Linear and non-linear mechanisms in pattern vision

Recent physiological results identify a visual mechanism that is sensitive to patterns defined by either luminance or contrast differences.

The objects that populate our visual environment may be distinguished from their backgrounds by variations in any of a number of attributes, including brightness, colour and surface texture. The mammalian visual system must thus be equipped with mechanisms to analyse how these different attributes vary in space and time. We already have a fairly clear understanding of the way early visual mechanisms may, by their selective sensitivity to spatio-temporal variations in luminance, begin the process of encoding objects that differ in brightness from their backgrounds. The results of psychophysical [1] and physiological [2] studies concur that an important feature of these early visual mechanisms is their selectivity for the spatial scale of luminance variations, and hence for size. This selectivity can be characterized by measuring neuronal responsivity to sinusoidal luminance patterns of different spatial frequencies (Fig. 1).

Because early visual mechanisms are approximately linear — they respond as if to the sum of excitatory and inhibitory signals generated by light falling within their receptive fields — Fourier analysis (see box) can be used to predict their sensitivity to other visual stimuli. Each cell (or psychophysical mechanism) is selective for a range of spatial frequencies, which are roughly inversely proportional to the sizes of the objects to which the cell responds best. Fourier analysis allows us to predict the optimal stimulus from the function relating sensitivity to spatial frequency [3].

Fourier analysis is a mathematical technique that allows any continuous waveform to be expressed as the sum of a set of simpler waveforms. In vision research, Fourier analysis can be used to express a stimulus as the sum of a set of sinusoidal luminance gratings. The utility of Fourier analysis stems from the fact that it is possible to predict performance – of a cell or psychophysical mechanism – in a task involving discrimination of luminance patterns from knowledge of the sensitivities of the cell or mechanism to the sinusoidal components of the patterns.

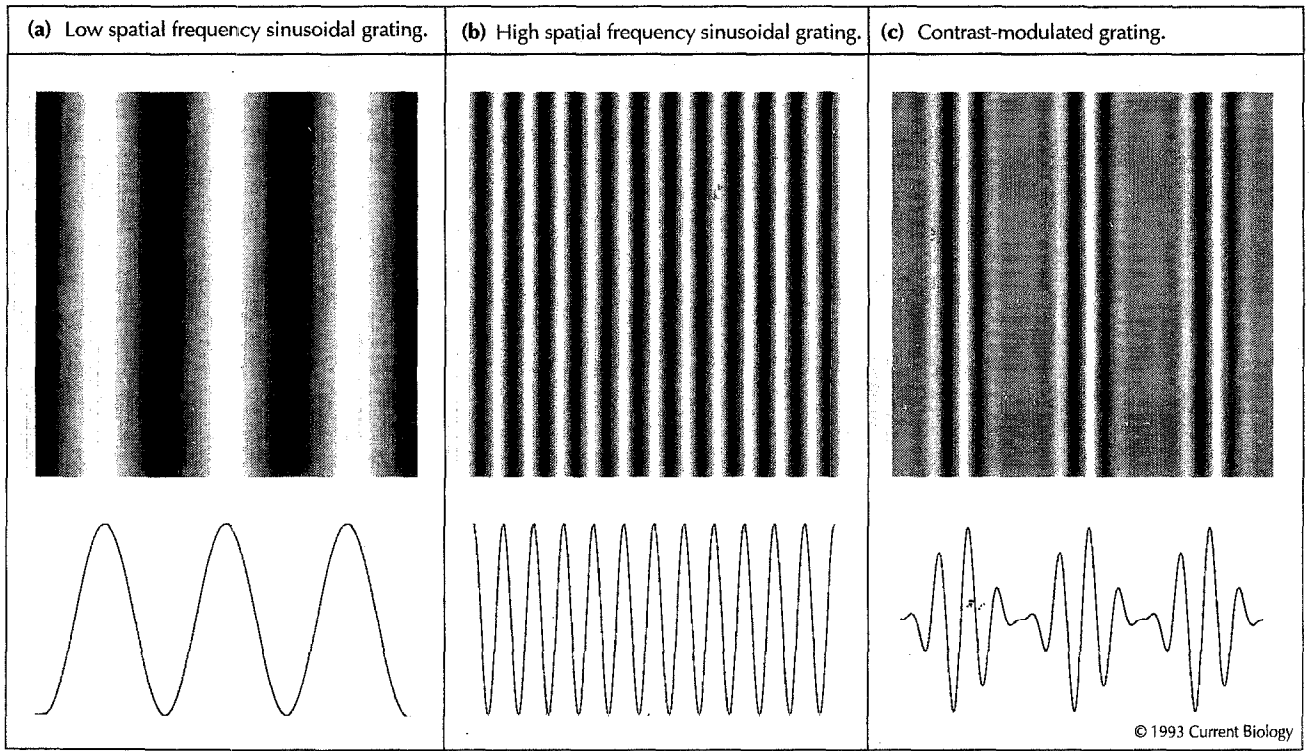

Fig. 1. Panels **(a)** and **(b)** show, at the top, sinusoidal gratings used to analyse response selectivities of neurons and psychophysical mechanisms. The luminance profiles of the gratings are shown at the bottom in each panel. A simple neuronal receptive field selective for either of the spatial frequencies illustrated in (a) and (b) would be divided into two or more sub-regions of alternating sensitivity (excited by brightening or excited by dimming), each about the same width as one bar (the spatial frequency is the reciprocal of the distance from one bright bar to the next). Cells responsive to the spatial frequency of grating in (a) would not respond to that of the grating in (b), and *vice versa*. The grating in **(c)** is contrast-modulated, and has a modulation frequency the same as the grating (a) and a carrier frequency the same as grating (b): Fourier analysis of this grating would reveal three components, all close in frequency to grating (b).

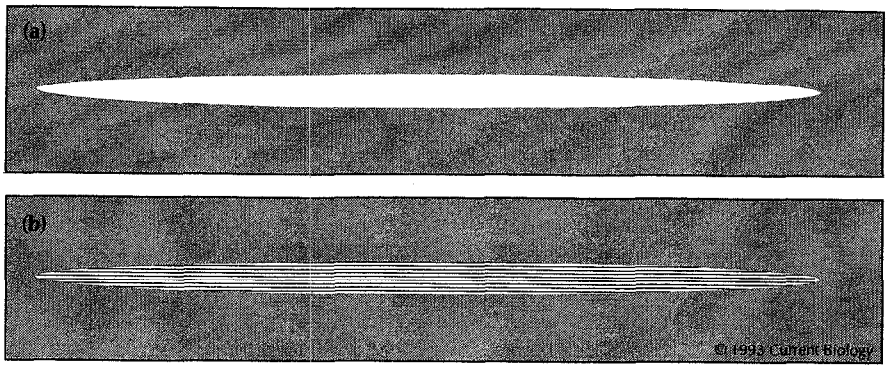

Fig. 2. **(a)** An example of an object differentiated from its background by a difference in luminance. **(b)** An example of an object differentiated from its background by contrast difference.

This concordance between the spatial period of the luminance variations that define an object and the size of the object does not hold for objects defined by local contrast. For example, a striped caterpillar can be discriminated from a background of the same brightness because of its stripes (Fig. 2). The stripes consist of variations in luminance, but these variations do not define the caterpillar directly. Mechanisms selective for luminance-defined objects the size of the caterpillar would not respond to either the caterpillar or its stripes, and spatial frequency selectivity does not allow one to predict selectivity for the size of contrast-defined objects.

What is required is a sort of 'second-order' analysis of selectivity for the spatial distribution of regions of high and low contrast. One way of achieving this is to represent the pattern with signals proportional to some non-linear function of the luminance at each image point (instead of signals proportional directly to the luminance). A non-linearity generates differences between signals from areas of low and high contrast, similar to the differences that a linear mechanism generates between areas of high and low luminance (Fig. 3) — the spatial distribution of the non-linear 'contrast' signal can then be analysed in the same way as luminance signals are. The simplest visual stimulus for studying responsivity to constrast-defined objects is a grating with a contrast that varies as a function of space, such as the contrast-modulated grating shown in Figure 1c. This consists of a sinusoidal grating of high spatial frequency (fine stripes, like those of the caterpillar), known as the carrier, the contrast of which is modulated by another sinusoid. The spatial and temporal parameters of the carrier and modulating waveform can be manipulated independently, allowing us to study the mechanisms responsible for analysing the caterpillar without affecting the mechanisms for analysing the caterpillar's stripes.

Psychophysical studies using patterns of this type have shown that the visual system takes longer to analyse the motion of contrast patterns than luminance patterns [4], which suggests that different mechanisms deal with the two types of pattern. However, a recent paper [5] describes recordings of the activities of single neurons in the cat visual cortex, and reports that most neurons in cortical area 18, and many in cortical area 17, respond to both luminance patterns (sinusoidal gratings) and contrast patterns (contrast-modulated gratings). These findings raise three questions. First, what is the relationship between the two kinds of selectivity in a given neuron? Second, what kind of mechanism endows these neurons with both kinds of selectivity? And third, are neurons like these likely to be the basis of our ability to extract information from such patterns?

The neurons described by Zhou and Baker [5] responded to the motion of both sinusoidal luminance patterns and constrast-modulated gratings in which the envelope moved and the carrier remained stationary (as if the caterpillar moved while its stripes stayed still). For each cell, the authors measured the effect of changing the spatial frequency of the carrier in the contrast-modulated grating (which determines the width of the caterpillar's stripes) and of changing the modulation frequency (which determines the fatness of the caterpillar). They found that only limited ranges of carrier and modulation frequencies were effective. Two surprising findings, which constrain both the possible mechanism of these responses and their likely significance in visual processing, emerged when the authors compared these ranges with the range of frequencies of simple sinusoidal gratings to which the cell responded.

First, without exception, the range of effective carrier frequencies was well above the range of frequencies of simple gratings to which the cell was responsive. It is as if the cell sees objects the size of the caterpillar that are visible to it because they have fine stripes that are invisible to it. This would be an ideal property for a cell designed to detect objects of a particular size and to generalize between contrast- and luminance-defined objects. However, it is unlikely that the cells generalize in this way, because of the second surprising finding — the range of modulation frequencies to which the cell responded was different again, being lower than the range of simple gratings. It is as if the cells confused fat striped caterpillars and thinner non-striped ones. Thus, in order to know the size of the object signalled by the cell one would need to know whether the object was contrast-defined or luminance-defined.

The responses to contrast variation observed by Zhou and Baker could be generated by a non-linear processing stage anywhere preceding the point at which at which they were recorded [6–8]. Any of a variety of

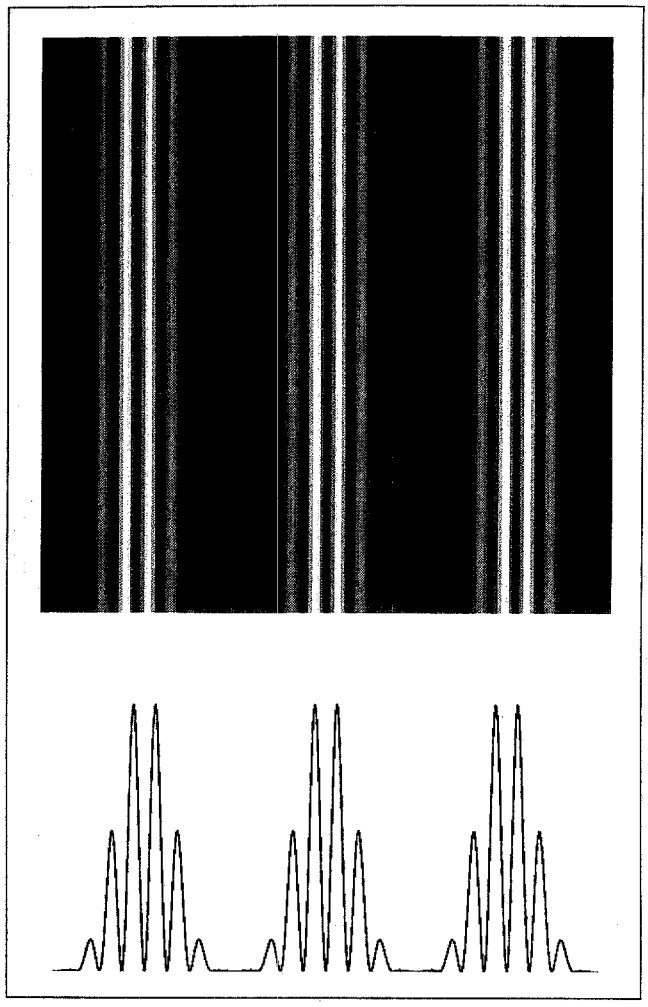

Fig. 3. An illustration of how non-linearities can be used to 'reveal' the modulation frequency of a contrast-modulated grating. Most non-linearities can be expressed as a polynomial or a power series — that is, their effect is to add to the pattern a series of extra terms proportional to the square and higher powers of the luminance at each point. Usually the magnitude of the added terms diminishes rapidly with increasing power. Brightness at each point in this pattern is proportional to the square of the brightness at that point in the contrast-modulated grating in Fig. 1c: it now has a strong luminance variation at the modulation frequency.

non-linearities would add a sinusoid at the modulation frequency to the internal represenation of the pattern (Fig. 3). The fact that the range of effective carrier frequencies is outside the range of spatial frequencies of simple gratings to which the cell is sensitive dictates that the non-linear stage precedes the cortical cell, as otherwise only frequencies to which the cell responded directly would be effective as carrier frequencies.

That the selectivity for modulation frequency also differs from the selectivity for sinusoidal grating frequency implies there is also a filter between the non-linear stage and the cortical cell, and that this has different characteristics from the filter that generates the frequency selectivity for sinusoidal gratings. Zhou and Baker [5] suggest that the non-linear and linear responses arise in independent pathways that converge in the cortex. An alternative source for the non-linear component occurs in the responses of cells in the lateral geniculate nucleus (LGN), which is the thalamic relay on the pathway from retina to cortex [9]. The LGN non-linearity is approximately equivalent to the addition to the response of each neuron of a component proportional to the square of the linear component of its response, and arises at a point where the visual signal is carried by complementary 'on-centre' and 'off-centre' cell types, which carry independent signals about local increases and decreases in illumination. Thus, the on-centre signal is the sum of a component representing luminance and a component representing the square of the luminance, whereas the corresponding components in the off-centre cell represent the negative of the luminance and its square. Of course, the two squared components will be equal, and the linear components will be equal but opposite.

Thus, a mechanism that summed the on-centre and off centre signals would have a response proportional only to the square of the luminance (the linear components would cancel) and, conversely, a mechanism that subtracted on-centre and off-centre responses would have a response with no non-linear components [10]. If the LGN non-linearity were the basis of the responses observed by Zhou and Baker, the different spatial filters associated with the linear and non-linear responses of cortical cells would reflect the spatial organization of the cortical connections that combine on-centre and off-centre responses in different ways. It follows that, if the non-linear responses observed by Zhou and Baker are a cortical reflection of the non-linearity in the LGN, the spatial frequency selectivity for carrier gratings should be the same in the cortex as it is in the LGN.

Finally, we should consider the likely significance of the non-linear responses observed by Zhou and Baker. First, it seems unlikely that they would provide a direct means of generalizing between luminance-defined and contrast-defined objects, because the size-selectivity of the linear and non-linear mechanisms is different. Further processing would be required in order to make such generalization possible. On the other hand, they do provide a potential mechanism for the interactions between luminance-defined and contrast-defined patterns that have been observed in psychophysical experiments [6,10]. Consequently, it would be most interesting to know whether the mechanism that generates these non-linear responses shows other properties characteristic of the psychophysical mechanisms that sense contrast patterns, such as poor temporal resolution [6] and lack of susceptibility to adaptation [12].

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