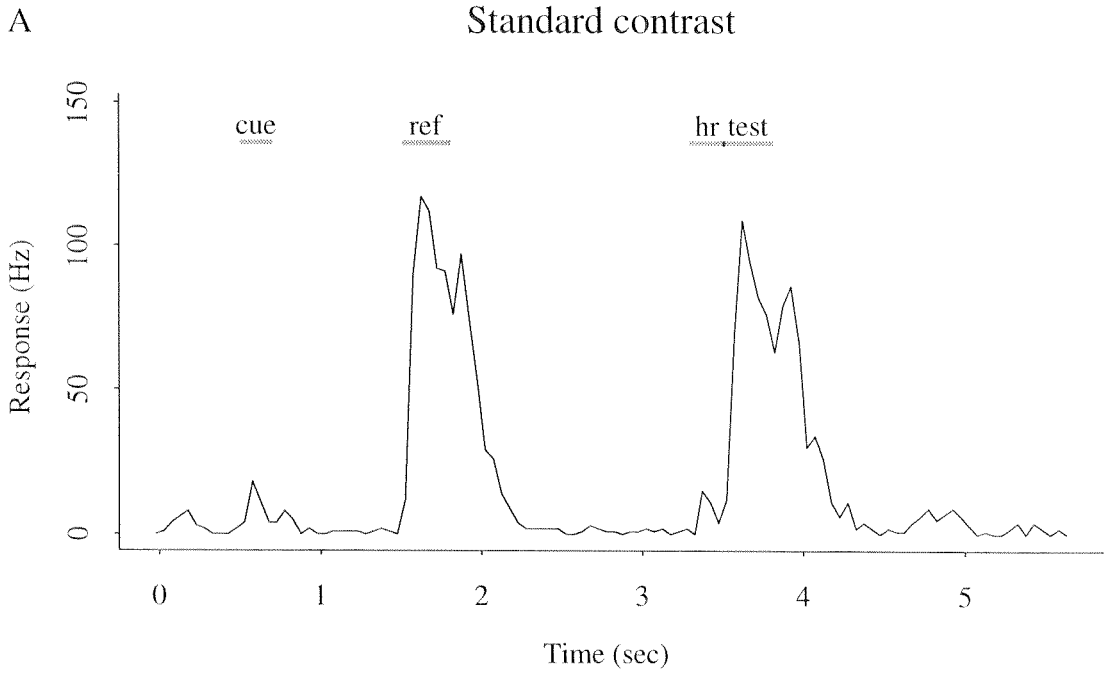


Figure 39. The effect of contrast on a cell's responses and interstimulus baseline activity. **A**. When standard contrast stimuli were displayed on the monitor, this cell demonstrated brisk, constrained responses to both the reference stimulus and test stimulus presented to the cell's CRF. This cell also showed subtle responses to the cue ring and the helper ring (hr), both of which circumscribed the cell's CRF. **B**. When high contrast stimuli were displayed, activity remained elevated throughout the one second interstimulus period, between the reference stimulus offset and the helper ring onset.

A


Standard contrast
cue
ref
hr test
Response (Hz)
0
50
100
150
0
1
2
3
4
5
Time (sec)

B

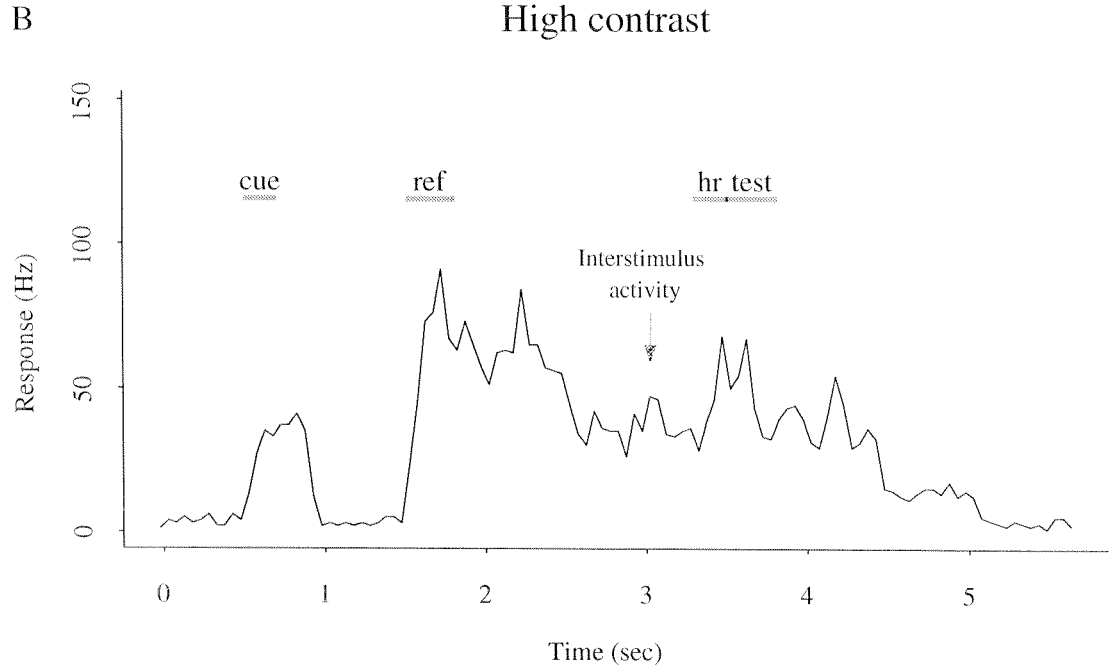

High contrast
cue
ref
hr test
Interstimulus
activity
Response (Hz)
0
50
100
150
0
1
2
3
4
5
Time (sec)

Figure 40. The effect of contrast on interstimulus baseline activity (period E2 in figures 1 and 2) compared to pre-cue baseline activity (period A). **A.** Mean pre-cue baseline and interstimulus baseline of each standard contrast cell (AT set, n=99). Filled circles indicate a significant difference in activity between these two periods for that cell. Under standard contrast conditions, two cells showed significantly elevated activity during the interstimulus period compared to the pre-cue period, while 21 cells showed significantly lower activity during the interstimulus period compared to the pre-cue period. **B.** A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. As a population, the pair-wise differences showed no significant difference between these two epochs. **C.** Mean pre-cue baseline and interstimulus baseline of each high contrast cell (n=28). Under high-contrast conditions, 14 cells showed significantly elevated activity during the interstimulus period, while only three showed significantly lower activity. **D.** A histogram of pair-wise differences across cells. As a population, the pair-wise differences showed a significant elevation during the interstimulus period ($p<0.01$).

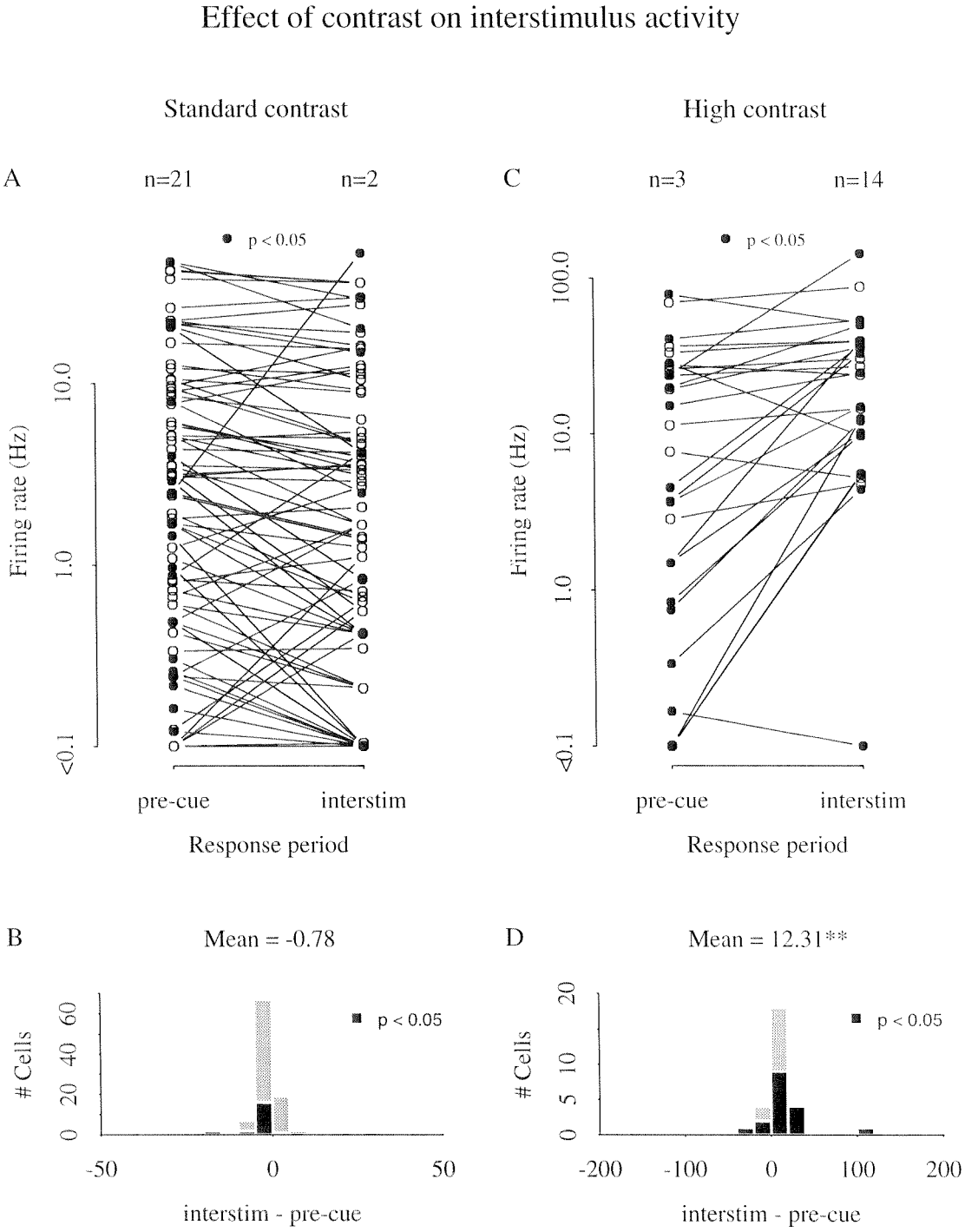
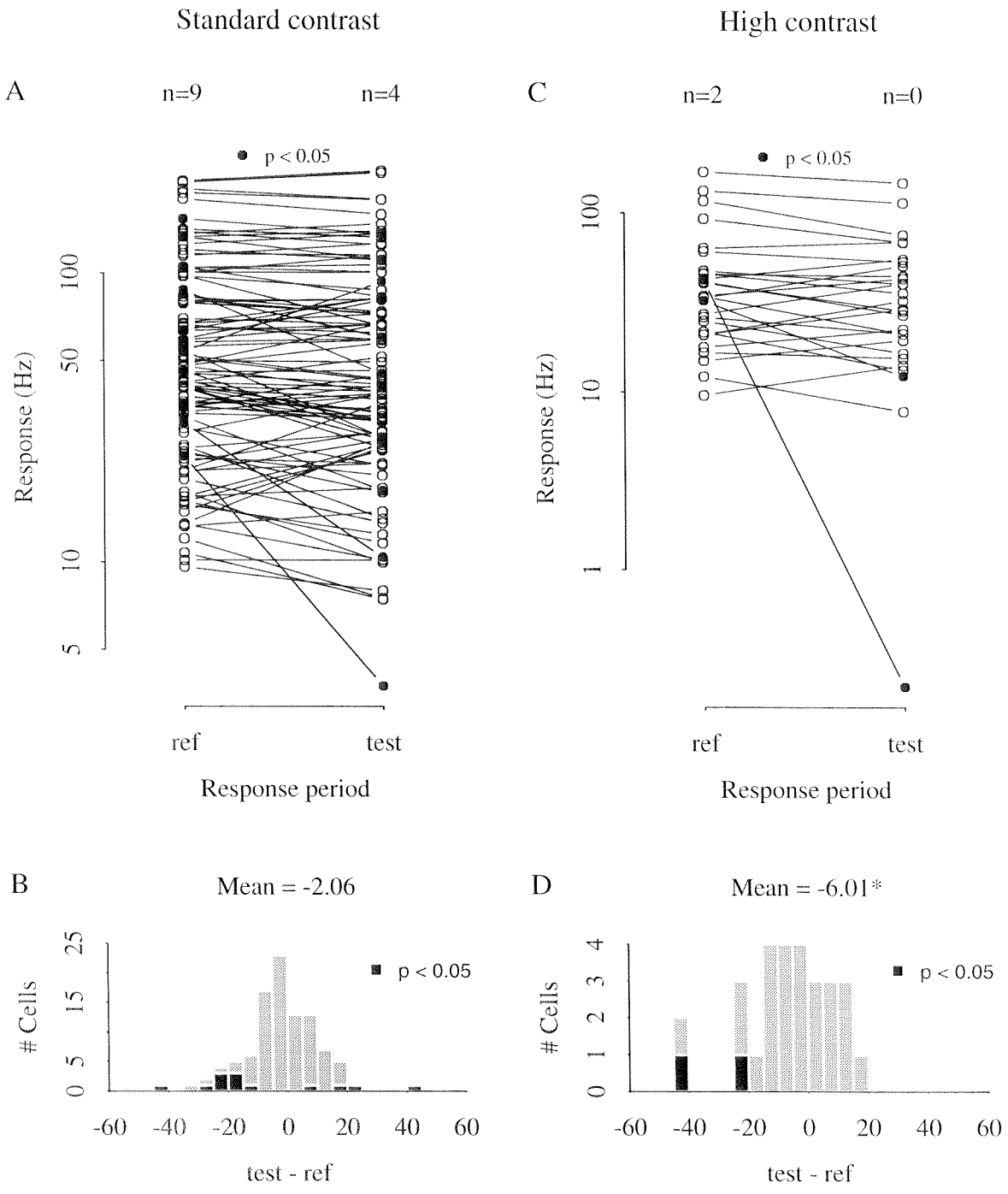

Effect of contrast on interstimulus activity
Standard contrast
High contrast
A
n=21
n=2
C
n=3
n=14
p < 0.05
Firing rate (Hz)
10.0
1.0
<0.1
100.0
pre-cue
interstim
Response period
B
Mean = -0.78
D
Mean = 12.31**
# Cells
0 20 40 60
0 5 10 20
-50
0
50
-200
-100
0
100
200
interstim - pre-cue

Figure 41. The effect of contrast on paired-pulse suppression (measured by comparing reference stimulus and test stimulus responses in match trials when attention is directed away from the CRF). **A.** Mean reference stimulus and test stimulus responses of each standard contrast cell (AT set, n=99). Filled circles indicate a significant difference in activity between these two periods for that cell. Under low-contrast conditions, nine cells have significantly reduced responses to the test stimulus, while four have significantly greater responses. **B.** A histogram of pair-wise differences across cells. Significant differences are shown as filled squares. As a population, the pair-wise differences show no difference between reference and test stimulus responses. **C.** Mean reference stimulus and test stimulus responses of each high contrast cell (n=28). Under high-contrast conditions, two cells have significantly reduced responses to the test stimulus. **D.** A histogram of pair-wise differences across cells. As a population, the pair-wise differences show that the test stimulus responses are significantly reduced relative to the reference stimulus responses ($p<0.05$).


Effect of contrast on paired-pulse suppression
Standard contrast
High contrast
A
n=9
n=4
C
n=2
n=0
p < 0.05
Response (Hz)
5
10
50
100
1
ref
test
Response period
B
Mean = -2.06
D
Mean = -6.01*
# Cells
0 5 15 25
0 1 2 3 4
-60 -40 -20 0 20 40 60
test - ref