Visual cortex neurons in monkey and cat: Contrast response nonlinearities and stimulus selectivity.

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ABSTRACT

The contrast response functions of cat and monkey visual cortex neurons reveal two important nonlinearities: expansive response exponents and contrast gain control. These two nonlinearities (when combined with a linear spatiotemporal receptive field) can have beneficial consequences on stimulus selectivity. Expansive response exponents enhance stimulus selectivity introduced by previous neural interactions, thereby relaxing the structural requirements for establishing highly selective neurons. Contrast gain control maintains stimulus selectivity, over a wide range of contrasts, in spite of the limited dynamic response range and the steep slopes of the contrast response function.

1. CONTRAST RESPONSE NONLINEARITIES

Neurons in the visual cortex of monkeys and cats are known to be quite selective along a variety of stimulus dimensions: spatial position, spatial frequency, temporal frequency, orientation, direction of motion, etc. Each neuron is analogous to a narrow-band filter, which transmits and signals only a limited portion of the available information. It seems reasonable to suppose that this type of stimulus selectivity plays a fundamental role in the overall process of vision and that one goal of the neural machinery is to produce individual neurons tuned to specific visual qualities. It is clear
that some of this selectivity is acquired through linear summation of inputs as described by the spatiotemporal receptive field, or the spatiotemporal transfer function.\textsuperscript{4-9} However there are nonlinear interactions that also contribute to this goal. Specifically, the contrast response functions of neurons recorded from area 17 in the visual cortex reveal two nonlinearities, expansive response exponents and contrast gain control, that have rather beneficial consequences with respect to establishing and maintaining stimulus selectivity.

A typical contrast response function is illustrated in Figure 1. The responses of a representative neuron recorded from the striate visual cortex of a monkey are plotted as a function of the contrast of an optimal spatial frequency grating pattern. As the contrast of the grating increases from zero, the response increases rapidly with a power function exponent greater than 1.0; that is, when plotted on log coordinates the slope is greater than 1.0. The value of this expansive exponent varies from cell to cell; for this particular cell the exponent was 3.2; for some cells it exceeds 5.0; the average value is approximately 2.5. The rapidly accelerating response rate soon saturates at a maximum value. These facts have been established through measurements on many hundreds of neurons, in both cat and monkey, in several different laboratories.\textsuperscript{9-14}

![Contrast response function](image)

**Figure 1.** Contrast response function of a typical visual cortex neuron. The smooth curve through the data points is the best fit of a saturating power function. This cell illustrates the two nonlinearities: as the contrast increases, the response increases rapidly (in this case with an expansive power function exponent of 3.2) and then saturates.
The properties of the saturation nonlinearity, seen in the contrast response functions of cortical cells, turned out to be rather interesting and certainly unexpected. By measuring the contrast response function at different spatial frequencies, we found that the saturation is not really tied to the overall level of the response, per se; rather, the saturation is determined by the overall level of the contrast.\textsuperscript{10} This fact, and other recent evidence\textsuperscript{13-16} lead to the conclusion that the saturation is due to a fast-acting, multiplicative, contrast gain control mechanism.

2. CONTRAST-GAIN/EXPONENT MODEL

We have developed a formal model, the contrast-gain/exponent (CGE) model which incorporates these two nonlinearities into the established notion of linear spatiotemporal filtering.\textsuperscript{14} This model is composed of three basic components: a linear spatiotemporal filter, contrast gain control, and an expansive response exponent. Heeger has developed and tested a similar model.\textsuperscript{17-20} Figure 2 illustrates the consequences of these various operations for an optimal stimulus and a nonoptimal stimulus. On the input side, the amplitude increases linearly with contrast and is equal for the two stimuli. After the contrast gain is applied, the saturation nonlinearity becomes apparent, although the two equal contrast stimuli continue to evoke equal responses. After the linear filter, the responses are no longer equivalent; the responses to the nonoptimal stimulus are shifted down, by a constant ratio, at all contrasts. Finally, after the expansive response exponent is applied, the differences in the responses to the two stimuli are greatly magnified.

Contrast-Gain Exponent Model

\begin{figure}
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\includegraphics[width=\textwidth]{contrast_gain_exponent_model.png}
\caption{The effect of each component of the contrast-gain/exponent model on the responses to an optimal stimulus (solid line) and a nonoptimal stimulus (dashed line). The three mechanisms are illustrated symbolically in the upper row of boxes. The resulting contrast response functions before and after each stage are shown in the lower row of boxes.}
\end{figure}
The basic idea is that the linear filter establishes a certain degree of stimulus selectivity through simple linear summation of inputs; the shape of the spatiotemporal receptive field produces a certain degree of orientation selectivity (due to the length of the receptive field), spatial frequency selectivity (due to the width, strength, and number of parallel excitatory and inhibitory regions), direction selectivity (due to the orientation in space/time), etc. If the output of the linear filter is passed through an expansive nonlinearity, the stimulus selectivity along all these dimensions will be greatly enhanced. Contrast gain control will ensure that these selectivities are maintained across a broad range of contrasts, in spite of the steep slope and the limited dynamic range of the contrast response.

3. EXPONENT ENHANCES SELECTIVITY

Consider the effect of an expansive exponent on stimulus selectivity. The basic effect of the exponent is to enhance stronger excitations disproportionately, relative to weaker excitations; and thus, optimal stimuli are disproportionately enhanced relative to nonoptimal stimuli.

Figure 3 illustrates the potential effect of an expansive exponent on spatial frequency selectivity. The circles connected by the solid line plot the responses of an LGN cell as a function of spatial frequency (the outermost curve). While this cell does show a certain degree of selectivity, due to its center/surround receptive field, it is rather broadly tuned --
it is not very selective for spatial frequency. It has a bandwidth of approximately 2.5 octaves. The circles connected by the dashed line illustrate what would happen to the responses if they were passed through a cell with an expansive exponent of 2.5; the circles connected by the dotted line illustrate the effect of an exponent of 5.0 (the innermost curve). As can be seen, the expansive exponent produces considerable narrowing or sharpening of the spatial frequency selectivity. An exponent of 2.5 reduced the bandwidth to approximately 1.5 octaves; an exponent of 5.0 reduced the bandwidth to approximately 1.0.

Figure 4 illustrates the effect of expansive exponents on the degree of direction selectivity. The direction selectivity of a strictly linear filter is plotted along the x-axis; the direction selectivity following expansion due to a power function exponent is plotted along the y-axis. The smooth curves show the effect of exponents ranging from one (the diagonal line -- no effect) through 6. The curves illustrate that expansive exponents can substantially increase the direction selectivity. For example, if the direction selectivity index were 0.3 before expansion, it is more than doubled by an exponent of 3.0. The exponent can make a very direction selective filter from a linear filter that is only partially direction selective.

Figure 4. Effect of expansive exponents on direction selectivity: each line plots the direction selectivity before (horizontal axis) and after (vertical axis) applying exponents ranging from 1.0 through 6.0. Direction selectivity is defined as $(R_P - R_N) / R_P$, where $R_P$ is the magnitude of response in the preferred direction and $R_N$ is the magnitude of response in the nonpreferred direction.14
4. EXPONENTS EASE STRUCTURAL REQUIREMENTS

Expansive exponents can potentially ease the structural requirements for producing highly selective neurons. Consider spatial frequency selectivity. Given strict linearity, as the number of parallel excitatory and inhibitory regions within the receptive field is increased, the spatial frequency selectivity is increased. Thus, in order to produce a linear cell with a high degree of spatial frequency tuning, the spatial receptive field must be composed of many flanking excitatory and inhibitory regions. For a cell to have a bandwidth of say 0.8 octaves the receptive field would have approximately eight spatially antagonistic regions. On the other hand, if an expansive exponent is introduced after the linear filter, the number of antagonistic regions can be reduced. An expansive exponent of 2.5 could decrease the number by a factor of approximately two.

Consider orientation selectivity. Given strict linearity, as the length of the receptive field is increased, the orientation tuning is increased. Thus, in order to produce a linear cell with a high degree of orientation tuning, the spatial receptive field must be very long. On the other hand, if an expansive exponent is introduced after the linear filter, then the length can be reduced. Again, an exponent of 2.5 could decrease the required length by a factor of approximately two.

Consider direction selectivity. Given strict linearity, as the strength of the oriented component of the receptive field in the space-time domain is increased, the direction selectivity is increased. Thus, in order to produce a linear cell with a high degree of direction selectivity, the cell must be very strongly oriented in space time. On the other hand, if an expansive exponent is introduced after the linear filter, the strength of space-time orientation can be reduced. DeAngelis et al. have recently demonstrated that the discrepancy between the measured spatiotemporal RF and the measured degree of direction selectivity was diminished when the effects of the measured exponent were taken into consideration.9

The effect of the response exponent can potentially help account for a number of discrepancies between the degree of stimulus selectivity and the exact shape of the receptive field. In general, the degree of spatial frequency selectivity, orientation selectivity, and direction selectivity are greater than what would be expected from the shape of the receptive field. In the past, we and others have proposed various factors which could potentially account for the lack of correspondence and the increased stimulus selectivity; for example, various kinds of inhibitions from nonoptimal stimuli. In fact, the increased selectivity may well be a simple consequence of the expansive exponents seen in the contrast response functions.
Figure 5 attempts to illustrate this point. The solid line on the left side of this figure is the spatial receptive field profile (more accurately, the impulse response) of a given linear filter; the solid line on the right is the spatial frequency selectivity of the linear filter. These two constitute a transform pair -- the space and spatial frequency representations of a hypothetical strictly linear filter. They are Fourier transforms of each other. If the output of this strictly linear filter is passed through an expansive exponent of say 2.5 then both the measured receptive field and the measured spatial frequency tuning would change -- as illustrated by the superimposed dashed lines. The bandwidth of the spatial frequency tuning becomes narrower. The stronger input from the optimal frequencies is disproportionately enhanced relative to the weaker input from the nonoptimal frequencies. Similarly, the width of the receptive field becomes narrower. The stronger responses from the center would be disproportionately enhanced relative to the weaker responses from the other flanking regions.

![Figure 5](image)

**Figure 5.** Spatial receptive field profile(A), and the corresponding spatial frequency tuning (B), before and after an expansive exponent. The solid lines plot the linear pair and the dashed lines plot the exponentiated pair.

These dashed lines would constitute the measured receptive field and the measured spatial frequency tuning of this filter, after exponentiation. Note that they are no longer a Fourier transform pair. The measured receptive field, following exponentiation, does not appear to have enough flanking regions to account for the narrow spatial frequency tuning. The exponent has simultaneously attenuated the weaker responses from nonoptimal/peripheral flanking regions and the weaker responses from nonoptimal/peripheral spatial frequencies. The expansive exponent has increased the
localization in both space and spatial frequency. The exponent has decreased the bandwidth of the spatial frequency tuning from 1.2 octaves to 0.7 octaves -- nearly a factor of two.

In order to produce spatial frequency tuning of 0.7 octaves using strictly linear mechanisms, the spatial receptive field profile would have to contain many flanking regions of excitation and inhibition -- as shown in Figure 6. The solid line is the receptive field profile of a linear mechanism with a spatial frequency tuning of 0.7 octaves. The superimposed dashed line is taken from Figure 5a -- it is the exponentiated receptive field that would correspond to the 0.7 octaves exponentiated spatial frequency tuning. Over the past few decades, many different laboratories have noted that the receptive fields of narrowly tuned cells generally do not have the receptive field expected from strictly linear mechanisms. The contrast response exponents can potentially help account for some of the these longstanding discrepancies.

![Predicted Mismatch of Linear Analysis](image.png)

**Figure 6.** Spatial receptive profile for a linear filter (solid line) and exponentiated filter (dashed line). The resulting spatial frequency tuning for both of these RFs is 0.7 octaves.

There is some evidence to support the above propositions. We have examples of individual cells which illustrate that the expansive exponent can help reconcile differences between the measured selectivity and the measured receptive field, and we are in the process of measuring and assessing the generality of the propositions for a large population of neurons. For example, we have completed one study of direction selectivity which clearly demonstrates the effects of the response exponent. We and
others\textsuperscript{21,22} had previously noted that the measured direction selectivity of cortical cells was greater than what would be expected from the measured responses to stationary flashing stimuli, if only linear summation of inputs is taken into account. As Reid et al. stated: "only about half of the direction selectivity could be accounted for on the basis of linear mechanisms (p. 8742)." However, if the effects of the expansive exponent are taken into account, then the measured direction selectivity is consistent with the measured responses to stationary stimuli.

![Figure 7](image-url)  
**Figure 7.** Amplitude and phase responses of a nondirection selective cell (A) and a direction selective cell (B) to stationary gratings counterphase flickering in different spatial positions. The smooth curves show what would be expected from a linear filter.\textsuperscript{14}

Figure 7 plots the expected and the measured responses of a direction selective cell and a nondirection selective cell to stationary counterphase flickering gratings, presented in different spatial positions. The panels on the left show the amplitude and phase of response for a nondirection selective simple cell as a function of the position of a counterphase flickering grating. From the work of Enroth-Cugell and Robson\textsuperscript{23} as well as Hochstein and Shapley,\textsuperscript{24} we know that the response should be a sinusoidal function of the spatial position of the grating, with two null phase positions (that is, two spatial phase positions which evoke little or no response); the smooth lines through the data points show the predictions of a strictly linear filter. For the nondirection selective cell on the left, the fit is reasonable.
Now consider the predicted and measured responses for the direction selective cell, on the right. This particular cell produced almost no response to gratings drifting in the nonpreferred direction -- it was very direction selective. Given a strictly linear cell with this degree of direction selectivity, the amplitude of response to a counterphase flickering grating would not change with spatial position and the phase would change continuously. This is because, a counterphase flickering grating can be decomposed into two gratings of equal contrast drifting in opposite directions. A strictly linear direction selective filter would only be affected by the component drifting in the preferred direction. The amplitude of this component remains constant -- and the phase changes continuously. These predictions are illustrated by the solid lines. As can be seen, this direction selective simple cell does not behave according to these strictly linear predictions.

We have shown that this kind of behavior can be readily accounted for if the expansive exponent of the contrast response function is taken into consideration. In Figure 8, the same responses are plotted along with the predictions of a model composed of a linear filter followed by the measured contrast response exponent. The fit is good for both the direction selective cell and the nondirection selective cell.

![Graphs showing amplitude and phase responses of a nondirection selective cell (A) and a direction selective cell (B) to stationary gratings counterphase flickering in different spatial positions. The smooth curves show the predictions from a model composed of a linear filter followed by the measured exponent of the contrast response function.](image-url)
5. CONTRAST GAIN MAINTAINS SELECTIVITY

The steep slopes of the contrast response function force most cortical cells to have a limited dynamic response range. As a function of contrast, the response increases rapidly and then saturates. While the steep slopes of the contrast response function may well enhance stimulus selectivity, the saturation nonlinearity could potentially have very deleterious effects on the overall stimulus selectivity of the cortical cells.

Consider, for example, what would happen to spatial frequency selectivity if the saturation were due to a limitation imposed by the final response generating mechanism of the cortical cell, after summation of inputs. Under these circumstances, the cell would exhibit very narrow spatial frequency tuning when measured at low contrasts, but then exhibit very broad spatial frequency tuning when measured at high contrasts. This is what we expected to find. The validity of these expectations can be tested by measuring the spatial frequency tuning at multiple contrasts, or equivalently, by measuring the contrast response function across a range of spatial frequencies -- particularly, optimal and nonoptimal spatial frequencies.

Figure 9 illustrates this point. The solid lines in the panel on the right are the predicted contrast response functions, measured at different spatial frequencies, given a saturation that is dependent upon the overall level of the final response of the cell. On log coordinates, the curves shift horizontally, the maximum response rate stays the same, only the semi-saturation constant changes. This is the response-set gain model: it is what
we were expecting to find. At a low contrast, say 5%, an optimal spatial frequency produces some 50 spikes/second whereas a nonoptimal frequency produces only 1 spike/second -- a 50-to-1 difference; the cell is very selective. However, at a high contrast, say 50%, the selectivity is gone since both the nonoptimal and the optimal evoke the same maximum saturated response. This is not how cortical cells behave; these predicted curves do not fit the measured responses.

The panel on the left shows the same measured responses along with the predictions of a different model. In this case, the saturation is not determined by the overall level of the response but rather the gain is set by the overall level of the contrast. On log coordinates, the curves shift vertically, the semi-saturation constant remains the same and only the maximum response changes. This is the contrast-set gain model of Albrecht and Hamilton,¹⁰ which we will shorten here to contrast gain model. As can be seen, the contrast gain model provides a much better fit to the measured responses. Saturation tends to occur at the same contrast level for all the different spatial frequencies, not at the same response level. Further, the magnitude of the saturated response is different for each spatial frequency. Thus, the relative response ratios between spatial frequencies are maintained across contrast.

Figure 10. Spatial frequency tuning functions measured at three different contrasts.¹⁰
One overall net effect of this contrast gain mechanism is to preserve the spatial frequency selectivity: the relative response ratios between spatial frequencies are maintained across contrast -- the responses of nonoptimal spatial frequencies remain non-optimal even at high contrasts. Figure 10 shows the spatial frequency tuning of a typical cell measured at different contrasts. As can be seen, the overall shape and bandwidth change very little as the contrast of the gratings is varied from a threshold value of 4% through a midrange value of 6.6% and a saturation value of 33%. The tuning remains relatively invariant with contrast. The bandwidth remains nearly fixed at 0.7 octaves. Over the last decade, many different laboratories have replicated and extended this basic finding to all of the important dimensions of stimulus selectivity: orientation selectivity, direction selectivity, ocular selectivity, spatial phase selectivity, etc. 10, 11, 14, 25, 26

6. ISOLATION OF CONTRAST GAIN CONTROL

We have just begun to explore the spatial and temporal properties of the contrast gain control mechanism using a new technique which we call the null-adaptor technique. 16 To isolate contrast gain control we vary the contrast of a counterphase grating which is (a) located at the null phase position and (b) confined in length and width to the conventional receptive field. This stimulus does not evoke a response from the cell but it does allow us to control the average contrast while holding other factors constant (such as response fatigue, slow adaptation, spatial frequency and orientation inhibition, etc.). To assess the effect of the adapting contrasts, we superimpose a drifting grating of the same spatial frequency, temporal frequency, orientation, length, and width. Figure 11A illustrates this basic stimulus configuration.

Figure 11B plots the contrast response function (measured with the drifting grating) in the presence of three adapting contrasts. As can be seen, the three null adaptor contrasts had little or no effect on the response of the cell when presented alone (i.e. when the contrast of the drifting test was zero); however, the adapting contrasts had a substantial effect on the responses to the superimposed drifting grating. Specifically, as the adapting contrast increased, sensitivity to the drifting contrast decreased; the contrast response function primarily shifts to the right.

These curves indicate that while the stationary flickering grating evokes no response from the cell in the null phase position, it nevertheless controls the overall sensitivity of the cell to contrast through a fast-acting, multiplicative, gain control mechanism.
Figure 11. (A) Stimulus configuration used to isolate contrast gain; a drifting grating is superimposed upon a counterphase grating flickering at the "null phase position." (B) Contrast response functions measured with a drifting grating in the presence of different null adaptor contrasts.16
Over the past few years, three different laboratories have performed a similar set of experiments that were designed to investigate the fundamental mechanism responsible for direction selectivity. In these studies, the responses to drifting sine wave gratings were compared with the responses to stationary counterphase flickering gratings. All three reports demonstrated that the results were not totally consistent with what would be expected based upon simple linear summation over a receptive field oriented in the space-time domain: for example, the direction selectivity predicted from responses to flickering gratings generally underestimated the direction selectivity measured from the responses to drifting gratings.

The results contained within the three reports were quite similar; further, all three reports seemed to agree that while linear summation could probably account from some of the direction selectivity, an additional nonlinear contribution would be required to account for the degree of direction selectivity. Reid et al. proposed a model in which the direction selectivity of a linear filter was "sharpened" by nonlinear suppression of the responses in the nonpreferred direction. Tolhurst and Dean proposed a similar model. As described above, Albrecht and Geisler incorporated the nonlinearities evident in the contrast response function (contrast gain control and expansive response exponent) and found that the discrepancies between the measured and predicted responses, to drifting and flickering gratings, were diminished.

Reid et al., and Tolhurst and Dean, compared the absolute magnitude of the response to drifting gratings with a simple linear prediction based upon the measured responses to flickering gratings. The linear predictions are straightforward: the response in the preferred direction of motion should be equal to the sum of the peak and the trough from the counterphase data while the response in the nonpreferred direction should be equal to the difference of the peak and the trough. They found that, for the preferred direction of motion, the measured responses were approximately equal to the linear predictions. However, for the nonpreferred direction of motion, the measured responses were considerably less than the linear predictions. This result may be consistent with what might be expected from a "nonlinear direction-selective suppression mechanism." However, this simple linear prediction ignores the well-known nonlinearities evident in the contrast response function (saturation due to contrast gain and expansive response exponents). As Heeger recently pointed out, this pattern of results is what might be expected when these two nonlinearities are taken into consideration.
Figure 12. Responses to stationary and drifting gratings along with a model composed of a linear filter, contrast gain control and expansive response exponent. (A) Responses to counterphase gratings in different positions and contrasts; the smooth curves show the fit of the contrast-gain/exponent model. (B) Contrast response function measured with drifting gratings in the preferred direction of motion (filled squares) and nonpreferred direction (filled circles); the smooth curves (solid lines) show the *predictions* of the contrast-gain/exponent model based upon the fit to the counterphase responses; open triangles and the dashed line replot the counterphase responses and fit near the peak; open diamonds and the dashed line replot the counterphase responses and fit near the trough.

Figure 12A plots the responses of a direction selective simple cell (recorded from the striate cortex of a macaque monkey) to a counterphase grating flickering in different spatial positions at four separate contrasts. The smooth curves show the fit of a model which incorporates the nonlinearities evident in the contrast response function; specifically, the contrast-gain/exponent model (formally described elsewhere). Given strict linearity, the null phase positions would lead to the erroneous conclusion that this cell was nondirection selective and that the responses to gratings drifting in either direction would be equal to the responses at the optimal position of the counterphase gratings. (The sum and the difference of the peak and the trough are obviously equal when the trough is zero.) Figure 12B plots the responses of the same cell to gratings drifting in the preferred and nonpreferred direction as a function of contrast; the responses to the counterphase grating (from 12A, near the peak and trough position), are superimposed. As can be seen, while the responses to the grating drifting in the preferred direction are approximately equal to the linear prediction (i.e., the responses are approximately the sum of the peak and the trough), the responses in the nonpreferred direction are far below the linear prediction (i.e., the responses are far below the difference of the peak and the trough). The smooth curves are the predictions of the
contrast-gain/exponent model using the optimized parameters from the counterphase data. As can be seen, the model conforms well to the measured responses.

Reid et al., and Tolhurst and Dean, summarize their data for the total sample of cells using scatter plots (one for each direction of motion), where the x-axis is the measured response to drifting gratings, and the y-axis is the linear prediction from the measured responses to counterphase gratings. We have performed a similar analysis on both a sample of cat and a sample of monkey striate cortex neurons; the results are very similar to what Reid et al. and Tolhurst and Dean reported. In general (across all laboratories, in both cat and monkey), for the preferred direction of motion, the data cluster around the diagonal (congruent with the linear predictions); however, for the nonpreferred direction of motion, the data cluster above the diagonal (contrary to the linear predictions).

Further, two clear differences are evident in a comparison of the scatter plot for the preferred direction of motion with the scatter plot for the nonpreferred direction: the nonpreferred data points are more dispersed and the regression line is shifted toward the upper left whereas the preferred data points are less dispersed and the regression line is shifted slightly toward the lower right corner. This pattern of results is consistent with what would be expected of a random sample of visual cortex neurons having contrast gain control, the known distribution of direction selectivities and the known distribution of response exponents. As summarized in Table 1, the location of the regression line and the degree of dispersion can be affected by: the contrast gain control, the degree of direction selectivity, and the value of the expansive exponent.

For the shift in the regression line, the arrows in Table 1 summarize the following relationships: (a) as the exponent increases from 1.0 (given any degree of direction selectivity), there is an asymmetric shift in the flicker predictions to overestimate the responses in the nonpreferred direction and underestimate the responses in the preferred direction; that is, the regression line shifts toward the upper left corner for nonpreferred and the lower right corner for preferred; (b) as the direction selectivity increases (given an expansive exponent), there is a similar asymmetric shift in the flicker predictions: that is, the regression line shifts toward the upper left corner for the nonpreferred direction and the lower right corner for the preferred direction; (c) as the contrast gain control factor is increased (given the difference in the spatiotemporal RMS contrast of a counterphase grating vs. a drifting grating -- equated using the conventional peak to trough "Michelson" contrast), the regression line shifts toward the upper left corner for both directions.
Table 1: Effects of the contrast gain control (Gain), the direction selectivity (Dir), and the expansive response exponent (Exp) on the shift of the scatter plot regression line and degree of dispersion for the preferred and nonpreferred directions of motion. Direction of the arrow indicates the direction of the effect: open arrows indicate that the effect is minor.

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For the degree of dispersion, the arrows in Table 1 summarize the following relationships: (a) as the exponent increases from 1.0 (given some level of variability in the degree of direction selectivity from cell to cell) there is a greater degree of dispersion for the nonpreferred direction of motion as opposed to the preferred direction of motion; (b) as the degree of direction selectivity is increased (given some level of variability in the exponent from cell to cell), there is a greater degree of dispersion for the nonpreferred direction of motion as opposed to the preferred direction of motion; (c) as the contrast gain factor is increased (given some level of variability in either/both the degree of direction selectivity or/and the exponent), the degree of dispersion increases for the nonpreferred but decreases for the preferred.

In summary, the data in the scatter plots reveal a consistent pattern: asymmetric shift of the regression line and the degree of dispersion, depending upon drift direction. This pattern of results is consistent with what one might expect given a random sample of cortical cells and the known effects of the nonlinearities seen in the contrast response function: the cell to cell variation in the degree of direction selectivity, along with the cell to cell variation in the value of the exponent, would combine with the differential contrast gain to produce the asymmetric shift and the asymmetric dispersion.
8. ACKNOWLEDGMENTS

This research was supported by TARP grant 003658-463, by AFOSR grant F49620-93-1-0307, by the Primate Vision Endowment (DGA), and by NIH grant EY02688 (WSG). The authors thank Larry Stern for his assistance in all phases of this research.

9. REFERENCES