Linear filtering precedes nonlinear processing in early vision
K. Langley*, D.J. Fleet[†] and P.B. Hibbard*

Background: Nonlinearities play a significant role in early visual processing. They are central to the perception of spatial contrast variations, multiplicative transparencies and texture boundaries. This article concerns the stage of processing at which nonlinearities first become significant.

Results: Subjects were adapted to a high contrast sinusoidal grating followed by a brief presentation of a contrast modulated test (plaid) pattern. Thresholds for the detection of the contrast modulation (the beat) were measured. Results show that threshold elevation is greatest when the orientation and spatial frequency of the adapting grating are close to the principal Fourier frequency (the carrier) of the test pattern. Adaptation to sinewave-gratings near the frequency of the contrast modulation has relatively little effect. The data also show that the processing of contrast is frequency selective, with a peak tuning frequency near 0.4 cycles per degree.

Conclusions: The data are consistent with a model in which the contrast beats are processed in a frequency-specific manner, after an initial stage of frequency-specific and orientation-specific linear filtering.

Addresses: *Department of Psychology, University College London, London, UK. [†]Departments of Computing Science and Psychology, Queen's University, Kingston, Canada.

Correspondence: K. Langley
E-mail: kl@psychol.ucl.ac.uk

Background
In order for us to have a complete model of the visual sensory nervous system and its detection of visual events, we need to understand how the visual system processes both linear and nonlinear image structures. The linear components of an image are regarded to be luminance defined edges, their spatial orientation and direction of motion. Nonlinear image structures include spatial contrast variations, texture boundaries and (multiplicative) transparencies. The work of Campbell and Robson [1] led to the assumption that that the initial stages of visual processing are primarily linear and can be modelled by a family of frequency- and orientation-selective bandpass filters. These ideas are still reflected in current models of visual processing (for example, see [2,3]). This early stage is linked anatomically to neurons (simple cells) in the primary visual cortex, which are thought to be responsible for the detection of linear features. Although models of these cells involve nonlinearities (such as contrast normalization and halfwave-rectification), their functional behaviour is remarkably linear over their dynamic range [4].

Nonlinearities have been incorporated into models of early visual processing to help account for the perception of stimuli that are (nonlinear) products of elementary image components. For example, several models include rectification of band-pass filter outputs [2,3]. A common source of nonlinear image components is the spatial variation in contrast that is caused by illumination

variations throughout a scene. Nonlinearities have been studied with the aid of contrast-modulated stimuli, similar to the sinusoidal plaid pattern shown in Figure 1. Interestingly, these signals can be viewed mathematically in two ways: they can be formed as a sum of three sinusoidal gratings, or they can be formed as a product of a low-frequency grating called the beat, and a high-frequency grating called the carrier. In Figure 1b, the perceptually compelling components are the two one-dimensional components in the product — the vertical carrier and the beats oriented at 45 degrees. A mathematical representation of these components is given by the Fourier transform of the image which is depicted in Figure 1c. The Fourier spectrum shows the locations of nonzero power in the frequency domain, as a function of spatial frequency. Note that, at the orientation and spatial frequency of the beat, there is no spectral energy in the Fourier transform. As a consequence, a linear neuron tuned to the frequency of the beat will not respond to this signal. The issue addressed in this article concerns the stage at which significant nonlinearities occur in relation to alternative models of visual processing and their predictions.

Burton [5] first showed that prolonged presentation of sinusoidal contrast modulations (spatial beats) affects the detection of sinusoidal gratings when the grating frequencies are close to the frequency of the beats. Because the Fourier transform of contrast-modulated stimuli does not contain power at the beat frequency, this result is

Figure 1
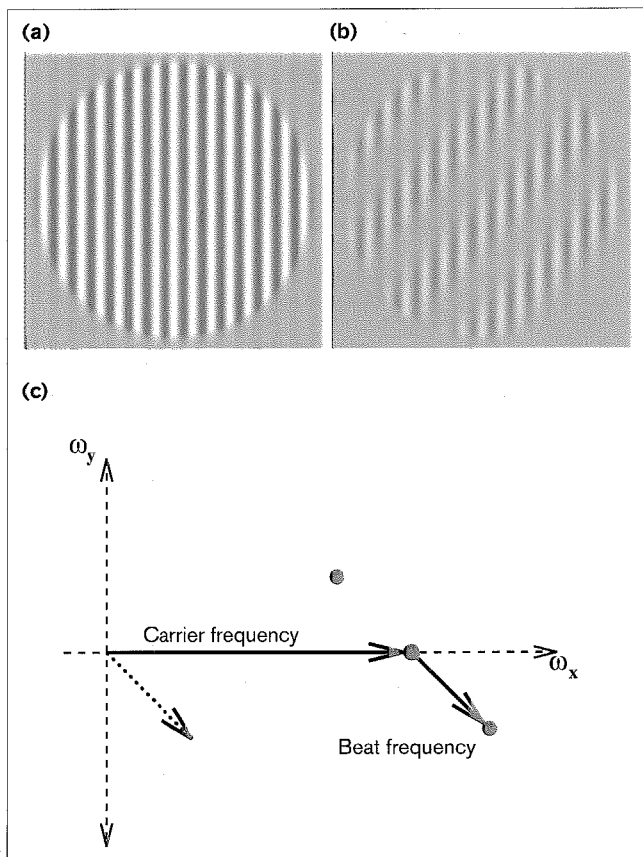
An example of (a) an adapting grating and (b) a test plaid stimulus. The plaid carrier and the adapting grating have the same orientation and frequency. The plaid beat is oriented at 45 deg. Adaptation to the carrier when the test plaid has low contrast reduces sensitivity to both the carrier and the beat. (c) In the Fourier domain, the test plaid has three non-zero sinusoidal components denoted by black circles. The carrier is located along the ω_x axis, shown by the solid vector that passes through the origin. The length and direction of the vector give its spatial frequency and orientation. The neighbouring locations of power are called side-bands. The beat spatial frequency is shown by the second solid vector from the carrier to one side-band [3]. The dotted vector shows the location where power would be introduced by an early nonlinearity.

inconsistent with a model of the human visual system that analyses spatial stimuli exclusively with a bank of frequency-selective, linear filters. Burton suggested that an early nonlinearity might occur at the very first stages of visual processing, distorting image intensities and introducing power not present in the original image at the beat frequency [6]. This distortion could then be sensed by conventional frequency- and orientation-selective channels that are associated with the visual cortex, leading to the detection of spatial beats.

To test whether the detection of spatial beats could be accounted for by an early nonlinearity, Derrington and Badcock [6] manipulated the contrast of one of the two

Fourier components in a sinusoidally modulated pattern. They reasoned that, if there was an early nonlinearity, then the beat amplitude would be proportional to the product of the amplitudes of the individual Fourier components. The detection of spatial beats should be unaffected by changes to the individual amplitudes, therefore, as the product of the amplitudes remains constant. Conversely, if the detection of spatial beats were based on local increments in contrast (the spatial gradient of the beat), then changes to individual amplitudes would affect the detection of beats, because contrast-increment detection thresholds increase with mean contrast.

Derrington and Badcock [6] found that raising the contrast of one component raises the contrast of the other component required to detect the beats. This result contradicts the early nonlinearity hypothesis. Derrington and Badcock reconciled their findings with those of Burton, however, by suggesting that small nonlinear distortions may occur in the visual system at high contrasts; such distortions might be caused by saturation, for example. Instead of an early nonlinearity, they proposed that the visual system detects and analyzes local changes in contrast explicitly. The site and nature of the process remain unclear. It may occur in the retina or lateral geniculate nucleus, with a nonlinearity in the responses of center-surround neurons [7]. This hypothesis is consistent with the two-pathway motion model of Chubb and Sperling [8]. In their model, one pathway detects motion by processing luminance information; the second pathway detects motion after broadband filtering and fullwave rectification. It is the second pathway that processes contrast beats. Because of the broadband nature of the initial processing before the rectification, we refer to this model as an early nonlinearity.

Other models posit a later nonlinearity that occurs after an initial stage of orientation- and frequency-specific filtering [2,3]. The likely site of such a nonlinearity would be the primary visual cortex. This article reports evidence that contrast information is extracted after bandpass orientation-tuned linear filtering. The data also suggest that the processing of contrast information is selective for spatial frequency. Our experiments are an extension of the adaptation studies of Blakemore and Campbell [9]. They showed that prolonged presentation of a high-contrast sinewave-grating reduces the sensitivity of the visual system to a selective range of frequencies; that is, the adaptation causes an elevation of the minimum contrast (the detection threshold) required to detect gratings at frequencies and orientations close to the adapting grating. The difference between the detection thresholds before and after adaptation are often used as a measure of the effect of adaptation. Because of the frequency- and orientation-selective nature of adaptation to sine gratings, it is often assumed to occur in primary visual cortex, where frequency- and orientation-selective neurons first occur.

Results

Our experiments involved adaptation to single sinewave gratings, followed by a brief presentation of a sinusoidal plaid pattern, such as that shown in Figure 1b. Subjects were asked to report the presence and orientation of the beat. The models outlined above yield different predictions for the outcomes of such experiments.

First, the early nonlinearity model posits that Fourier power at the beat frequency is introduced by a nonlinearity (a distortion product [7]). This power at the beat frequency is then analyzed by the same frequency- and orientation-specific channels that process luminance gratings. Thus, if the visual system detects the beat with an early nonlinearity [4,9], then one might expect that adaptation to frequencies near the beat frequency would have a significant effect on subjects' perception of the beats. One might also predict that peak sensitivity should occur at beat frequencies close to 5 cycles per degree (cpd), which is the peak sensitivity of luminance sinewave gratings [1].

If the nonlinearity occurred after orientation- and frequency-selective processing, then we might predict that the perception of the beats would be influenced by adaptation to frequencies near the plaid carrier, where Fourier power is concentrated in the plaid pattern (see Fig. 1). Hence, we would expect an elevation of detection thresholds when the adapting sinewave grating is similar to the plaid carrier, but not when the adapting grating is similar to the beat frequency.

From the late nonlinearity model, one might also predict those threshold elevations should be greatest for lower frequency beats. In this case, as illustrated in Figure 1, the sidebands of power that define the beat would be closer to the carrier frequency. Adaptation to a single sinewave grating at the frequency of the carrier will affect the sidebands more, therefore, than if they were further from the carrier (when the beat frequency is higher).

If the early nonlinearity occurred before orientation-selective processing but after band-pass processing (at the on and off centre-surround neurons in the retina, for example), then one might expect somewhat different behaviour. Here, one would predict that the orientation between the adapting grating and the carrier would have little or no effect on the perception of the beat, as processing at this stage is not orientation-specific.

A final prediction for these experiments can be made if the detection of beats were based solely upon the spatial gradient of the beat itself [6]. In this case, one would predict that (unadapted) detection thresholds to the beats would decrease as the beat frequency increased over a wide range of beat frequencies. The reason is that higher frequencies have a higher gradient, which might be more easily detected because local differences in contrast are greater.

In order to test these predictions, the stimuli were presented to the subjects as described in the Materials and methods section. Figure 2 shows the threshold elevations for the discrimination of the beat orientation when the frequency of the adapting sinewave-grating was close to the carrier frequency of the plaid. The threshold elevation is the ratio of the contrast thresholds in the adapted and the unadapted conditions. Figure 2a shows the threshold elevation as a function of the frequency of the adapting grating. The two curves correspond to different carrier frequencies — 1.7 and 3.4 cpd. In both cases, the maximum threshold elevation occurred when the frequency of the

Figure 2

(a) The mean threshold elevation for the discrimination of beat orientation following adaptation is plotted on log–log axes as a function of the frequency of the adapting grating. These threshold elevations are averaged over all sessions of the three subjects. The two curves correspond to carrier frequencies of 1.7 and 3.4 cpd, which are marked on the horizontal axis. The threshold elevations are maximal when the frequencies of the adapting gratings matched the carrier frequencies. (b) Mean threshold elevation is plotted as a function of the difference in orientation between the carrier and the adapting grating. Standard error bars are also plotted, which reflect the variation between subjects and across sessions. The threshold elevations are maximal when the orientations are identical.
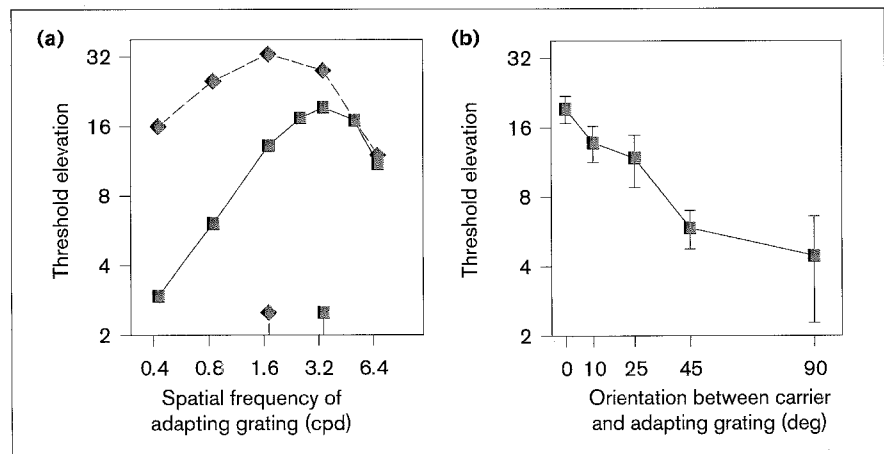
Figure 3
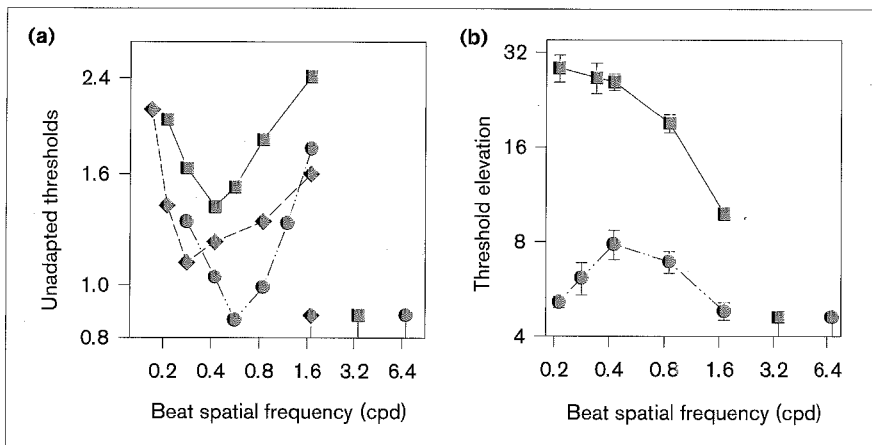
(a) Mean normalized thresholds (75 %-correct contrast thresholds) for the discrimination of beat orientation are plotted on log–log axes as a function of the beat frequency. As discussed in the text, the three curves correspond to three different carrier frequencies. The carrier frequencies are marked on the horizontal axis. (b) Mean threshold elevation after adaptation is plotted as a function of the beat frequency. The adapting gratings had the same orientation as the plaid carrier. The spatial frequency of the adapting gratings, marked on the horizontal axis, were 3.4 and 6.8 cpd. The spatial frequency of the plaid carrier was 3.4 cpd.

adapting grating was close to the carrier frequency. The threshold elevations decreased as the difference in frequency between the adapting grating and plaid carrier increased. Figure 2b shows threshold elevation as a function of the difference in orientation between the adapting grating and the plaid carrier. It was maximal when the plaid carrier and the adapting grating had the same orientation. The detection of spatial beats was significantly affected, therefore, by the orientation and frequency of the adapting sinewave grating. When the adapting grating had the same frequency and orientation as the plaid carrier, the subjects required a higher level of plaid contrast to do the task.

Figure 3a shows contrast thresholds for the discrimination of the beat orientation as a function of the beat frequency, without prior adaptation to a sinewave grating. For each of three carrier frequencies, 1.7, 3.4 and 6.8 cpd, we measured discrimination thresholds for six different beat frequencies (for each carrier frequency, there is one curve in Fig. 3a). As described in the Materials and methods section, the data shown in Figure 3a have been normalized with respect to the perceived contrast of the plaid carrier. From these curves, note first that the discrimination thresholds for the beats changed as the beat spatial frequency was varied. The threshold minima (maximal sensitivity) for each curve occurred for beat frequencies of approximately 0.4 cpd. The threshold minima also depended, to a small degree, on the carrier frequency.

Finally, Figure 3b shows how discrimination thresholds changed with adaptation; that is, it shows how threshold elevation in the adapted condition depended on the spatial frequency of the beat. In this experiment, we ran two conditions: one with the frequency of the adapting grating equal to the carrier frequency; and the other with the adapting frequency one octave higher. When the adapting grating was equal to the plaid carrier, threshold

elevations increased as the beat frequency decreased. When the adapting grating was one octave higher, however, threshold elevations peaked close to 0.4 cpd. Threshold elevations were also consistently lower when compared with the first case in which the adapting grating matched the plaid carrier.

Discussion

The data presented here are not consistent with a model in which contrast beats are detected primarily because of an early nonlinearity, before orientation- and frequency-specific filtering. Adaptation to a sinewave grating affects the perception of the beat most when the adapting grating is similar in both frequency and orientation to the carrier of the plaid, rather than to the beat. This suggests that the adapted mechanism is selective to both frequency and orientation, whereas the early nonlinearity model would predict that the angle between the adapting grating and the plaid carrier should be insignificant.

One can also see in Figure 2a that the threshold elevation curves are nearly symmetric about the peak. The curves decay by a factor of two from the peak after about 0.5 octaves in spatial frequency, and about 25 ° in orientation. They are similar to the elevation in detection thresholds to individual sinewave gratings found by Blakemore and Campbell [9], which are often thought to arise from processing in the primary visual cortex [10].

The results in Figure 3a, which show how sensitivity to spatial beats in the unadapted condition depends on beat frequency, are also inconsistent with the early nonlinearity model. The minimum threshold (maximal sensitivity) for each curve occurs for beat frequencies near 0.4 cpd. By comparison, contrast thresholds for single sinewave gratings are smallest at approximately 5 cpd [11]. Therefore, if the perception of contrast beats were the result of an early nonlinearity followed by conventional frequency-specific

channels, one would have expected a minimum at 5 cpd instead of 0.4 cpd. Figure 3a also shows that the threshold minima depend on the carrier frequency. An early nonlinearity model would predict no dependence on the spatial frequency of the carrier.

If the detection of contrast beats were based upon local spatial changes in contrast [6], then, by manipulating the beat frequency and controlling for the perceived contrast of the plaid carrier, one would expect that thresholds for beat detection would decrease as beat frequency increases. Hence, as the beat frequency increases so does the beat gradient, which should yield larger local contrast variations, while the mean contrast remains constant. The data shown in Figure 3a are inconsistent with this scheme. Rather, they are consistent with a contrast processing mechanism that is selective for spatial frequencies near 0.4 cpd.

The results shown in Figure 3b provide some confirmation of our main results. As explained above, if the contrast beat is processed after orientation- and frequency-specific filtering, then one would predict that beat discrimination thresholds should increase as one reduces the spatial frequency of the beat, but only when the adapting grating is equal to the plaid carrier — when the beat frequency decreases, the sidebands of power (see Fig. 1) move closer to the carrier. As a result, adaptation to the carrier should have a greater influence on the sidebands, and thereby attenuate the effective strength of the beat along with the carrier.

Indeed, the data in Figure 3b agree with this prediction. Beat threshold elevations rise as the beat frequency decreases, and then saturate at a relatively higher level for beat frequencies below approximately 0.4 cpd. The saturation may be explained by an elevation in unadapted detection thresholds, as shown in Figure 3a, which counterbalances the elevation in adapted beat detection thresholds as beat frequency is reduced. To confirm this, note that when the adapting grating has a frequency an octave higher than the carrier, threshold elevations are not as remarkable and they no longer saturate. Rather, they peak at close to 0.4 cpd, where Figure 3a suggests that the visual system is most sensitive to the beat.

Conclusions
The data collected from these four experiments are consistent with a late nonlinearity: a nonlinearity that occurs after an initial stage of frequency- and orientation-specific filtering (for example, see [2,3]). The data also suggest that the processing of contrast is itself selective for spatial frequency. The experiments are not, however, restricted to contrast thresholds or spatial vision. We have replicated these experiments in stereopsis with similar results (our unpublished observations). Our ideas may also transfer to

other sensory modalities, such as audition, where related stimuli are used [12]. Moreover, at high contrasts, a condition where early nonlinearities are likely to be significant [6], we can make a prediction. Given the assumption that the functional basis of contrast adaptation is to increase discrimination about the level of adaptation [13], then beat detection thresholds should decrease relative to their baselines when presented at the contrast of the adapting grating. Here, we would predict reciprocal frequency- and orientation-specific tuning curves to those shown here, if late nonlinearities are significant at high as well as low levels of contrast.

Materials and methods
Stimuli
Figure 1 shows an example of the stimuli. Each image was presented within a circular window with a smoothed boundary. For the plaids, the orientation of the carrier was vertical or horizontal; this was randomized between trials. The spatial frequency of the carrier was 1.7 cpd on one set of trials, and 3.4 cpd on another set of trials. The beat orientation was either 45 deg or −45 deg, and randomized between trials. In the first two experiments (Fig. 2) the spatial frequency of the beat was two octaves below the carrier. The beat modulation depth was fixed at 0.75. The method of constant stimuli was used. For each condition, there were two sessions, each with 12 trials at each of 10 contrast levels. Stimuli were presented on a linear JOYCE DM 4 monitor, and subtended a visual angle of 15.98 deg. The mean luminance of the monitor was 8.8 cd m^{-1}. Test stimuli were presented to an accuracy of 12 bits using a VSG2/3 graphics display card. The results reported here are averaged over three subjects with normal vision.

Baseline task
The baseline task (without adaptation) used a yes–no contrast discrimination task, and a yes–no orientation discrimination task. On each trial, subjects were presented with a plaid pattern for 80 msec. The spatial frequency of the beat was 0.43 cpd. The maximum contrast of the plaid defined at the peak of the beat was fixed at 0.6 %. The beat orientation was either 45 deg or −45 deg, and was randomized between trials. This was followed by a 1 sec interstimulus interval, after which subjects were shown another plaid pattern for 80 msec. The carrier frequencies in the first and second plaids were equal, but the contrast and beat spatial frequency varied across trials and sessions. Subjects responded to two questions: whether the contrast of the carrier in the second plaid was greater than that of the first plaid; and whether the beat in the second plaid was oriented at either 45 deg or −45 deg.

Adaptation task
Each session began with a baseline measurement, as described above, followed by a 2 min period of adaptation to a sinewave-grating. The adapting grating was counterphase flickered at 4 Hz to avoid phase-dependent after-effects [14]. Subjects were then presented with a test plaid pattern for 200 msec, and asked to report whether the orientation of the beat was 45 deg or −45 deg. Subsequent trials were preceded by a 'top-up' adaptation period of 3 sec. Subjects were required to respond to each trial during the 'top-up' period. In separate sessions, we adjusted the spatial frequency of the adapting grating, the orientation of the adapting grating and the spatial frequency of the beat.

Analysis
In the orientation discrimination task, we measured the contrast threshold at which subjects could report the orientation of the beat correctly on 75 % of the trials. To obtain this threshold, a psychometric function (ranging between 1 and 0.5) was fitted to the percent correct for each subject in each session as a function of plaid contrast. The 75 %-correct contrast thresholds were obtained from the fitted psychometric

functions. Adapted 75 %-correct thresholds were then normalized by baseline 75 %-correct contrast thresholds. These baseline measurements are made without prior adaptation, to consider differences in baseline discrimination thresholds between sessions. The resulting threshold elevation, shown in Figure 2, is equal to the adapted contrast threshold divided by the baseline threshold.

In the baseline task, we conducted a yes–no contrast discrimination task which required a different analysis to the orientation discrimination task. This task was included to consider differences in the perceived brightness of each plaid's carrier while we measured beat orientation discrimination thresholds. The perceived brightness of the plaid carrier may influence beat detection thresholds because the spatial gradient of the beat is dependent on the contrast of the plaid carrier. For each session, a psychometric function (ranging between 1 and 0) was fitted to each subject's data. The point of subjective equality (PSE) was taken from the fitted functions as the contrast at which the second plaid was judged to have higher contrast on 50 % of the trials. This gave us a measure of the perceived contrast (compared with the reference plaid) of each plaid carrier in the baseline task. To the (unadapted) 75 %-correct contrast thresholds (Fig. 3a), each condition was divided by the contrast at which the PSE occurred in the contrast matching task. This normalization allowed us to correct for differences in contrast thresholds in the beat orientation task that occur owing to differences in perceived contrast of the plaid carrier [15].

References

1. Campbell FW, Robson JG: **Application of Fourier analysis to the visibility of gratings.** J Physiol 1968, **197:**551–566.
2. Wilson HR, Ferrera VP, Yo C: **A psychophysically motivated model for two-dimensional motion perception.** Vis Neurosci 1992, **9:**79–97.
3. Fleet DJ, Langley K: **Computational analysis of non-Fourier motion.** Vis Res 1994, **34:**3057–3079.
4. Heeger D: **Normalization of cell responses in cat striate cortex.** Vis Neurosci 1992, **9:**181–198.
5. Burton GJ: **Evidence for non-linear response process in the visual system from measurements on the thresholds of spatial beat frequencies.** Vis Res 1973, **13:**1211–1255.
6. Derrington AM, Badcock DR: **Detection of spatial beats: nonlinearity or contrast increment detection?** Vis Res 1986, **26:**343–348.
7. Derrington AM: **Mechanisms for coding luminance patterns: are they really linear?** In Vision: Coding and Efficiency. Edited by Colin Blakemore. Cambridge: Cambridge University Press; 1990:175–184.
8. Chubb C, Sperling G: **Drift-balanced random-stimuli: a general basis for studying non-Fourier motion perception.** J Opt Soc Am 1988, **5:**1986–2007.
9. Blakemore C, Campbell FC: **On the existance of neurons in the human visual system selectively sensitive to the orientation and size of retinal images.** J Physiol 1969, **203:**237–260.
10. Hubel DH, Wiesel TN: **Receptive fields, binocular interaction and functional architecture in the cat's visual cortex.** J Physiol 1962, **160:**106–154.
11. Henning GB, Hertz GB, Broadbent DE: **Some experiments bearing on the hypothesis that the visual system analyses patterns in independent bands of spatial frequency.** Vis Res 1975, **15:**887–897.
12. Tansley BW, Suffield JB: **Time-course of adaptation and recovery of channels selectively sensitive to frequency and amplitude modulation.** J Acoust Soc Am 1983, **74:**765–775.
13. Greenlee MW, Heitger F: **Functional role of contrast adaptation.** Vis Res 1988, **28:**791–797.
14. Georgeson M: **Temporal properties of spatial contrast vision.** Vis Res 1987, **27:**765–780.
15. Georgeson M, Shackleton TM: **Perceived contrast of plaids.** Vis Res 1994, **34:**1061–1075.