RESEARCH NOTE

SUBHARMONICS IN ADAPTATION TO SINE WAVE GRATINGS[1]

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In 1969, Blakemore and Campbell reported that the human visual system could be selectively adapted to stimuli of given spatial frequency and orientation. For several seconds following the prolonged viewing of a high contrast sinusoidal grating, subjects experienced a significant increase in their threshold for detecting gratings at or near the spatial frequency and orientation of the adapting stimulus. The threshold elevation decreased gradually as the test grating frequency moved away from that of the adapting grating, reaching half its maximum value about one half octave on either side of the adapting frequency.

In fact, however, the threshold elevation is not symmetrical about the adapting frequency but skewed toward the low frequencies (Stromeyer, Klein and Sternheim, 1977). Blakemore and Campbell (1969) do not mention this asymmetry although they implicitly include it in the mathematical function they chose to represent their data. Also implicit in their threshold elevation function is the assumption that the elevation decreases smoothly on both sides of the adapting frequency. A quick glance at the individual curves in Figs. 7, 9 and 11 of their article does not seem to justify this assumption. Nine of the eleven curves show secondary maxima and four of these lie well above the stated level of significance.

To investigate this further, Blakemore and Campbell's data for the frequencies 3.5–10.0 cycles/degree (their Fig. 8) are replotted in Fig. 1. Whereas their smooth function appeared not unreasonable for the superimposed data which they presented, the averaged data[2] plotted here shows suggestive evidence of
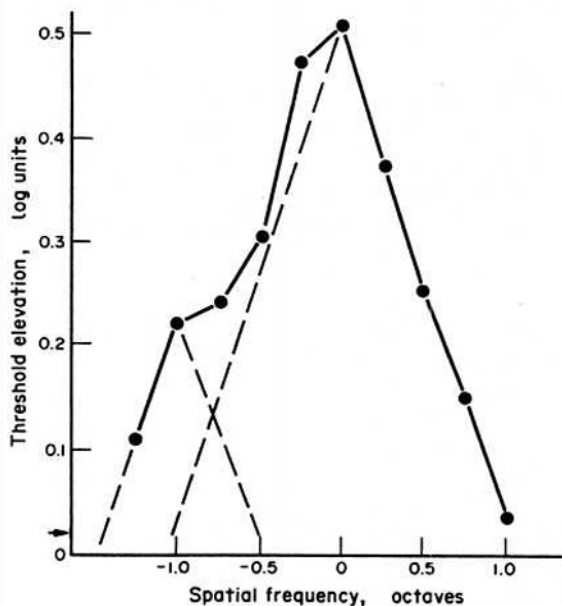

Fig. 1. Average threshold elevation[2] following adaptation to sine wave gratings of 3.5, 5, 7.1 and 10 cycles/degree. Spatial frequency is expressed in octaves relative to the frequency of the adapting grating. Data taken from Blakemore and Campbell, 1969, Fig. 8. Dashed lines indicate the possible presence of two symmetrical adaptation curves: one centred at the adapting frequency, the other at a frequency one octave lower. Arrow indicates statistically significant level which is one half that stated by Blakemore and Campbell in order to reflect the averaging of four values.

a secondary threshold elevation peak at a frequency one half that of the adapting grating.

Reanalysis of another portion of their data adds strength to this finding. In Blakemore and Campbell's Fig. 11 (1969) the threshold elevations resulting from four different contrasts of a 10 cycles/degree adapting grating are shown. The authors superimposed the four curves to make the point that the shape of the spatial frequency tuning curve does not depend on the adapting contrast. Their smooth function again provided a reasonable fit to the superimposed data. On the other hand, a more informative measure of the effect of adapting contrast on the shape of the threshold elevation curves is obtained by dividing the elevation obtained at one contrast by that obtained at another. In this manner, the *relative* effect of an increase in adapting contrast is shown at each test frequency and any variations in the rate of adaptation

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[2] Blakemore and Campbell (1969) plotted relative threshold elevation which they define as $(TC_A/TC_B)-1$, where TC is the threshold contrast after adaptation and TC_B is the threshold contrast before adaptation. These values were read off the curves for adapting frequencies of 3.5, 5, 7.1 and 10 cycles/degree in their Fig. 8 and converted to simple threshold elevation ratios: TC_A/TC_B. The geometric mean of the four ratios (e.g. the arithmetic mean of the logs of these ratios) was then computed for each test frequency/adaptation frequency ratio for which all four values were available. The values for adapting frequency 14.2 cycles/degree were not included as it alone did not have data for -1.00 and -1.25 octaves.

[3] That is, $(TC_{A2}/TC_B)/(TC_{A1}/TC_B)$ which is just TC_{A2}/TC_{A1} where TC_{A1} and TC_{A2} are threshold contrasts following two different adaptation conditions and TC_B is threshold contrast before adaptation. TC_B is assumed to be independent of the adaptation condition.
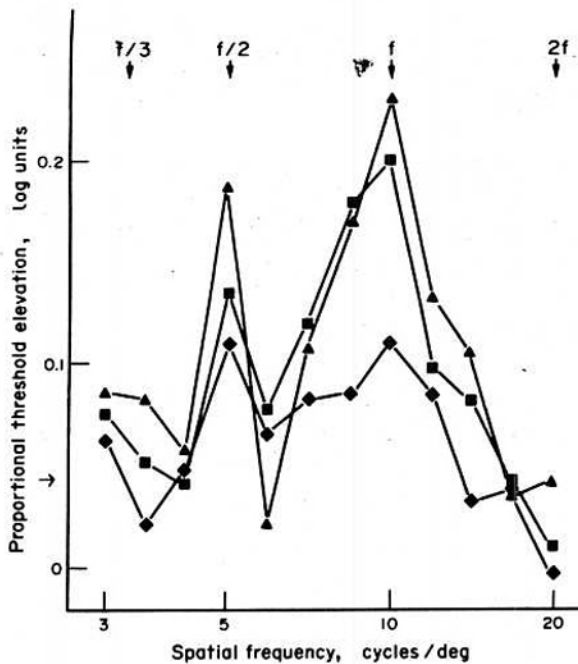
Fig. 2. Proportional threshold elevation at 2.0 (triangles). 1.5 (squares), and 1.0 (diamonds) log units of adapting contrast relative to threshold elevation for 0.5 log units of adapting contrast. Data taken from Blakemore and Campbell, 1969, Fig. 11, for adaptation at 10 cycles/degree. The horizontal arrow indicates the statistically significant level of elevation equivalent to their stated value. Vertical arrows indicate the adapting frequency and its harmonics and subharmonics.

with test frequency should be revealed. Fig. 2 depicts the ratios obtained by dividing the threshold elevations observed for adaptation as contrast of 2.0, 1.5, and 0.1 log units, by the threshold elevations observed following adaptation at 0.5 log units contrast.

The proportional threshold elevations in Fig. 2 are strongly bimodal. It appears that the rate of adaptation as a function of contrast is greatest at the adapting frequency (f) and less everywhere else except, again, at one half the adapting frequency ($f/2$).

Why should there be a second peak and why specifically at a subharmonics of the adapting frequency? Pollen, Andrews and Feldon (1978) have recently reported that many of the complex cells that they record in area 17 respond to moving sinusoidal gratings with a modulated discharge. When tuning curves are plotted based on the levels of this modulated activity, the cells show two distinct spatial frequency response bands: a broadly tuned band of about 1.0 octaves bandwidth at half amplitude and a narrowly tuned band of less than 0.5 octaves bandwidth. Pollen et al. (1978) find that the narrow band is centered at a frequency one octave above the center frequency of the broad band. The modulated output of these cells can therefore be characterized as responding to both a fundamental frequency and to second harmonic of that frequency.

The second harmonic response band is thus the most probable source of the threshold elevation seen at $f/2$ in Figs. 1 and 2. That is, if an adapting grating of frequency f equal to, for example, 10 cycles/degree (cpd) is presented, it will stimulate not only cells, both

simple and complex, that respond maximally to 10 cpd but also those complex cells tuned to 5 cpd that have a second harmonic response band (necessarily at 10 cpd). If these latter cells are fatigued by their modulated activity (the mean activity of these cells remains relatively constant across the bandwidth of the second harmonic response band), then a threshold elevation will be produced at 5 cpd as a result of adapting to 10 cpd.

By the same argument, some of the cells fatigued by adaptation to a 10 cpd stimulus should have a second harmonic band at 20 cpd and, as a result, a threshold elevation at 20 cpd might be expected. There is, however, no evidence for such a peak in Fig. 1 or 2. The asymmetry of the effect can be understood if it is assumed that a grating is detected when any part of the distribution of cells responding to it crosses a threshold value. Following adaptation to a 10 cpd grating, a 5 cpd test grating will be detected first by the cells that respond maximally to 5 cpd. Some of these cells have been adapted due to their second harmonic response to the 10 cpd grating and a threshold elevation is thus produced. A 20 cpd test grating will be detected first by the cells responding maximally to 20 cpd. Although some cells maximally tuned to 10 cpd and having a second harmonic band at 20 cpd will respond, they are not located at the part of the response distribution that will initiate the detection. Consequently, the adaptation of these cells will not produce a threshold elevation.

The subharmonic threshold elevation thus appears to be a psychophysical reflection of the "periodic" complex cells reported by Pollen and Ronner (1975) and Pollen et al. (1978). Whatever analysis these cells are performing, the presence of harmonic response bands rules out the possibility of a simple Fourier transform. On the other hand, these cells should be sensitive to the relative phase of their harmonic components. Evidence of the importance of such relative phase information has been shown recently in adaptation to rectangular gratings (De Valois, 1977) and in the McCollough effect (Stromeyer, Lange and Ganz, 1973).

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