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Neural Correlates of Contrast Detection at Threshold

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Summary

Human psychophysical studies have demonstrated that, for stimuli near the threshold of visibility, detection of motion in one direction is unaffected by the superimposition of motion in the opposite direction. To investigate the neural basis for this perceptual phenomenon, we recorded from directionally selective neurons in macaque visual area MT (middle temporal visual area). Contrast thresholds obtained for single gratings moving in a neuron's preferred direction were compared with those obtained for motion presented simultaneously in the neuron's preferred and anti–preferred directions. A simple model based on probability summation between neurons tuned to opposite directions could sufficiently account for contrast thresholds revealed psychophysically, suggesting that area MT is likely to provide the neural basis for contrast detection of stimuli modulated in time.

Introduction

How the visual system is able to detect moving stimuli that are barely visible (like a ship at sea on a foggy night) is a much studied question in the field of vision research. Results from human visual psychophysical experiments suggest that the detection of such "near-threshold" patterns is mediated by directionally selective mechanisms in the brain. One well-established paradigm for demonstrating this involves comparing the contrast threshold for the detection of two patterns of black and white stripes (i.e., gratings) superimposed and moving in opposite directions (which is mathematically equivalent to a stationary grating that undergoes contrast reversal over time, referred to as a counterphase grating) with the contrast threshold for the moving gratings presented alone. When these experiments are performed in human subjects, the counterphase grating is found to be as detectable as the single moving gratings. In other words, the contrast threshold for detecting the presence of a grating moving in one direction is unaffected by the superimposition of a second grating moving in the opposite direction (e.g., Levinson and Sekuler, 1975; Watson et al., 1980; Stromeyer et al., 1984; Dobkins and Teller, 1996). In fact, human subjects are slightly more sensitive to counterphase gratings as compared with single moving gratings (i.e., they exhibit lower thresholds for the former), a finding attributed to probability summation between detectors tuned to opposite directions (Watson et al., 1980; Dobkins and Teller, 1996). In sum, these findings provide strong evidence that directionally selective mechanisms tuned for opposite directions underlie the detection of counterphase gratings and further suggest that such directional mechanisms do not antagonize each another at contrast threshold.

To investigate the neural basis of this perceptual phenomenon, we recorded the responses of single neurons in macaque area MT (middle temporal visual area), a region of extrastriate visual cortex known to contain a high proportion of directionally selective neurons and thought to play a key role in motion perception. Across a range of luminance contrasts, responses elicited by single gratings moving in an MT neuron's preferred direction were compared with those elicited by counterphase gratings, the latter produced by the superimposition of motion in the neuron's preferred and anti–preferred (i.e., opposite) directions. For each neuron, responses were analyzed using a method derived from signal detection theory known as receiver operator characteristic (ROC) analysis. This analysis yields a neuronal contrast threshold, based on the predicted performance of an ideal observer who listens to the activity of that neuron. If MT responses to motion in the preferred direction are unaffected by simultaneous motion in the anti–preferred direction, neuronal contrast thresholds for counterphase (Thr_{CP}) and preferred motion (Thr_{PM}) gratings are expected to be comparable (i.e., yielding threshold ratios, Thr_{CP}/Thr_{PM}, near 1.0). Conversely, if preferred motion responses are opposed by the addition of anti–preferred motion, neuronal contrast thresholds for counterphase gratings should be higher than those for preferred motion gratings (i.e., yielding threshold ratios >1.0).

The results of our study reveal differences across MT neurons in threshold ratios; while the majority of neurons exhibited ratios near 1.0, suggesting a lack of opponent input from the anti–preferred direction, others exhibited threshold ratios far greater than 1.0, suggestive of opponency. On average, the mean threshold ratio was 1.54, indicating that, as a population, MT responses to motion in the preferred direction were somewhat suppressed by simultaneously presented motion in the anti–preferred direction. Despite this suppression, however, the mean threshold ratio observed in MT could well account for threshold ratios observed psychophysically when probability summation between pairs of neurons tuned for opposite directions was considered. These results thus suggest that responses in area MT are sufficient to account for the detection of near-threshold patterns that are modulated in time.

Results

Example Data

Data from two MT neurons are shown in Figure 1, with results plotted as a function of luminance contrast for each of the three stimulus conditions: single gratings

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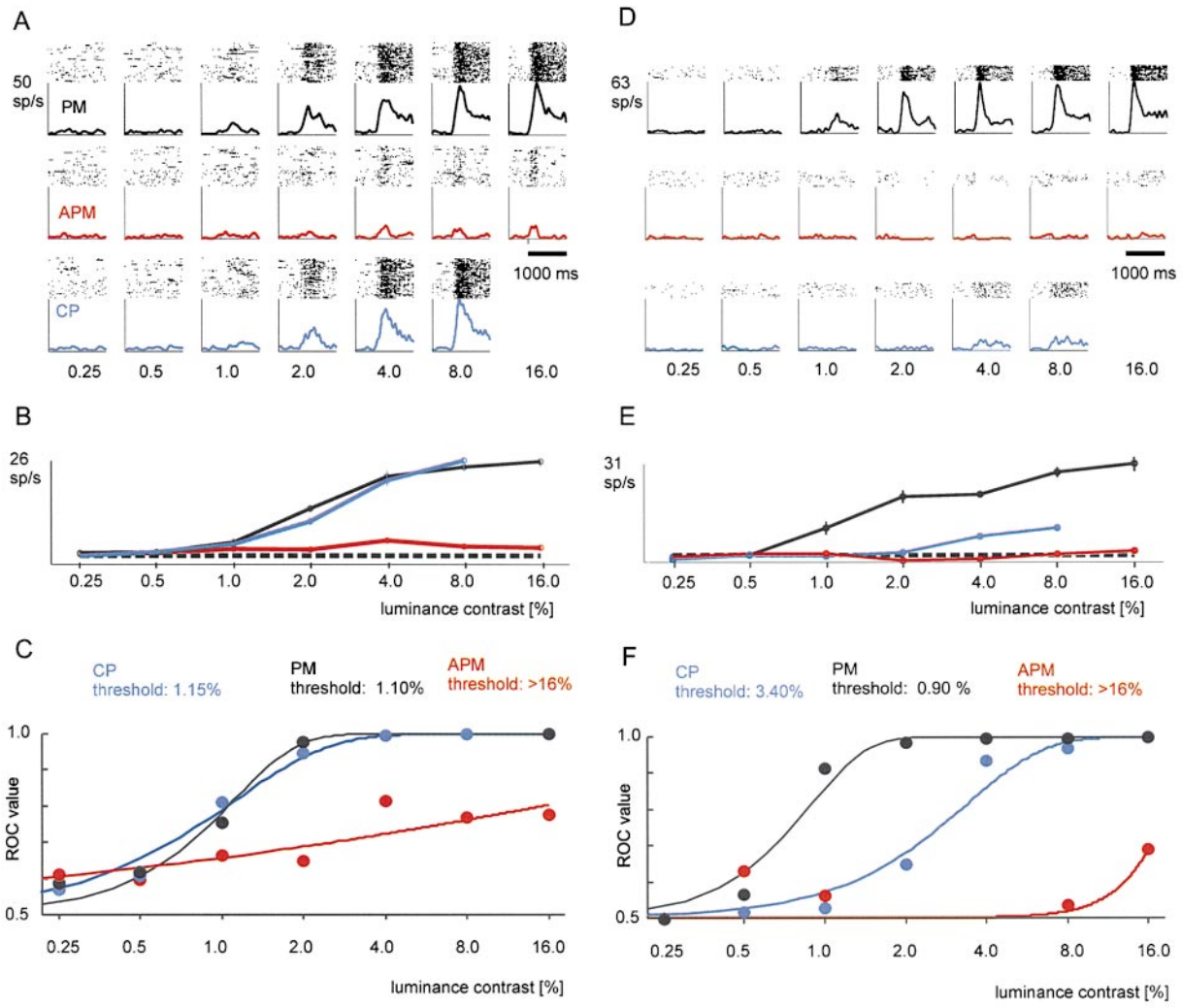

Figure 1. Example Data from Two MT Neurons

The neuron shown on the left-hand side exhibited comparable thresholds for counterphase and preferred motion gratings ($Thr_{CP}/Thr_{PM} = 1.05$). The neuron shown on the right-hand side exhibited a higher threshold for counterphase, as compared with preferred motion, gratings ($Thr_{CP}/Thr_{PM} = 3.8$).

(A and D) Rasters and histograms.

(B and E) Contrast–response functions obtained from mean responses. Error bars denote standard error of the mean.

(C and F) Weibull functions fitted to ROC values derived from MT responses.

Symbols: black lines = preferred motion, red lines = anti–preferred motion, blue lines = counterphase gratings, and dashed horizontal line = mean baseline activity in the absence of a stimulus.

moving in the preferred direction ("preferred motion" [PM], black lines), single gratings moving in the anti–preferred direction ("anti–preferred motion" [APM], red lines) and counterphase gratings (CP, blue lines). In the upper panels (A and D), neuronal responses are plotted in the form of individual trial rasters and cumulative spike histograms. The middle panels (B and E) plot mean responses (spikes/s) as a function of luminance contrast (i.e., contrast–response functions). In the bottom panels (C and F), ROC values are plotted, and the data have been fitted with Weibull functions in order to obtain neuronal contrast thresholds for counterphase (Thr_{CP}) and preferred motion (Thr_{PM}) gratings (threshold = 82% correct). Note that thresholds could not be obtained for motion in the anti–preferred direction, since ROC values remained below 82%.

For the neuron shown on the left-hand side of Figure 1, the contrast–response function for preferred motion was almost identical to that observed for counterphase gratings, while the response to anti–preferred motion hovered around baseline (dashed horizontal line). Thus, at all luminance contrasts, this neuron was largely unaffected by motion in the anti–preferred direction when that motion was presented alone or concurrently with motion in the preferred direction. The derived contrast thresholds for counterphase gratings and preferred motion gratings were extremely similar (1.15% versus 1.10%, respectively), resulting in a threshold ratio (Thr_{CP}/Thr_{PM}) close to 1.0. By comparison, the neuron shown on the right-hand side of Figure 1 exhibited a much higher contrast threshold for counterphase gratings as compared with preferred motion gratings (3.4% versus

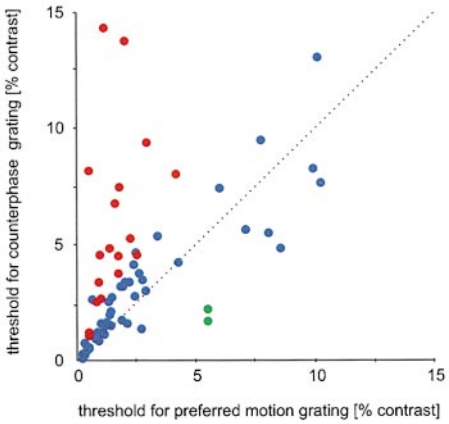

Figure 2. Population Data: Thresholds for Counterphase versus Preferred Motion Gratings

Data are shown for 78 MT neurons (of 96) for which a reliable threshold could be obtained for both preferred motion and counterphase gratings (based on the goodness of the Weibull function fit). Blue circles represent neurons classified as nonopponent (i.e., statistically indistinguishable thresholds for counterphase and preferred motion gratings). Red circles represent neurons classified as opponent (i.e., statistically higher thresholds for counterphase gratings than for preferred motion gratings). The rare green circles represent neurons that exhibited neural summation (i.e., statistically lower thresholds for counterphase gratings than for preferred motion gratings). The diagonal line depicts a threshold ratio (Thr_{CP}/Thr_{PM}) of 1.0.

0.9%, respectively), resulting in a threshold ratio of 3.8. For this neuron, sensitivity to motion in the preferred direction was markedly suppressed by simultaneous motion in the anti–preferred direction. For both neurons, the contrast sensitivity for moving gratings was extremely high, which was typical for the population of MT neurons (see Sclar et al., 1990; Dobkins and Albright, 1994; Gegenfurtner et al., 1994, for similar observations). The vast majority (83%) of neurons exhibited contrast thresholds $<3.0\%$.

Population Data

To observe the relationship between contrast thresholds for moving versus counterphase gratings across the population of neurons, we plotted individual data for our sample of 78 MT neurons in Figure 2. For each neuron, the derived contrast threshold obtained for counterphase gratings is plotted against that obtained for preferred motion. The diagonal line depicts a threshold ratio (Thr_{CP}/Thr_{PM}) of 1.0. As can be observed in this plot, threshold ratios varied across the population of MT neurons, indicating that differences exist in the degree to which responses to motion in the preferred direction are opposed by motion in the anti–preferred direction. To evaluate this effect further, we determined statistically, for individual neurons, whether contrast thresholds for counterphase and preferred motion gratings were significantly different from one another. Specifically, if a given neuron's thresholds for the two stimulus types were statistically indistinguishable from one another (determined by a χ^2 statistic, $p > 0.05$; see Experimental Procedures), we took this as evidence for negligible opposing effects of anti–preferred motion when superimposed upon motion in the preferred direction. A neuron that yielded this result was thus classified as "nonopponent." Conversely, if the threshold obtained for counterphase gratings was significantly higher than that obtained for preferred motion, we took this as evidence for significant opposing effects, and the neuron was classified as "opponent." By this criterion, the majority (74%, blue circles) of sampled MT neurons were nonopponent, with Thr_{CP}/Thr_{PM} ratios close to 1.0. The bulk of the remaining neurons (23%, red circles) were classified as opponent, with Thr_{CP}/Thr_{PM} ratios significantly >1.0. In addition, for a very small minority of neurons (3%, green circles) thresholds for preferred motion were actually lowered by the addition of anti–preferred motion (i.e., Thr_{CP}/Thr_{PM} ratios were significantly <1.0). These neurons were classified as consistent with neural summation, since the oppositely moving grating components in the counterphase grating, in effect, summed their individual contrasts.

Although the majority of MT neurons were classified as nonopponent based on our statistical criterion, as a population, these neurons exhibited a significantly higher mean contrast threshold for counterphase gratings ($Thr_{CP\text{-}mean} = 1.92\%$) as compared with preferred motion gratings ($Thr_{PM\text{-}mean} = 1.54\%$), with a mean threshold ratio of 1.25 ($p < 0.001$, paired t test $= 3.55$). This overall greater sensitivity for moving versus counterphase gratings was augmented when thresholds were averaged across the entire sample of MT neurons ($n = 78$). Here, the mean threshold for counterphase gratings (2.37%) was significantly higher than the mean threshold for preferred motion gratings (1.54%), with a mean threshold ratio of 1.54 ($t = 5.37$, $p < 0.001$). Note that, because we used geometric means in our analyses, the mean of threshold ratios is equivalent to the ratio of threshold means.

If area MT is the critical neural substrate underlying contrast detection of moving and counterphase gratings, we expect the threshold ratios observed in MT to account for the relative thresholds for moving versus counterphase gratings reported in the human psychophysical literature. Implicit in this proposal, however, is the assumption that neuronal data from macaques can be used to model psychophysical data from humans. Although a reasonable inference to make in light of the known similarities in motion processing and contrast sensitivity between the two species (e.g., De Valois et al., 1974; Golomb et al., 1985), we nonetheless thought it important to ensure that macaques exhibit threshold ratios similar to those observed for human subjects. To this end, we obtained psychophysical data from one macaque subject, as described below.

Macaque Psychophysical Data

Contrast thresholds for counterphase and single moving gratings were obtained from one macaque subject using a two-alternative forced choice (2-AFC) paradigm (see Experimental Procedures). Shown in Figure 3 is the percent correct performance of the animal plotted as a function of luminance contrast for both single moving gratings (black lines) and counterphase gratings (blue lines). As for neuronal ROC data, Weibull functions were fitted to the data to determine threshold (i.e., contrast

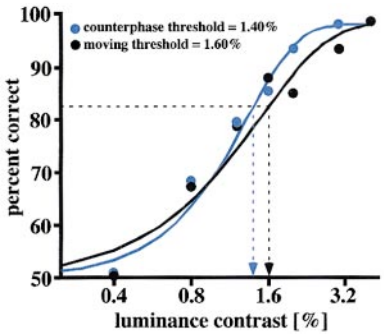

Figure 3. Psychophysical Data from One Macaque Subject

The psychophysical contrast threshold for this macaque was 1.60% for moving gratings (black lines) and 1.40% for counterphase gratings (blue lines), with a resulting threshold ratio ($Thr_{counterphase}/Thr_{moving}$) of 0.88.

yielding 82% correct performance), which was determined to be 1.60% for moving gratings and 1.40% for counterphase gratings.

There are two things to note about these results. First, the psychophysical threshold for moving gratings (1.60%) was extremely close to the mean neuronal threshold in MT derived from ROC analysis (1.54%; see above). Although comparing absolute neuronal and psychophysical thresholds was not the purpose of our study, the similarity between the two measures serves to support the view that area MT underlies contrast detection of moving stimuli. The second point is that, as for human data, the macaque subject exhibited a slightly lower threshold for counterphase gratings than for single moving gratings (although the difference was not statistically significant, $p > 0.05$, χ^2 statistic). The resulting threshold ratio ($Thr_{counterphase}/Thr_{moving}$) for the animal was 0.88, a value quite close to those reported for human subjects ($\sim$0.7 to 0.9) tested under low–spatial/high–temporal frequency conditions similar to those employed in the present study (e.g., Watson et al., 1980; Dobkins and Teller, 1996). Thus, it appears safe to assume that humans and macaques perform similarly with respect to their relative sensitivities to moving versus counterphase gratings. Having demonstrated this likeness, we now turn to a discussion of how threshold ratios in MT might account for psychophysically obtained threshold ratios.

Modeling Psychophysical Data

As discussed in the Introduction and in the previous paragraph, psychophysical data reveal slightly lower contrast thresholds for counterphase gratings as compared with single moving gratings. These psychophysical threshold ratios below 1.0 are typically explained by positing that the oppositely moving components of the counterphase grating are detected by independent directionally selective mechanisms, with probability summation occurring between them. Probability summation predicts a slight advantage for detecting the counterphase stimulus simply because it is composed of two, rather than a single, moving components (e.g., Watson, 1979; Nachmias, 1981). That is, while the counterphase stimulus can be detected if either of two directional mechanisms reaches threshold (each selective for one of the two moving components in the counterphase stimulus), detection of a moving grating stimulus relies on a single directional mechanism reaching threshold. The degree to which this phenomenon is expected to lower the psychophysical threshold ratio below 1.0 depends on the slope of the Weibull function relating contrast to performance, as described further below.

At first glance, the fact that humans and macaques exhibit slightly lower contrast thresholds for counterphase, as compared with moving, gratings appears to contradict our neuronal data demonstrating the converse, i.e., that on average, MT neurons are more sensitive to moving gratings. This apparent discrepancy can be reconciled when probability summation is considered. To model the effects of probability summation using our neuronal data, we assume that the psychophysical contrast threshold for counterphase gratings is determined by the thresholds of pairs of MT neurons tuned for opposite directions. Although, in our experiments, we recorded from only one neuron at a time, we can assume that for each neuron sampled, there existed an exact counterpart, i.e., an antineuron with the same preferences and contrast threshold but tuned for the opposite direction. In other words, the responses to counterphase gratings that we observed in the sampled neuron were assumed to be simultaneously occurring in the antineuron (from which we did not record). The theory behind this model, which is described in detail in the Experimental Procedures, predicts that the psychophysical threshold ratio ($Ratio_{PSY} = Thr_{counterphase}/Thr_{moving}$) will be related to the ratio of mean neuronal thresholds ($Thr_{CP\text{-}mean}/Thr_{PM\text{-}mean}$) as follows: $Ratio_{PSY} = (Thr_{CP\text{-}mean}/Thr_{PM\text{-}mean}) * (0.5)^{1/\beta\text{-}mean}$, where β-mean corresponds to the geometric mean slope of the Weibull functions derived for MT neurons under the counterphase condition. In our neuronal sample, the mean threshold ratio was 1.54, and the mean slope of the function for counterphase gratings was 1.04. Based on these values, the predicted psychophysical threshold ratio is 0.79, which is consistent with values observed in previous human psychophysical studies and close to the psychophysical value obtained from the macaque subject of the present study. Thus, our model incorporating probability summation between directionally selective MT neurons appears to be sufficient to account for the relative thresholds for moving versus counterphase gratings revealed psychophysically.

Mean Contrast–Response Functions

In addition to investigating neuronal contrast thresholds, our data also allowed us to determine the mean population response (i.e., spikes/s) as a function of luminance contrast. In particular, we investigated whether a reduced response to counterphase, as compared with preferred motion, gratings is dependent on the amount of luminance contrast in the stimulus. Evaluating the effects of luminance contrast was motivated, in part, by a dichotomy in the psychophysical literature suggesting that directional mechanisms exhibit opponency for suprathreshold stimuli (Stromeyer et al., 1984; Qian et al., 1994; Zemany et al., 1998) but not for near-threshold stimuli (Levinson and Sekuler, 1975; Watson et al., 1980;

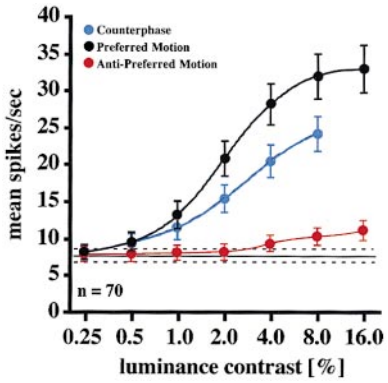

Figure 4. Mean Contrast–Response Functions

Mean responses and standard errors are plotted for counterphase (blue lines), preferred motion (black lines), and anti–preferred motion (red lines) gratings. Horizontal solid and dashed lines denote mean baseline activity ±1 standard error, respectively. Responses are averaged across 70 neurons. (Data from 8 of a total of 78 neurons are not included, since these neurons were tested at a slightly different range of contrasts.)

Stromeyer et al., 1984; Dobkins and Teller, 1996; Raymond and Braddick, 1996). Based on these psychophysical findings, we expected anti–preferred motion to suppress preferred motion responses at high, but not low, luminance contrasts.

In Figure 4, we have plotted mean MT responses and standard errors separately for counterphase (blue lines), preferred motion (black lines), and anti–preferred motion (red lines) data. Horizontal solid and dashed lines denote mean baseline activity ±1 standard error, respectively. (Note that, for this analysis, data from all neurons—classified as opponent, nonopponent, or "neural summation"—were combined.) There are two things to point out in these contrast–response functions. First, anti–preferred motion elicited no discernible response at contrasts below 4.0%. Above this contrast, the response was significant, yet extremely small. This finding indicates that, on average, single gratings moving in the anti–preferred direction do not inhibit activity below baseline. Second, differences between the contrast–response functions for counterphase and preferred motion gratings grew larger as luminance contrast was increased. At the two lowest contrasts (0.25% and 0.5%), the mean responses to moving and counterphase gratings were essentially identical to each other (paired t test comparisons: 0.25% contrast: $t = 0.08$, $p = NS$; 0.5% contrast: $t = 0.47$, $p = NS$). Note that this is not a simple consequence of a lack of response to counterphase and moving gratings at low contrasts, since both stimulus types elicited responses significantly greater than baseline activity at 0.25% contrast ($t_{CP} = 2.00$, $p < 0.05$; $t_{PM} = 2.46$, $p < 0.01$) and at 0.5% contrast ($t_{CP} = 2.35$, $p < 0.02$; $t_{PM} = 2.58$, $p < 0.01$). Only at contrasts >0.5% were the responses elicited by counterphase gratings significantly reduced as compared with those elicited by preferred motion gratings ($p < 0.05$). At 1.0%, 2.0%, 4.0%, and 8.0% contrast, ratios of mean responses ($Resp_{CP\text{-}mean}/Resp_{PM\text{-}mean}$) were 0.87, 0.74, 0.73, and 0.75, respectively.

In sum, these data demonstrate differential effects at low versus high luminance contrasts. At relatively low contrasts, neurons faithfully respond to motion in the preferred direction regardless of motion simultaneously presented in the anti–preferred direction. At contrasts ≥2.0%, the addition of anti–preferred motion serves to reduce the neuronal response by a roughly constant percentage (~25%). This differential effect of luminance contrast may explain why studies that employ suprathreshold stimuli typically observe antagonistic interactions between opposite directions, while studies conducted near threshold do not, an issue we return to in the Discussion.

Directional Opponency or Contrast Normalization?

We have considered the possibility that the suppressive effects of counterphase gratings are due to opponent input from anti–preferred motion. It is also possible that the suppression reflects contrast gain control mechanisms invoked under the counterphase condition, which has twice the contrast as the single moving gratings. In this scenario, which has previously been put forth (Heeger, 1993; Tolhurst and Heeger, 1997) to account for the responses of cat V1 neurons to moving and counterphase gratings of suprathreshold contrast (Dean et al., 1980; Reid et al., 1987; Albrecht and Geisler, 1991; Tolhurst and Dean, 1991; Geisler and Albrecht, 1992), contrast normalization within a neuron arises due to divisive input from a neighborhood of active neurons tuned for the full range of directions. That such a divisive normalization might account for some of our results is supported by the finding that, for gratings containing between 2.0% and 8.0% luminance contrast, the suppressive effect of counterphase gratings was roughly proportional to the amplitude of the response to motion in the preferred direction (~25%; see Figure 4).

One way to discern whether the suppression observed in MT neurons is a consequence of opponency versus contrast gain control is to study those neurons that exhibited significantly higher thresholds for counterphase, as compared with preferred motion, gratings (classified as opponent; see Figure 2). If the suppressive effect of counterphase gratings results from directionally opponent input, anti–preferred motion presented by itself should inhibit activity in these neurons below baseline (see Simoncelli and Heeger, 1998). To study this, we investigated ROC values for the anti–preferred motion condition (e.g., see Figures 1C and 1F, red lines). Here, ROC values are predicted to be <0.5 if anti–preferred motion inhibits neuronal activity. Note that we chose to use ROC data, as opposed to mean activity data (i.e., spikes/s), since the former are a more accurate measure of detectability.

In Figure 5, mean ROC values for anti–preferred motion obtained from opponent neurons are plotted as a function of luminance contrast (open red squares). For comparison, ROC values are also plotted for neurons classified as nonopponent (open blue squares), i.e., neurons that exhibited comparable thresholds for counterphase and preferred motion gratings (see Figure 2). As expected, if suppression arose from directionally selective inhibition, the neurons classified as opponent were inhibited by single gratings moving in the anti–preferred direction, as evidenced by ROC values that

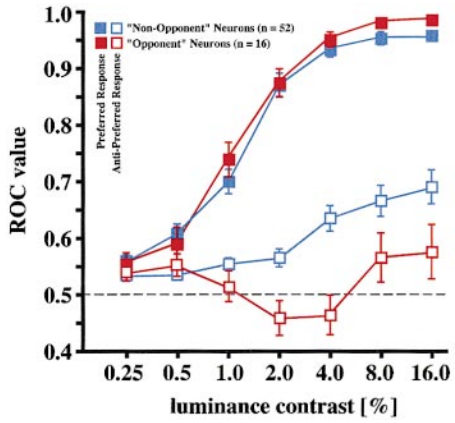

Figure 5. ROC Values for Opponent and Nonopponent Neurons

Mean ROC values and standard errors are plotted as a function of luminance contrast. Symbols: red squares = opponent neurons, blue squares = nonopponent neurons, open squares = ROC values for anti–preferred motion, and closed squares = ROC values for preferred motion. As for Figure 4, data from eight neurons are not included, since these neurons were tested at a slightly different range of contrasts. In addition, data from the two neurons that exhibited neural summation (Figure 2, green circles), i.e., that were neither opponent nor nonopponent, are not included.

fell below 0.5 at low contrasts (~2% to 4%). Although ROC values <0.5 were not observed at all contrasts, values were significantly lower for opponent neurons, as compared with nonopponent neurons ($F(1,66) = 7.42$, $p < 0.001$).

For further comparison, ROC values obtained from preferred motion responses are also plotted separately for opponent (closed red squares) and nonopponent (closed blue squares) neurons. Unlike the data for anti–preferred motion, ROC values for preferred motion were essentially identical for opponent and nonopponent neurons ($F(1,66) = 0.45$, p = NS). Thus, while opponent and nonopponent neurons are equally sensitive to motion in their preferred direction, they differ markedly in their response to motion in the anti–preferred direction. Taken together, these results suggest that the significant suppressive effect of counterphase gratings, which was observed in a minority of MT neurons, is due (at least partially) to opponent input from anti–preferred motion and is not just a result of contrast normalization.

Discussion

These experiments provide a demonstration of contrast thresholds in area MT derived from an ideal observer analysis of neuronal responses. Here, we find that, for the majority of MT neurons, the contrast threshold for counterphase gratings is statistically indistinguishable from that obtained for motion in the preferred direction. This indicates that responses to preferred motion in these neurons are not significantly affected by simultaneously presented motion in the anti–preferred direction, a result that provides evidence for nonopponent directional processes in a proportion of MT neurons. Other neurons, however, exhibit markedly elevated thresholds for counterphase, as compared to preferred motion, gratings, and, thus, their responses are consistent with opponent processes in MT. Most importantly, regardless of the degree of opponency in individual neurons, the population threshold data from MT can adequately account for psychophysical data when probability summation between neurons tuned for opposite directions is considered. That is, our MT data predict a slight overall advantage for detection of counterphase gratings at the perceptual level, which is in line with results from psychophysical experiments. In sum, these experiments suggest that responses in MT are sufficient to account for the perceptual ability to detect time-modulated patterns at contrast threshold (but see Pasternak, 1986, for arguments, based on cat behavioral data, against directional mechanisms underlying detection of counterphase gratings).

In the remainder of this section, we discuss our results in the context of previous findings. First, we address the literature on motion opponency and discuss whether the degree of opponency depends on stimulus contrast. Second, we discuss the results of previous experiments investigating opponency in area MT. On a final note, we raise the possibility for the existence of two generally distinct neuronal types in MT—opponent versus nonopponent—and discuss whether these divisions might map onto the previously described pattern versus component neuronal distinction.

Does Motion Opponency Depend on Stimulus Contrast?

The degree to which motion detectors exhibit opponency (i.e., antagonism between pairs of detectors tuned for opposite directions) has been an issue of longstanding debate. Early models of motion processing proposed an opponent stage of processing, in which detectors tuned to opposite directions mutually inhibit each other (e.g., Adelson and Bergen, 1985; van Santen and Sperling, 1985). In human psychophysical studies, the notion of opponency has been supported by results demonstrating antagonistic interactions between stimuli moving in opposite directions (e.g., Qian et al., 1994; Zemany et al., 1998). Contrary to these findings, however, several psychophysical studies have shown that the detectability of moving patterns is unabated by the addition of motion in the opposite direction (e.g., Levinson and Sekuler, 1975; Watson et al., 1980; Dobkins and Teller, 1996). These latter results support nonopponency of directional mechanisms (see Raymond and Braddick, 1996, for similar conclusions based on motion adaptation experiments).

The discrepancy across studies is likely explained by stimulus differences; it is generally the case that studies reporting opponency employ stimuli of suprathreshold contrast, whereas studies reporting nonopponency employ stimuli near contrast threshold. In fact, the influence of stimulus contrast on the degree of motion opponency has previously been observed within a single psychophysical study by Stromeyer et al. (1984). These investigators employed counterphase gratings in a paradigm that allowed them to assess whether the motion system performs a subtraction between signals for leftward and rightward motion—an indicator of opponent processes. The results of their study demonstrated opponency at

suprathreshold levels of luminance contrast but not at contrast threshold.

Similar to the results from these psychophysical experiments, the mean contrast–response functions of the present study suggest that opponency is dependent on luminance contrast (Figure 4). Specifically, suppression of MT responses by counterphase gratings was observed at higher (~1.0% to 8.0%), but not lower (0.25% to 0.5%), luminance contrasts. It is this differential effect of luminance contrast observed for MT neurons that may account for differences in the degree of opponency observed across various psychophysical studies.

Relationship to Previous MT Studies

The issue of opponency has been addressed in several previous neurophysiological experiments in MT. Unlike the present study, however, these earlier studies employed only suprathreshold contrast stimuli. In general, their results are consistent with those of the present study demonstrating suppressive effects at higher luminance contrasts (see Figure 4). For example, studies employing moving dot fields of suprathreshold contrast have shown that the responses of MT neurons to motion in the preferred direction are suppressed by concomitant motion in the anti–preferred direction (Snowden et al., 1991; Qian and Andersen, 1994; Recanzone et al., 1997; see Qian and Andersen, 1995, for related findings in area V1). Similar results have been observed in a recent study by Heeger et al. (1999), which employed functional magnetic resonance imaging (fMRI) to measure responses in human area MT+ (analogous to macaque area MT) to suprathreshold counterphase and single moving gratings. In addition to obtaining fMRI data from human subjects, Heeger et al. also used their stimuli to obtain neurophysiological data from 12 isolated MT neurons (and several multiunit MT sites) in macaques. These investigators found that responses (in human MT+ and macaque area MT) elicited by suprathreshold counterphase gratings were reduced, as compared with those elicited by suprathreshold single moving gratings.

In sum, there is strong consensus across MT studies that opponent processes operate at suprathreshold levels of contrast. A contribution of the present study is the finding that opponent mechanisms are less effective at contrasts near threshold. We base this conclusion on two main results. First, many MT neurons exhibited contrast thresholds for counterphase and preferred motion gratings that were nearly identical to one another (e.g., Figure 1C). Thus, for these neurons, motion in the anti–preferred direction had negligible opposing effects near contrast threshold. Second, across the entire population of MT neurons, mean responses (spikes/s) elicited by counterphase and preferred motion gratings were equivalent at the two lowest contrasts tested (Figure 4). Taken together, the results of the present and previous studies suggest that opponent effects depend on the amount of luminance contrast in the stimulus—a finding that mirrors and thus potentially underlies results from psychophysical studies.

Two Types of MT Neurons?

In the present study, we categorized neurons as nonopponent or opponent, depending on whether thresholds were significantly elevated for counterphase, as compared with preferred motion, gratings. By this criterion, the ratio of nonopponent versus opponent neurons was ~3:1. We should point out, however, that we did not observe any bimodality in the data set, i.e., the distribution of threshold ratios (Thr_{CP}/Thr_{PM}) across neurons did not divide neatly into two populations. Although the opponent/nonopponent distinction is probably more of a continuum, it is nonetheless tempting to draw a connection between our nonopponent versus opponent dichotomy and the "component" versus "pattern" dichotomy reported in plaid motion experiments, which also appears to exist in an ~3:1 ratio (e.g., Movshon et al., 1985; Rodman and Albright, 1989).

Plaid motion experiments employ stimuli consisting of two component gratings, superimposed and moving in different directions. When human subjects view this stimulus, they perceive a rigidly moving plaid pattern, and not the individual motions of the components, a phenomenon that is interpreted as evidence for the integration of local motion signals into a coherent global motion percept (reviewed by Stoner and Albright, 1994). When these moving plaid patterns are presented to MT neurons, two generally distinct neuronal types are observed. One type (referred to as a pattern neuron) responds best when the plaid pattern is moved in its preferred direction, indicating that the neuron integrates the motion of the component gratings. The other type (referred to as a component neuron) responds best to motion of either component in its preferred direction, indicating a lack of integration.

It would perhaps not be surprising to discover that pattern neurons are also opponent, since opponency requires an integration (i.e., a subtraction) of signals from opposite directions. In fact, one could argue that pattern neurons, which signal global motion, should exhibit no response to counterphase gratings, since this stimulus does not, in fact, appear to move (rather, it appears to flicker over time). By comparison, component neurons would be well suited to signal the contrast of motion in their preferred direction regardless of concomitant motion in other directions. Further studies will be required to determine whether the opponent/nonopponent dichotomy observed herein maps onto the previously described pattern/component distinction.

Experimental Procedures

Experiments were conducted using neurophysiological and animal training methods described previously (e.g., Dobkins and Albright, 1994). In brief, macaque monkeys (*M. mulatta*) were trained to fixate a small spot on a video screen situated 63 cm away. Simultaneously, we recorded the responses from single isolated neurons in area MT, using microelectrodes lowered into that region of visual cortex. Protocols for all experiments were approved by the Salk Institute Animal Care and Use Committee and conformed to United States Department of Agriculture regulations and National Institutes of Health guidelines for the humane care and use of laboratory animals. Further details about experimental procedures are provided below.

Apparatus

Visual stimuli were generated using an SGT Pepper Graphics board (Number Nine Computer, 640 by 480 pixel resolution, 60 Hz frame rate) residing in a Pentium-based PC and were displayed on a 20 inch analog RGB monitor (Sony GDM 2000TC, 60 Hz, noninterlaced). The outputs of the red and green guns were combined, such that

a resolution of 12 bits/pixel was achieved (Pelli and Zhang, 1991). This manipulation allowed for a presentation of contrasts on the monitor that were low enough to obtain luminance contrast thresholds.

MT Recordings

Visual responses were recorded from a total of 96 directionally selective MT neurons in three awake, fixating macaques. For each MT neuron tested, the receptive field was mapped using a black bar moving on a gray background. The preferred direction for the neuron was determined from its directional tuning curve, obtained by presenting moving black/white sinusoidal gratings (0.7 cycles/degree, 4 Hz, 100% Michelson contrast) in eight different directions. The optimal spatio–temporal frequency for the neuron was determined by presenting gratings at various spatial frequencies (range = 0.4 to 1.4 cycles/degree) and temporal frequencies (range = 1 to 8 Hz). The preferred direction and spatio–temporal frequency for the neuron were then used for subsequent testing. In our sample, most MT neurons preferred (and were thus tested at) higher temporal frequencies (mean = 5.4 ± 2.6 Hz) and lower spatial frequencies (mean = 0.56 ± 0.7 cycles/degree). Other stimulus parameters were as follows: mean luminance of gratings and background = 20 cd/m^2; CIE coordinates = 0.327, 0.341; duration = 1000 ms; and size = 5° diameter for neurons with receptive field sizes <5° and 10° diameter for neurons with receptive field sizes >5°. The mean receptive field eccentricity of the sample was 4.12° ± 2.8°.

Neuronal responses were obtained for three different stimulus conditions: (1) single gratings moving in the preferred direction (preferred motion), (2) single gratings moving in the anti–preferred (i.e., opposite) direction (anti–preferred motion), and (3) counterphase gratings composed of preferred and anti–preferred motion superimposed. Each neuron was tested at six to seven different levels of luminance contrast (ranging in octave steps from 0.25% to 16% Michelson contrast). Luminance contrast in the counterphase grating is described in terms of the contrasts of its moving components (which were equal to one another), rather than by its total contrast (which is twice that of the component contrast). The different stimulus conditions and contrasts were interleaved in random order across trials.

Obtaining Neuronal Contrast with ROC Analysis

To derive contrast thresholds from MT responses, we employed an "ideal observer" approach, which supposes that a hypothetical observer detects a stimulus whenever the neuronal activity elicited by that stimulus is greater than baseline neuronal activity. This approach is implemented by using ROC analysis based on signal detection theory, which calculates the overall probability that a random sample of neuronal activity (i.e., spikes/s) selected during the presence of the stimulus is larger than a sample selected in its absence (Green and Swets, 1974; see Tolhurst et al., 1983, for its application to neuronal data). The fidelity of this judgment depends on the degree of overlap between the stimulus-elicited activity distribution and the baseline activity distribution (i.e., the less overlap, the more reliable the judgment). In our ROC analysis, baseline activity distributions were drawn from estimates of spontaneous activity (occurring within a 500 ms epoch prior to stimulus onset) and were compared against stimulus-elicited activity distributions (obtained from a 1000 ms epoch, starting 50 ms after stimulus onset) separately for each luminance contrast tested. This yielded ROC values (i.e., percent correct ideal observer performance) for each condition that were then fitted with Weibull functions (Weibull, 1951; Quick, 1974) to obtain neuronal contrast thresholds. The Weibull function is described as follows: $P = 1 - (0.5 * \exp[-(c/\alpha)^\beta])$, where P corresponds to probability correct, c is stimulus contrast, α corresponds to contrast threshold (yielding 82% ideal observer performance), and β corresponds to the slope of the function.

Only neurons for which at least 10 trials/condition (a total of at least 210 trials) could be obtained and which yielded data points that could be reliably fitted with Weibull functions (based on χ^2 fitting, $p < 0.05$) were included in our analysis. A total of 78 (of 96) neurons from three macaques met these criteria. In this sample, the mean number of trials/condition was 23, resulting in a mean of 460 total trials/neuron. To observe mean effects, the neuronal data across our three macaque subjects were averaged. Due to the skewed nature of distributions for threshold data (e.g., see Figure 2), geometric rather than linear means were calculated.

Statistical Comparisons of Threshold Values

For each neuron, we determined whether the threshold for preferred motion was significantly different from the threshold for counterphase gratings. For this analysis, the goodness of the Weibull fits (χ^2) obtained separately for counterphase and preferred motion data were compared with the χ^2 obtained from a multiple fitting procedure that provided a common Weibull function for the two data sets fitted jointly. If the common fit was as good as the fit to the separate data sets (i.e., if the χ^2 for the common fit was not significantly different from the χ^2 for separate data sets, χ^2 distribution; degrees freedom = 2, $p > 0.05$), the thresholds for preferred motion and counterphase gratings were deemed indistinguishable. By contrast, if a common fit was worse than separate fits ($p < 0.05$), thresholds for the two stimulus types were considered significantly different.

Macaque Psychophysical Experiments

Psychophysical contrast thresholds for single moving and counterphase gratings were obtained from one macaque subject. Using a 2-AFC paradigm, this animal was trained to indicate the location of a grating stimulus that appeared in one of two visual field locations. Each trial began with the animal fixating a small spot on the video screen. Successful fixation was followed by a 1000 ms period in which the stimulus was presented either to the left side or right side of fixation (centered at 4.12° eccentricity along the horizontal meridian). At the end of this period, a small target appeared at each of the two potential stimulus locations (i.e., at 4.12° to the left and right of fixation). The animal then indicated the perceived location of the stimulus with a saccadic eye movement to the appropriate (of the two) target. A juice reward was administered when the animal correctly indicated the stimulus location for 3 trials in a row.

Data were obtained for both single moving gratings (horizontally oriented, moving upward or downward) and counterphase gratings (horizontally oriented). Stimuli were set at a spatio–temporal frequency (0.4 cycles/degree, 5.6 Hz) and eccentricity (4.12°) that approximated the mean conditions of our neurophysiological experiments (see above). Six to seven different luminance contrasts were employed, ranging from 0.4% to 4.0%. The different stimulus conditions and luminance contrasts were interleaved in random order across trials. As for neuronal experiments, percent correct performance data were fitted with Weibull functions to obtain contrast thresholds (i.e., contrast yielding 82% correct performance). This was performed separately for single moving gratings (data combined for upward and downward motion) and counterphase gratings, and the resulting threshold ratio (i.e., $Thr_{counterphase}/Thr_{moving}$) was determined. For the psychophysical data presented in Figure 3, a total of 1160 trials were obtained (348 trials for the counterphase stimulus and 406 trials for each of the two directions of motion).

Modeling the Effects of Probability Summation

Here, we outline the equations underlying probability summation between detectors tuned for opposite directions of motion (see Watson et al., 1980; Graham, 1989). The probability that a mechanism selective for upward motion will detect an upwardly moving grating (P_U) is described by a Weibull function:

$$P_U = 1 - (0.5 * \exp[-(C_U/\alpha_U)^\beta]), \quad (2)$$

where C_U is the contrast of the upwardly moving grating, α_U is the contrast threshold of the mechanism (yielding 82% correct ideal observer performance), and β is the slope of the function relating contrast to performance.

If upward selective and downward selective mechanisms are independent, then the probability of detecting a counterphase grating (P_{CP}), which contains both an upward and a downward moving component, is

$$P_{CP} = 1 - (1 - P_U)(1 - P_D). \quad (2)$$

Combining Equations 1 and 2,

$$P_{CP} = 1 - (0.25 * \exp[-R^\beta]), \quad (3)$$

where

$$R = [(C_U/\alpha_U)^\beta + (c_D/\alpha_D)^\beta]^{1/\beta}. \quad (4)$$

If the upward selective and downward selective mechanisms are equally sensitive (i.e., $\alpha_U = \alpha_D$), the contrast in the upward and downward components ($C_{U,D}$) required to yield contrast threshold for the counterphase grating (i.e., $P_{CP} = 82\%$ correct) can be solved as follows:

$$C_{U,D} = \alpha_{U,D} * (0.5)^{1/\beta}. \quad (5)$$

The term $C_{U,D}$ thus reflects the predicted psychophysical contrast threshold for the counterphase grating (i.e., $Thr_{counterphase}$). Note that in the original derivation of these equations (e.g., Watson et al., 1980), $\alpha_{U,D}$ referred to the psychophysically determined contrast threshold for single moving gratings (i.e., upward or downward). This was based on the assumption that the upward (or downward) mechanism's threshold and slope for single moving gratings were identical to the threshold and slope for counterphase gratings (i.e., that the directional mechanism's response to preferred motion was unaffected by simultaneous motion in the opposite direction). When using our neuronal data to model the effects of probability summation, we do not make this assumption, since we found that the mean neuronal thresholds for the two stimulus types were not identical. In this situation, it is more appropriate to use the directional mechanism's threshold and slope for counterphase gratings. Thus,

$$Thr_{counterphase} = \alpha_{CP\text{-}mean} * (0.5)^{1/\beta\text{-}mean}, \quad (6)$$

where $\alpha_{CP\text{-}mean}$ corresponds to the mean neuronal contrast threshold for counterphase gratings, and β-mean corresponds to the mean slope of the neurons' Weibull functions for those gratings.

Because the psychophysical contrast threshold for moving gratings is expected to be determined by the mean neuronal threshold for single moving gratings (i.e., $Thr_{PM\text{-}mean}$), the predicted psychophysical threshold ratio ($Ratio_{PSY} = Thr_{counterphase}/Thr_{moving}$) is simply described as

$$Ratio_{PSY} = (Thr_{CP\text{-}mean}/Thr_{PM\text{-}mean}) * (0.5)^{1/\beta\text{-}mean}. \quad (7)$$

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