Direction Selectivity of Neurons in the Striate Cortex Increases as Stimulus Contrast Is Decreased

Matthew R. Peterson, Baowang Li, and Ralph D. Freeman

Group in Vision Science, School of Optometry, Helen Wills Neuroscience Institute, University of California, Berkeley, California

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Introduction

Contrast is a fundamental parameter of visual scenes and has been the variable of interest in many behavioral and physiological studies. Single neuron investigations demonstrate that preferred tuning parameters of cortical cells are relatively independent of stimulus contrast. In particular, peak and bandwidth values for orientation (Sclar and Freeman 1982) and spatial frequency (Skottun et al. 1987) remain constant at different contrast levels. However, spatial summation is reported to increase at low contrast levels with a subsequent broadening of spatial frequency bandwidth (Sceniak et al. 2002). In addition, contrast appears to be inversely and directly related, respectively, to response latency and temporal frequency tuning (Albrecht 1995). Therefore at low contrasts, a cell’s temporal integration time is increased, which results in relatively long latencies and shifts in sensitivity to lower temporal frequencies. Considered together, as contrast within the visual stimulus changes, the response alterations appear to be in the temporal domain.

Direction or directional selectivity (DS) is also a fundamental property of neurons in the central visual pathway of animals with frontally positioned eyes. We have recently considered how cells in the visual cortex may derive DS from inputs which are nondirectional (Peterson et al. 2004). The encoding of stimulus direction requires both spatial and temporal components, and it is of interest to know how changes in a fundamental parameter such as contrast, affects DS. Results of previous studies are contradictory. In one report, DS is found to be contrast invariant (Li and Creutzfeldt 1984) and in another, it is thought to be highly dependent on stimulus contrast levels (Albrecht 1995).

We have conducted a detailed study of this issue using single cell recordings of neurons in primary visual cortex. As noted above, the temporal integration times of cells at low contrasts are increased, which causes longer latencies and shifts in sensitivities to lower temporal frequencies. This would be expected to cause changes in DS as stimulus contrast is varied. The expectation is derived from a linear model of DS in which two spatiotemporal filters with phase differences near 90° (quadrature) are added together to form a space-time inseparable receptive field (RF). This is a form of the energy model (Adelson and Bergen 1985; Watson and Ahumada 1985) that has been employed extensively in previous work (DeAngelis et al. 1999; McLean et al. 1994).

The energy model provides two opposing predictions regarding contrast and direction selectivity. In one, contrast-induced changes in neuronal response latency are uniform, which causes a shift to lower temporal frequencies at reduced contrasts (Alitto and Usrey 2004). This would result in relatively small temporal phase differences between the two spatiotemporal filters, which would decrease the degree of DS. The second and opposing prediction is made on the assumption that contrast changes in the stimulus affect temporal latencies of the two spatiotemporal filters by differing amounts. Relatively large temporal phase differences would apply for low contrasts. In this case DS would increase at low contrast levels. Our neurophysiological findings are consistent with the second prediction. Our results appear to be directly relevant to recent behavioral investigations of human subjects. These studies show clear increases in the ability to discriminate direction of a visual target, as pattern contrast is reduced (Bett et al. 2005; Tadin et al. 2003).

Methods

Physiological procedures

Cats are tranquilized, anesthetized, and paralyzed according to a standard protocol described in detail in previous publications (e.g., Peterson et al. 2004). In brief, anesthesia is induced with isoflurane and femoral veins are cannulated. A thermistor probe is inserted to monitor core body temperature. A tracheostomy is performed and a tracheal cannula is positioned. Isoflurane is discontinued and anesthe-

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sia is continued with thiopental. The animal is positioned in a stereotaxic apparatus and craniotomy and durarumy procedures are performed. Once a steady-state level of anesthesia is reached, as determined for each animal, a muscle relaxant (pancuronium) is given and artificial respiration is instituted. Various physiological functions are monitored continuously throughout the experiment, which generally lasts for several days. Monitored parameters include: core body temperature, intra-tracheal pressure, expired end-tidal CO₂, heart rate, blood pressure, electroencephalogram (EEG) and electrocardiogram (ECG).

Recording procedures

Single neurons are recorded in area 17 of mature cats. Generally, two tungsten electrodes are inserted at an angle of around 10° medial and 20° anterior with the intention of traversing down the medial bank of the postlateral gyrus (H-C coordinates P4 L2). Single units are isolated and identified by waveform and spike response characteristics. After noting the boundaries of the RFs, preliminary estimates are made of spatial and temporal tuning parameters of isolated cells. Custom made search software is used to provide a display of a variety of visual stimuli parameters. Computer-generated stimuli are displayed on CRTs. These stimuli are frame-locked to the data acquisition computer. Following preliminary estimates of optimal stimuli parameters, tuning functions are obtained quantitatively with drifting sinusoidal gratings of 50 cd/m² mean luminance.

For 15 cells, complete space-time RFs are mapped at multiple contrast levels. This facilitates determination of linear and nonlinear factors underlying observed responses as grating contrast is changed. For this procedure, we use visual noise in a reverse correlation procedure (DeAngelis et al. 1993a,b; Freeman and Ohzawa 1990; Jones and Palmer 1987). The noise consists of small black or white bars presented at an optimal orientation for 40 ms at random locations within the RF. Resulting spike trains are cross-correlated with the stimulus sequence. Since the response of a cortical cell may be thought of as a push-pull process, dark bar responses may be considered to be equivalent to inhibitory responses to bright bars. Therefore the differences between bright and dark bar response fields provide estimates of RFs. The result is an accurate space-time description of the RF for each neuron.

After tuning parameters are determined and fixed, tests are conducted in which both direction and contrast are varied. Tuning parameters, including spatial and temporal frequencies, and RF size, determined with 50% contrast gratings, are fixed for all DS and contrast runs. The two-parameter tuning run consists of a four second presentation of a sinusoidal grating drifting at the preferred orientation of the cell. Direction of drift and contrast are randomized. Long inter-stimulus intervals (10 s) are used to avoid contrast adaptation effects. Contrast is the main variable of interest and we generally use five contrast values ranging in logarithmic steps from 4 to 50%. Contrast is defined in the usual way, as the ratio of the difference over the sum of dark and bright grating bar luminances. Multiple repetitions were used (generally 10 or more). Data are included only for contrast levels for which responses are significant ($P < 0.05$, t-test).

**RESULTS**

We have recorded from a total of 62 neurons located in the primary visual cortex (Area 17) of the cat. We classified 30 as simple cells and 32 as complex based on subjective classical criteria (Hubel and Wiesel 1962) and the degree of modulation of responses at the drift rates of the gratings. For all 62 cells, we measured neural response values for drifting gratings at 14, 26, and 50% contrasts. We also determined responses at 4 and 7% contrasts for 19 and 39 cells, respectively. Our results for simple and complex cells are not distinguishable so all cells are combined.

By use of a reverse correlation visual stimulation procedure, we may derive a space-time RF, as described in previous work (e.g., DeAngelis et al. 1993a; Freeman and Ohzawa 1990; Jones and Palmer 1987). Is this procedure, a neural spike train is cross-correlated with a visual stimulation pattern. By considering different amounts of time delays between the visual stimulus and the neural response, it is possible to derive two-dimensional spatial plots for several time delays between stimulus presentation and spike activity. By integrating along the $y$-axis, one can derive an XT plot which gives space along one dimension and time along the other. When the XT plot shows different temporal response values at various spatial locations, the RF is spatiotemporally inseparable. In this case, the space-time plot will be tilted at an angle. An inseparable space-time plot indicates that the neuron is sensitive to the direction of movement of the stimulus (Peterson et al. 2004; Reid et al. 1991). In the opposite kind of space-time RF profile, responses are not tilted. In this separable case, temporal changes in responses occur at relatively constant spatial locations. The 2D XT profile can be represented as the product of two 1D profiles, one a function of space and the other of time. Details of the analysis with respect to DS are given in our previous report (Peterson et al. 2004).

Results for two neurons are shown as XT plots in Fig. 1. For one cell, data for stimuli of 50% and 14% contrasts are given in A and B, respectively. In this case, there is a clear tilt or inseparability in the XT plots for both contrast levels which indicate that the cell is DS. Because the XT tilt is to the left, the cell is predicted to be selectively sensitive to rightward motion (DeAngelis et al. 1993a). To quantify the degree of DS, we use a direction selectivity index (DSI) as derived and used previously (DeAngelis et al. 1993a; Peterson et al. 2004)

$$\text{DSI} = 1 - \frac{NP}{P}$$

where DSI is the direction selectivity index, P and NP represent response values for preferred and nonpreferred directions, respectively, of a visual stimulus that consists of a sinusoidal grating. Mean response levels (DC values) are used for complex cells and first harmonic amplitudes of the PSTH data are employed in the case of simple cells. For space-time RFs, P and NP represent values of the spatiotemporal amplitude spectrum in preferred and nonpreferred directions, respectively. For the data shown in Fig. 1A and B, the DSI values which are predicted based on the XT plots, are 0.4 and 0.64, in A and B, respectively. In this case, the degree of predicted DS is higher for the lower contrast stimulus condition. Actual values of DSI for this cell, as determined from measurements with grating stimuli are 0.63 and 0.71, in Fig. 1A and B, respectively. In the second example of Fig. 1, presented in C and D, there is very little tilt in the XT plot for 50% contrast (C) and the RF is nearly space-time independent. The predicted and measured DSI values are 0.21 and 0.12, respectively. At the low contrast value of 7%, shown in Fig. 1 D, there is a slight amount of XT tilt and the predicted and measured DSI values are 0.36 and 0.73, respectively. Although this latter difference in values is substantial, most of the comparison data we have found previously are quite similar (Peterson et al. 2004). For the 15 simple cells tested, results are generally consistent with those illustrated in Fig. 1. Specifically, 12 of 15 cells exhibit stronger
predicted DS values at low compared with high stimulus contrasts. Mean DSI values at low and high contrasts are 0.53 ± 0.22 and 0.38 ± 0.12 (SD), respectively. This difference is significant (P = 0.02, t-test).

In the examples in Fig. 1, it is apparent that lower contrast visual stimuli produce a latency delay with a corresponding expansion of the temporal profile of the RF. These factors produce a change in the space-time separability of the RF which is given by the tilt of the XT plot. Results for these cells are representative of our sample and illustrate our general finding that DS changes with contrast as measured with drifting sinusoidal gratings. To investigate the expansive nonlinear component of these 15 cells, we computed the exponents required for matches between predicted and measured DSI values for low and high contrast values. Mean exponents for high and low contrasts are 1.8 ± 0.3 and 1.5 ± 0.2. The difference between these values is not significant (P = 0.4, t-test), and it is not clear if a larger sample size would yield a different result. However, we also measured changes in the first and second temporal phases of the responses. This requires fits by skewed Gabor functions (DeAngelis et al. 1993a). We examined temporal changes in the first and second phases of the responses as a function of contrast. To do this, we took slices of the spatiotemporal RFs parallel to the time axis at points of maximal responses. Durations of first and second phases are estimated at points of 10% or greater of the maximum 1D RF responses. In general, the most pronounced effects, showing low contrast stimuli to be delayed and expanded, are found in the second temporal phase values. Mean first phase durations are quite similar, i.e., 98 ± 29 ms and 100 ± 54 ms for low and high contrasts, respectively (P = 0.9, t-test). For second temporal phases, mean values are 222 ± 84 ms and 149 ± 125 ms, for low and high contrasts, respectively (P = 0.07, t-test).

For all 62 cells studied here, two directions of the visual stimulus, preferred and nonpreferred, were tested at optimal orientations at several contrasts. For 11 neurons, orientation tuning curves were obtained at several contrast levels and an example of one cell tested in this way is shown in Fig. 2. A–C. Orientation tuning functions are presented for the cell measured with high (50%), medium (26%), and low (14%) contrast values. This cell prefers stimuli oriented at 30° (where 0° represents horizontal gratings drifting downwards). At the highest contrast condition (50%), this cell’s response to grating drift in the nonpreferred direction (210° in this case) is around 80% of that for the preferred direction. The measured DSI value for this cell is 0.24 at 50% contrast. At a medium contrast level, (26%), the overall response strength is lower at all orientations, relative to those recorded at high contrast levels. As a result, the measured DSI value is slightly higher (0.27). At the lowest contrast (14%), DS is even higher (DSI = 0.45). Thus as contrast levels decrease, DS increases, as predicted by the spatiotemporal changes observed in the RFs shown in Fig. 1. This effect is observed for 8 of the 11 cells studied in this way. For the remaining three cells, one showed an opposite effect and data for the other two neurons are mixed.

In previous work, we suggested that nonlinearities can enhance the DS generated within a linear RF (Peterson et al. 2004). In the case of the example shown above in Fig. 2, A–C, contrast-dependent changes in responses of the cell could be due to nonlinear enhancements that are not necessarily related to alterations in the space-time RF as illustrated in Fig. 1. However, this possibility appears unlikely because of data such as those illustrated in Fig. 2, D–F. The cell whose responses
are shown here is not DS at the high and intermediate contrast levels of 50% (Fig. 2D) and 26% (Fig. 2E) as evident from the equal response amplitudes to the two directions of stimulus motion. In this case, the measured DSI values for 50% and 26% contrasts are 0.1 and 0.16, respectively. However, for a lower contrast level (14%), DS increases. For the data shown in Fig. 2F, overall response is weak, but DS is clear and the measured DSI value is 0.82. This implies that there is more than a simple change in enhancement of nonlinearities and it suggests that alterations in the linear space-time RF tend to increase DS under low compared with high contrast stimulus values. To investigate this quantitatively, we tested all 62 cells at optimal orientations for preferred and nonpreferred directions of motion at 4, 7, 14, 26, and 50% contrast levels. In Fig. 3A, contrast response functions are illustrated for preferred and nonpreferred directions for five cells. Corresponding DSI values for these cells are given in Fig. 3B. For two cells, DSI values increase markedly as contrast is reduced. For two others, the same trend is seen but effects are minimal and for one cell there is no effect. If we examine the distribution of DSI values for low and high contrasts, as depicted in Fig. 3C, there is a clear preponderance of points above the diagonal line of unity. DSI values tend to be higher for lower stimulus contrasts. This difference is significant ($P = 0.03$, t-test). Low contrasts refer to the lowest levels tested for which we found significant responses. For low contrast response levels, we obtained 19, 20, and 23 cells at contrasts of 4, 7, and 14%, respectively. Histograms of DSI values for all three low contrasts as compared with those for the 50% high contrast level are shown in Fig. 3D. The difference is highest and significant for the 4%/50% comparison, but it is small and not significant for the other contrast cases shown.

These results are consistent with two general types of models; a variable phase model, that we consider here, and an iceberg effect model as described below (see DISCUSSION). In the variable phase model, DS RFs are derived from the sum of two space-time separable inputs with different spatial and temporal phase offsets (Peterson et al. 2004). DS increases monotonically with an increase of temporal phase difference between two space-time separable inputs. The phase offsets can vary in
range from $0^\circ$ to $90^\circ$, i.e., they are not limited to quadrature conditions. The magnitude of the phase difference determines the degree of DS (Peterson et al. 2004). The effects of phase offsets for a model simple cell are illustrated in Fig. 4. The RFs shown in Fig. 4A cover a full range of temporal phase differences from $0^\circ$ to $90^\circ$. In Fig. 4B, plots of temporal phase difference are presented as a function of predicted DSI values. Curves for three different exponents are included. The exponent is the result of the simple cell model as a linear filter followed by an expansive nonlinearity. The expansive function may be half-squaring and serves to sharpen the output tuning of the cell (Heeger 1992a,b). As the graphs of Fig. 4B show, small temporal phase differences are associated with low DSI values. Maximal DSI levels are seen for the highest temporal phase difference ($90^\circ$).

To see how this model accounts for changes in DS with contrast, we consider how the temporal phase difference of the input components change with contrast. We have shown in previous work that there is a wide-range of temporal phase differences between the two input components that generate directionally selective RFs (Peterson et al. 2004, Fig. 10). We reported data suggesting that the two inputs could be non-DS simple cells. However, if the non-DS simple cells derive their phase differences from lagged and nonlagged cells, they are predicted to exhibit larger temporal phase differences under low compared with high contrasts. This is because of the different effects of contrast on response latency for lagged and nonlagged cells (Hartveit and Heggelund 1992). Lagged cells are more affected by contrast than nonlagged cells and that would result in an increase in the latency difference between the two groups at low contrasts. That is what is found for lagged and nonlagged cells (Hartveit and Heggelund 1992).

Considered together, the data we present here show clearly that space-time RFs of cortical cells change with stimulus contrast. Specifically, DS is enhanced at low contrast levels, which is a somewhat counterintuitive result. Under low contrast conditions, the temporal profile of a RF tends to be expanded and it exhibits relatively long latencies compared with measurements at high contrast values. What is relevant for DS is that RFs tend to be more space-time inseparable under low contrast levels and this provides a prediction of increased DS. Consistent with the observed RF changes, cells exhibit higher levels of DS to drifting gratings under low compared with high contrast conditions. The observation that there are neurons which are not DS for high contrast stimuli, but which become DS under low contrast stimulation, implies that the mechanism underlying the effect is a change in the RF structure and not just a simple enhancement due to nonlinearities.

**DISCUSSION**

We have shown here that space-time RFs of 80% of the cortical cells we studied change with stimulus contrast. Under low contrast levels, the temporal profiles of RFs tend to be expanded and exhibit longer latencies compared with RFs measured under high contrast conditions. With regard to DS, RFs tend to be more space-time inseparable under low con-
DeAngelis et al. 1993a; Peterson et al. 2004). This means that the best fit by a skewed Gabor function as shown in previous work (1993a). For example, the temporal response of a simple cell is slowed temporal response profiles exhibited by cells in the central visual pathway (Cai et al. 1997; DeAngelis et al. 1997). The skewed temporal profile suggests that responses slow down over the course of the impulse response function. As a consequence, induced latency changes at the early part of the response are relatively small compared with those that occur later. This difference in latency change is evident by the temporal expansions that have been observed previously and assumed to be due to decreases in both luminance and contrast (e.g., Peterson et al. 2001, 2004). In this study, we find that overall responses are delayed and expanded with low contrasts. The first phase remains approximately the same in duration, while the second is substantially expanded in time. The unequal scaling in time implies that the contrast-dependent change in latency difference between lagged and nonlagged cells may be due to a general slowing of the temporal response throughout the central visual pathway. This slowing process results in long-latency responses that exhibit large timing changes compared with those associated with short-latency responses.

In general, contrast-dependent response characteristics of cortical cells have been observed in previous studies of cats (Jagadeesh and Ferster 1990; Nolt et al. 2004) and monkeys (Cavanaugh et al. 2002; Kapadia et al. 1999; Sceniak et al. 2002). In one investigation, RF size is reported to increase as stimulus contrast is reduced (Sceniak et al. 1999). In addition, temporal integration in visual cortex is reported to be contrast dependent. In particular, preferred temporal frequency decreases and response latency increases as contrast is reduced. DS is generally reduced at nonpreferred temporal frequencies (Alitto and Usrey 2004; Bair and Movshon 2004; Moore et al. 2005). In our current study, we used constant size stimuli and temporal frequency for all contrast conditions. It is possible, therefore that manipulation of these variables might alter our findings but it is unlikely to affect our main conclusion.

We have presented above (see RESULTS) a model of a variable phase mechanism that could account for our results. However, another potential underlying mechanism could be a simple threshold nonlinearity in the form of the well known iceberg effect. The assumption here is that there is a fixed threshold nonlinearity at the spike generation stage of the neuron. The membrane potential of the cell must exceed a fixed threshold to cause an action potential. If the cell is slightly DS at high contrasts, employment of a low contrast can increase the selectivity by simply reducing the cell’s response amplitude overall. This has the effect of lowering part or most of the orientation tuning curves to below the threshold level. The overall effect is an increase in the ratio between preferred and nonpreferred direction responses and that can account for results such as those illustrated in Fig. 2. The iceberg effect also predicts that there should be an increase in orientation selectivity in addition to that of direction selectivity as contrast is reduced. However, previous work shows that orientation selectivity is independent of stimulus contrast (Sceniak et al. 2002; Sclar and Freeman 1982). Models have been devised to account for why orientation doesn’t change with stimulus contrast as would be expected by an iceberg effect. For example, inhibition at off-orientations has been suggested as a way to maintain tuning widths in spite of threshold effects (Troyer et al. 1998). With this type of model, contrast response functions of preferred and nonpreferred directions would exhibit the same slopes. This prediction follows from the central

**FIG. 4.** A variable phase model is illustrated here to indicate how it may account for differences in DS as a function of stimulus contrast. In this model, a DS RF is obtained by the sum of inputs from two non-DS cells with separable space-time RFs. Selectivity for stimulus direction is determined by the temporal phase difference between these two separable RFs. A 0° phase difference generates an RF with no DS whereas a 90° phase difference leads to high DS. High and low stimulus contrasts result in small and large temporal phase differences, respectively. A: space-time (XT) plots are illustrated for a range of temporal phases from 0° to 90° that represent different degrees of space-time inseparability. Space and time are represented, respectively, on horizontal and vertical axes. B: associated DSI values for various temporal phase differences are indicated in by three functions with different exponent ($e$) values. A linear prediction is given by an $e$ value of 1. Nonlinear predictions with squaring ($e = 2$) and cubing ($e = 3$) output nonlinearities are illustrated in the other two functions. (see Peterson et al. 2004 for details of this model.)

Contrasts. This predicts an increase in the incidence of DS that is consistent with the observed RF changes; i.e., cells generally exhibit higher levels of direction selectivity to drifting gratings under low as compared with high contrast gratings. The observation that there are cortical cells which are not DS under high contrast but that exhibit selectivity under low contrast, implies that the mechanism underlying the effect is a change in the RF structure and not a simple enhancement of nonlinearities. Both an iceberg effect and a variable phase model may be considered to account for the results obtained here.

Regarding timing issues, increased latency differences are expected for relatively low contrast gratings based on the slowed temporal response profiles exhibited by cells in the central visual pathway (Cai et al. 1997; DeAngelis et al. 1993a). For example, the temporal response of a simple cell is best fit by a skewed Gabor function as shown in previous work (DeAngelis et al. 1993a; Peterson et al. 2004). This means that temporal response functions show faster and slower changes at the start and finish, respectively, of the response. This same dynamic is observed in the LGN (Cai et al. 1997). The skewed temporal profile suggests that responses slow down over the course of the impulse response function.
assumption of the iceberg effect that responses at all orientations decrease with contrast at approximately the same rate. While this applies to some of our data, other contrast response functions for preferred and nonpreferred directions have different slopes.

The iceberg effect assumes a fixed threshold nonlinearity at the output stage of the cortical neuron. However, there is evidence that the output nonlinearity is characteristic of a power function with exponents in the region of two to three (Gardner et al. 1999; Heeger 1992a). By recording membrane potentials and action potentials simultaneously, it has been shown that the variability in the threshold produces a power function relationship between these two response stages. This result in contrast-independent orientation tuning widths (Anderson et al. 2000). A power-function output nonlinearity predicts that DS will exhibit contrast invariance. But the results presented here demonstrate that DS depends substantially on contrast, and therefore effects of output nonlinearities are not sufficient to account for our data.

Results presented here may be relevant to perceptual findings. Human observers discriminate direction of motion better at low compared with high contrast levels. In one investigation of human observers, a broad range of contrasts was studied (Derrington and Goddard 1989). The plot of percent correct versus contrast is quite similar in form to the DS1 versus contrast data reported here (Fig. 3). In other perceptual work, center/surround interaction has been investigated in connection with motion processing. For a given moving pattern, an increase of either size or contrast reduces acuity for direction of the stimulus (Tadin et al. 2003). Essentially the same study was repeated with the intention of investigating potential differences between young and old subjects. Again, there was a clear effect in which motion perception increased improved under low contrast conditions (Betts et al. 2005). This perceptual increase in DS at low contrasts is similar to the physiological results reported here and may be accounted for by the variable phase model mentioned here and described previously (Peterson et al. 2004). With this model, a decrease in contrast results in an increase in temporal phase difference between inputs to DS cells. This results in an increase in DS for phase difference values of 90° or less. For values of 90° or more, selectivity peaks and then decreases at larger phase differences. It is possible that DS at lower contrasts in single cells may also peak and then decrease in their DS1 versus contrast functions.

Considered together, these findings suggest that contrast-dependent changes in DS arise via alterations in the linear RF according to a variable phase model where temporal phase differences are small at high contrasts and relatively large at low contrasts. These changes in temporal phase differences agree with contrast-dependent latency changes observed in the LGN and are consistent with a slowing of the temporal response of visual cells in general. In addition, an iceberg effect could contribute to our results. The neurophysiological data reported here are consistent with perceptual findings in human subjects in which motion discrimination has been determined under different contrast levels.

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