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PERCEPTUAL BISTABILITY WITH COUNTERPHASE GRATINGS*

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Abstract—Suprathreshold counterphase modulated gratings induce a bistable percept of drift or flicker. It is argued that these perceptual alternations might provide a new means for the investigation of directional selective mechanisms. The prevalance of either of the two perceptions has been studied as a function of the spatio-temporal characteristics of the stimulus and compared with: (1) the spatio-temporal contrast sensitivity surface for counterphase modulated gratings; (2) the motion/counterphase sensitivity ratio. Drift perception elicited by suprathreshold counterphase gratings attains a maximum for 8 c/deg, 12 Hz stimuli and decreases for any other experimental condition. For spatial frequencies below 1 c/deg, or temporal frequencies below 2 Hz, only flicker perception is reported. These phenomenal experiences do not show any systematic dependence on the involuntary eye movements of the observer. Comparison with the threshold measurements does not support their explanation in terms of the transient-sustained dichotomy, nor does it allow for a straightforward equivalance between the spatio-temporal characteristics of direction-selective mechanisms at threshold and at suprathreshold levels. It is suggested that the balance between flicker and motion is the perceptual outcome of the competition between lower and higher order motion detectors.

INTRODUCTION

A suprathreshold counterphase grating is perceived either as a drifting stimulus whose direction alternates with time, or as a temporally modulated, directionless grating. Although the manipulation of the spatiotemporal characteristics of the stimulus does not seem to induce any obvious changes in the average perception time of the two directions of drift, it strongly affects the total time during which the subject perceives the nondirectional pattern ("flicker" as opposed to "movement" perception). We shall briefly develop below the reasons why the study of these phenomenal alternations can shed light upon how the human visual system processes "movement" information.

Levinson and Sekuler (1975a) have shown that the contrast threshold for a counterphase grating was twice as high as the contrast threshold for a drifting grating with the same spatio-temporal characteristics. Knowing that a counterphase modulated pattern may be analysed as the algebric sum of two half-contrast gratings moving in opposite directions, this result has been taken as strong evidence for the independent processing of the two drifting components.

More recent studies have nevertheless shown that this directional selectivity does not hold over the entire spatio-temporal domain (Stromeyer, Madsen, Klein and Zeevi, 1978; Kulikowski, 1978; Watson, Thompson, Murphy and Nachmias, 1980). More specifically, it breaks down in that frequency region where the sustained mechanisms are supposed to be optimally stimulated (Tolhurst, 1973; Kulikowski and Tolhurst, 1973). It is thus theoretically convenient to infer that the loss of directional selectivity results from the activation of these movement insensitive mechanisms.

Even within the limits of the "transient" region of the spatio-temporal domain the sensitivity ratio for drifting and counterphase modulated gratings may be significantly less than 2. As noted by Watson *et al.* (1980) this may be due both to "probability summation" (e.g. Graham, 1977) and to "direction uncertainty" (Sekuler and Ball, 1977) effects. The former is inherent to the simultaneous presentation of the two motion components and it increases the relative sensitivity to the compound (counterphase) stimulus. The latter is dependent upon the experimental procedure. Intermixing leftward, rightward and counterphase modulated stimuli within one experimental session (e.g. Stromeyer *et al.*, 1978; Watson *et al.*, 1980, who have used forced choice procedures) will decrease sensitivity to moving but not to counterphase modulated gratings, thereby decreasing their sensitivity ratio. These uncertainty effects will play a minor role in experiments where one single stimulus is presented during the whole experimental session (e.g. Levison and Sekuler, 1975a; Kulikowski, 1978; Kelly, 1979; Panish, Swift and Smith, 1983, who have

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used adjustment procedures). It is therefore not surprising that the reported sensitivity ratio may vary from author to author and for the same spatio-temporal parameters by as much as a factor of 4 dB. Since none of these studies covered the whole spatio-temporal domain, we repeated these experiments in order to allow for more extensive comparisons with the phenomenal reports (concerning movement and/or flicker perception) elicited by the suprathreshold, counterphase modulated gratings. This was intended to bring new evidence concerning the relationship between optimal movement perception at suprathreshold levels and the spatio-temporal sensitivity envelope of the visual system.

Directional sensitivity mechanisms show strong inhibitory interactions at suprathreshold levels (Levinson and Sekuler, 1975b; Gorea and Fiorentini, 1982). These interactions, combined with time dependent adaptation effects, may account for the alternating perception of the rightward and leftward drifting components of a suprathreshold counterphase grating. The dynamics of such an oscillatory system has been advanced a long time ago to account for the water-fall effect (Sutherland, 1961; Barlow and Hill, 1963) and it can be taken within this interpretative framework as evidence of activation of movement selective mechanisms. It can consequently be proposed that a counterphase grating which does not induce any (alternating) drift perception, but whose temporal (directionless) modulation is still visible, is processed by directional-insensitive ("flicker") mechanisms. Although several authors have already suggested a possible dichotomy between flicker and movement mechanisms (King-Smith and Kulikowski, 1975; Gorea, 1979, 1982; Watson *et al.*, 1980; Green, 1981), such a dichotomy may not be structural. A "flicker" mechanism might include all the motion mechanisms whose spatio-temporal characteristics are inappropriate with respect to the physical parameters of the stimulus, their directional selectivity being thereby "impaired" (see the Discussion section). In some experimental conditions to be reported in the Results section, a counterphase grating never elicited a movement perception. It is difficult to account for such an observation by assuming that the two opposed movement mechanisms are stimulated but are in an indefinitely long lasting state of equilibrium. On the basis of these considerations, the overall time of movement and flicker perception when looking at a counterphase grating may be used as an experimental tool to study how directional sensitivity may be affected by the spatio-temporal characteristics of highly suprathreshold stimuli. Some other considerations justifying what may appear as an arbitrary separation between these two phenomenal perceptions will be discussed on the basis of the results presented below. It should be finally noted that the "bistability" label used throughout this paper is specifically referred to the alternation of flicker and motion percepts as opposed to any other type of perceptual alternation, e.g. among different possible direction vectors.

METHODS

Vertical sinusoidal gratings were displayed on the face of a Tektronix 608 (phosphor P4) oscilloscope. The observer looked at a circular, 40 cd/m^2, 7° dia inspection field with a tiny central fixation point and a large surround closely matched in luminance and hue. The whole display was viewed binocularly from a distance of 100 cm. The modulation in space and time, $M(x, t)$, of the two types of stimuli is described by:

$$M(x, t) = m \cos[2\pi (f_S x \pm f_T t)] \quad (1)$$

and by:

$$M(x, t) = 2m [\cos(2\pi f_S x) \times \cos(2\pi f_T t)] \quad (2)$$

where m is the contrast and f_S and f_T are the spatial and temporal frequencies in c/deg and Hz, respectively. Equation 1 describes a leftward or rightward (depending on the $+/-$ sign) drifting grating with a velocity (in deg/sec) given by f_T/f_S. Equation 2 describes the counterphase modulated stimulus which is simply the trigonometrical sum of a leftward and a rightward drifting grating as described in equation 1. Only the counterphase modulated stimulus was used in the suprathreshold experiments. Spatial frequencies ranging from 1 to 16 c/deg and temporal frequencies ranging from 3.1 to 25 Hz were used. All the spatio-temporal combinations have been studied with one observer (A.G.). The 16 c/deg and 25 Hz conditions were omitted for observer J.L. A cosine, two-dimensional spatial window set the amplitude envelope of the signal. The cosine envelope function allowed for a 2.5° plateau of maximum contrast with a 1° peripheral region of decreasing contrast. The maximum contrast of the stimuli was set at 38 dB above their detection threshold. The different experimental conditions were run in a random order with four repetitions each.

A 2-alternative forced choice experiment (2AFC) was run with one of the authors (A.G.) and another observer in order to assess the threshold sensitivity for all stimuli used in the suprathreshold experiments as well as for drifting gratings with the same spatio-temporal characteristics. In addition to the suprathreshold experimental setup the threshold stimuli were temporally modulated by a cosine envelope in order to prevent transient effects. The envelope function had a 1 sec plateau of maximum contrast with increasing and decreasing transitions of 0.5 sec each. Percentages of correct detection were computed from 50 trials/data point at four contrast levels. The contrast threshold was interpolated at 75% correct detection on the psychometric function estimated by means of a maximum likelihood fitting procedure described by Watson (1979).

In the suprathreshold experiments one experimental session consisted in the presentation of a grating of a given spatial and temporal frequency during a 150 sec inspection period. The observer, who was provided with three response-buttons, always began an experimental session by pushing the "flicker"-button and changed his response as soon as his flicker perception was replaced by the perception of drift ("rightward" or "leftward"-button). His responses were fed into a Mostek microprocessor which computed individual times for and corresponding frequencies of each type of perception, as well as their averages and standard deviations throughout the inspection period.

In order to be sure that the phenomenal experience of the observer was not dependent on his oculomotor behaviour, horizontal eye movements were recorded during at least one of the four replications of each experimental condition. The recording was made through a corneal reflection technique using a photoelectric device connected to a long time-constant, multiple channel Hewlett–Packard 7702B recorder. The experimental setup permitted a resolution of the position of the eye of at least 7′ of arc. Observer's manual responses were simultaneously recorded through a second channel of the Hewlett–Packard polygraph. The recording device did not allow for their labeling in terms of the three possible phenomenal events.

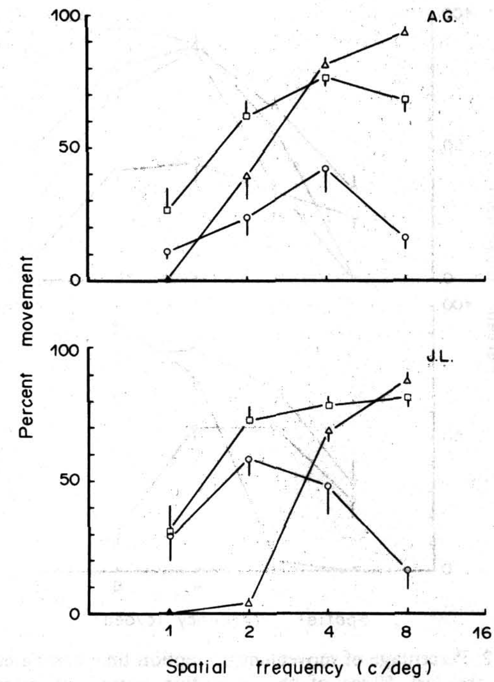

Fig. 1. Percentage of movement perception time computed over the 150 sec inspection period as a function of the spatial frequency of the suprathreshold counterphase grating. Each datum point is the average of four repetitions. Vertical bars represent 1 SE Circles: 3.1 Hz; squares: 6.2 Hz; triangles: 12.5 Hz. The inspection stimulus was set at 38 dB above its contrast threshold. Observer A.G. and J.L., upper and lower panel, respectively.

RESULTS

Suprathreshold experiments

Neither observer showed any practice effects during the main experiment, although observer J.L. showed a slight increase in the time of motion perception during preliminary trials. Figure 1 displays the total time of motion perception expressed as a percentage of the 150 sec inspection period. Leftward and rightward movement perception times did not show any systematic differences and were thus summed together. Movement perception time is displayed as a function of spatial frequency and for three temporal frequencies of the inspection stimulus (3.1 Hz, circles; 6.2 Hz, squares; 12.5 Hz, triangles). Every datum point is based on four repetitions in different, randomly distributed experimental sessions. The two observers (upper and lower pannels) show very similar results: total time of movement perception increases with spatial frequency up to about 2–4 c/deg for low and medium temporal frequencies; it is nevertheless still increasing at 8 c/deg for a 12.5 Hz modulation attaining in this condition 93 and 88% for observer A.G. and J.L., respectively. At the lowest spatial and the highest temporal frequencies both observers reported only flicker perception throughout the 150 sec of inspection. (Within this spatio-temporal range motion perception could not be elicited even by voluntarily trying to pursue one of the two moving components of the compound stimulus.) The first major point to be noted on the basis of these results is that a suprathreshold counterphase grating can elicit, depending on its spatial and temporal characteristics, all the intermediate movement perception times ranging from 0% to almost 100%.

The data of Fig. 1 are very similar to those obtained when the percentages of total movement perception are computed over the last 50 sec of the inspection period only (Fig. 2). The 25 Hz condition (inverted triangles) is included in this computation for observer A.G. (upper panel). It is now quite clear, at least for this observer, that all the curves show a spatial frequency optimum, whatever the temporal frequency of the stimulus. The very strong similarity between the data computed over the whole inspection period and those obtained for the last 50 sec deserves more detailed comment.

Figure 3 displays the average perception times of one movement and one flicker experience as a function of the inspection time. The overall numbers of both movement (N_m) and flicker (N_f) perceptions reported during the 150 sec period were divided into five segments of equal numbers ($N_m/5$ and $N_f/5$). Thus, segments are not precisely aligned in time, but represent equal sample numbers of response durations. The average time for each response (movement and flicker) during a segment is then plotted in Fig. 3 at the time corresponding to the midpoint of each segment. The average time of one movement

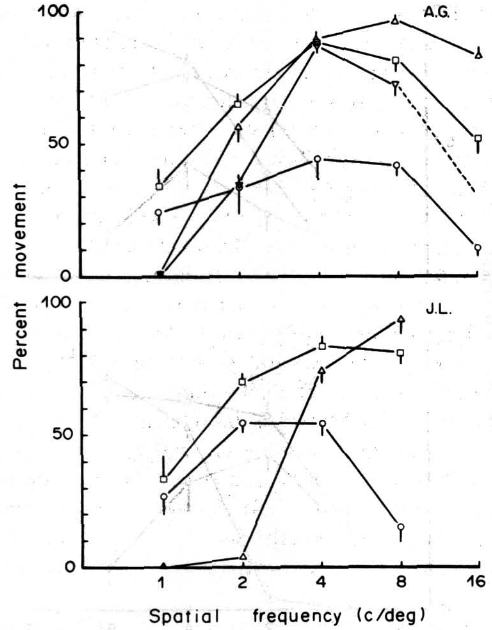

Fig. 2. Percentage of movement perception time computed over the last 50 sec of the inspection period. Inverted triangles refer to a 25 Hz modulation. Otherwise the same as in Fig. 1.

report did not show any strong systematic variation with either inspection time, or frequency parameters of the stimulus. The horizontal dashed line in each panel of Fig. 3 represents the mean of the average time of one movement report pooled across all spatial frequencies and over the five partitions of the inspection period. For observer A.G. (left panel in Fig. 3) the average time of one flicker report was strongly dependent on the inspection time decreasing in some cases by as much as a factor of 4 (2 c/deg, 12.5 Hz). This finding can be taken as further evidence that movement and flicker reports are based on two distinct types of perception presenting different time-courses. Durations of individual flicker and movement reports do not change any more beyond 50–60 sec of inspection. This explains why the data of Fig. 1 (averaged over the whole inspection period) and the data of Fig. 2 (averaged over the last 50 sec) are quite similar. For observer J.L. (right panel in Fig. 3) the average durations of individual movement and flicker reports are time independent. Consequently, the data displayed in Figs 1 and 2 for this observer should be (as they are) practically identical. It is not clear why the time dependent effects displayed in Fig. 3 show such strong inter-subject differences.

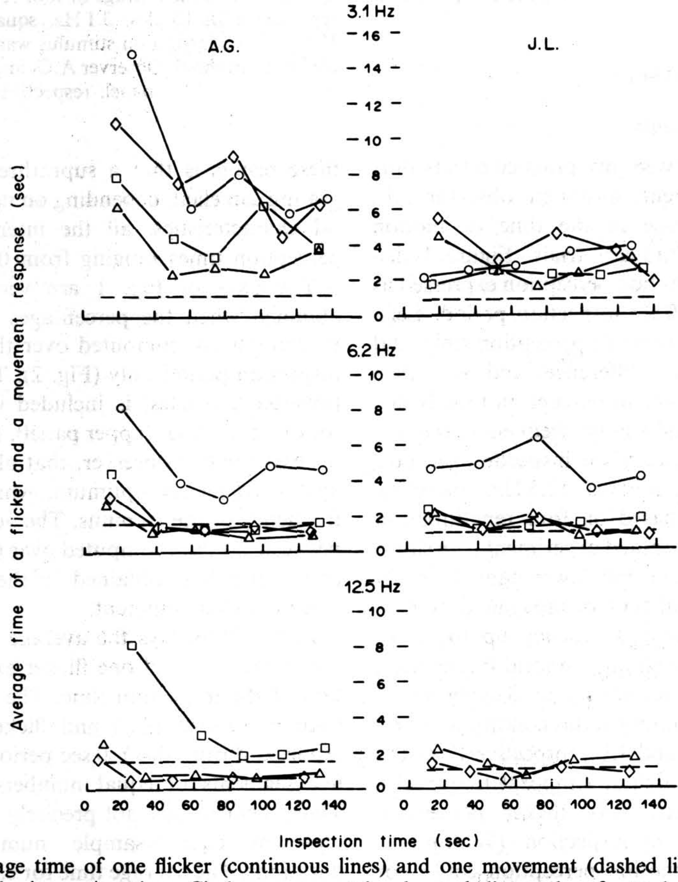

Fig. 3. Average time of one flicker (continuous lines) and one movement (dashed lines) percept as a function of the inspection time. Circles, squares, triangles and diamonds refer to 1, 2, 4 and 8 c/deg gratings, respectively. Temporal frequency is given as parameter. Observer A.G. and J.L., left and right side of the Figure, respectively. Average times of the movement percepts have been pooled across all spatial frequencies and over the whole inspection period. See text for further details.

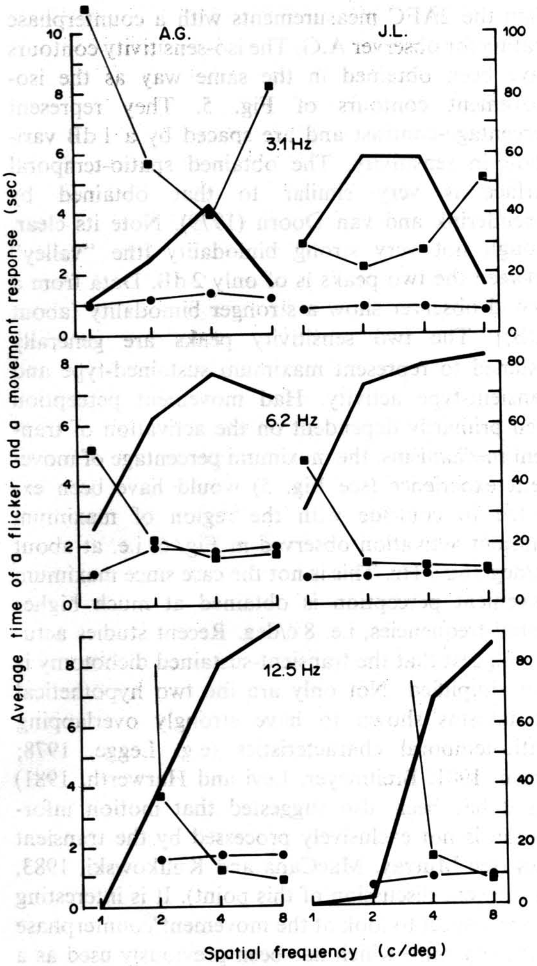

Fig. 4. Average time of individual movement (circles) and flicker (squares) percepts computed over the last 50 sec of the inspection period as function of the spatial frequency of the stimulus. The temporal frequency is given as a parameter. Average times of the flicker percepts at 12.5 Hz were too high to be plotted. The heavy lines show movement perception percentages (right hand ordinate) replotted from Fig. 2.

The average durations of movement (circles) and flicker (squares) reports have been computed over the last 50 sec of the inspection period and are shown in Fig. 4 (left-side ordinate) as a function of the spatial frequency with the temporal frequency as a parameter. Additionally, percentages of total movement perception (right-side ordinate), already displayed in Fig. 2, have been replotted in heavy lines. It can be seen that the average duration of each movement report is almost independent of the experimental condition. On the contrary, the average duration of the flicker reports strongly depends on the spatial and temporal parameters of the stimulus. It can thus be concluded that the overall time of movement perception is mainly dependent on the frequency, rather than on the duration, of the individual movement reports. The reverse is true for the total time of flicker perception which is mostly dependent on the average duration of individual flicker reports, rather than on their frequency. As a consequence, the total amount of motion perception is positively correlated with the number of response shifts from one perceived direction to the opposite direction and negatively correlated with the number of response shifts between motion and flicker. These additional considerations provide new evidence that our distinction between flicker and movement experiences is justified.

In order to provide a clearer description of the movement perception time variations as a function of the spatio-temporal characteristics of the suprathreshold counterphase grating, the data of Fig. 2 have been reanalysed and plotted in Fig. 5 as iso-movement (in percentage) contours. The contour lines are obtained by linear interpolation between the datum points of observer A.G., without any smoothing operation. The interval between adjacent contour lines corresponds to a 1 dB change in the percentage of movement perception. Such a plot will facilitate the comparison with sensitivity data to be presented below.

The peak of the iso-movement contour lines (96.7%) is obtained for a 8 c/deg, 12.5 Hz grating. The total amount of movement perception decreases with almost equal slopes for any other spatio-temporal condition. Movement perception does not depend on the velocity of the stimulus (in Fig. 5, any straight line with a slope of 1 designates a constant velocity). Had this been the case, the iso-movement contours should have been elongated (and not circular as they are) along one velocity line. Almost 100%

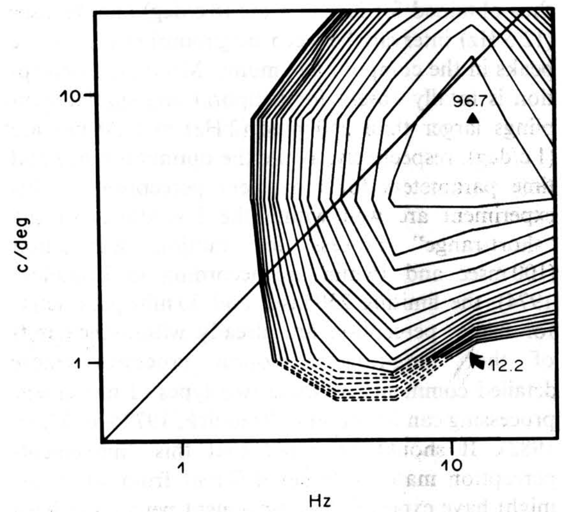

Fig. 5. Iso-movement contour lines in the spatio-temporal frequency plane. The contour lines are computed from the data of Fig. 2 (observer A.G.). The digits refer to the maximum observed (96.7%) and to the minimum measured (12.2%) movement perception. The dashed lines refer to extrapolations within the spatio-temporal region where data were not available. Adjacent contour lines are separated by a 1 dB difference between percentages of movement perception. The 45° oblique line designates the spatio-temporal locus of a constant 1 deg/sec velocity. The spatio-temporal loci for any other constant velocity lie on parallel lines.

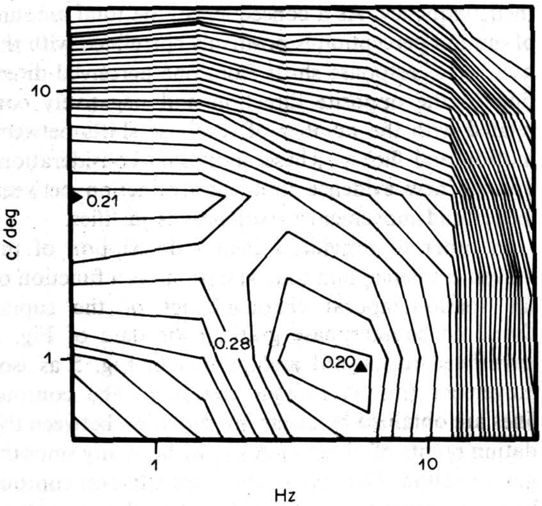

Fig. 6. Iso-sensitivity contour lines in the spatio-temporal frequency plane obtained with a counterphase modulated grating (observer A.G.). Digits in the Figure refer to percentage contrast. Adjacent contour lines are separated by a 1 dB difference in contrast sensitivity.

flicker perception (0% movement) is attained for temporal frequencies below 2 Hz independently of the spatial frequency of the stimulus. One hundred per cent flicker perception is also observed for spatial frequencies below 1 c/deg, whatever the temporal frequency of the stimulus.

It may be interesting to express these frequency limiting intervals into their equivalents in the space and time domains: optimum movement perception is thus obtained for 3.75 min arc (8 c/deg) and 40 msec (12.5 Hz) intervals between neighbouring luminance peaks in the compound stimulus. Movement perception is totally absent for temporal and spatial samplings larger than 250 msec (2 Hz) and 30 min arc (1 c/deg), respectively. While the optimum space and time parameters for movement perception in this experiment are well within the boundaries of the "short-range" process for motion segregation (100 msec and 15 min arc according to Braddick, 1974), the limiting 250 msec and 30 min parameters for flicker perception are already within the limits of the "long-range" motion processes (more detailed comments on these two types of movement processing can be found in Braddick, 1979 and Marr, 1982). It should be noted that this "movement-perception map" is rather different from what one might have expected had movement perception been entirely dependent upon the activation of the transient mechanisms. The experiments reported below were intended to provide sensitivity data for both counterphase and drifting gratings in order to permit extensive comparisons between the suprathreshold and threshold behaviour of the visual system.

Threshold experiments

Figure 6 displays iso-sensitivity contours derived from the 2AFC measurements with a counterphase grating for observer A.G. The iso-sensitivity contours have been obtained in the same way as the iso-movement contours of Fig. 5. They represent percentage-contrast and are spaced by a 1 dB variation in sensitivity. The obtained spatio-temporal surface is very similar to that obtained by Koenderink and van Doorn (1979). Note its clear, though not very strong bimodality [the "valley" between the two peaks is of only 2 dB. Data from a second observer show a stronger bimodality (about 4 dB)]. The two sensitivity peaks are generally assumed to represent maximum sustained-type and transient-type activity. Had movement perception been primarily dependent on the activation of transient mechanisms, the maximum percentage of movement experience (see Fig. 5) would have been expected to coincide with the region of maximum transient activation observed in Fig. 6, i.e. at about 1 c/deg and 7 Hz. This is not the case since maximum movement perception is obtained at much higher spatial frequencies, i.e. 8 c/deg. Recent studies actually suggest that the transient-sustained dichotomy is over simplified. Not only are the two hypothetical mechanisms shown to have strongly overlapping spatio-temporal characteristics (e.g. Legge, 1978; Green, 1981; Breitmeyer, Levi and Harwerth, 1981) but it has been also suggested that motion information is not exclusively processed by the transient ones (see Murray, MacCana and Kulikowski, 1983, for a recent discussion of this point). It is interesting in this respect to look at the movement/counterphase sensitivity ratio which has been previously used as a measure of the directional selectivity of movement mechanisms at threshold (Levinson and Sekuler, 1975a; Kulikowski, 1978; Stromeyer *et al.*, 1978; Kelly, 1979; Watson, 1980). As already discussed in the Introduction, a ratio of 2 (6 dB difference) is taken as direct evidence of the independent activation of such direction selective mechanisms.

Figure 7 displays the absolute sensitivity ratio (in dB) between counterphase and drifting gratings. For the sake of the comparison with the rest of the data the dB differences are plotted as iso-difference contours. Given the ± 1.5 dB standard deviation of each particular measure, the standard deviation of their difference was about ± 2.1 dB. Compared to this, the sensitivity differences are often rather small. As a consequence, the movement and counterphase sensitivity curves have been smoothed by visual interpolation and only afterwards subtracted. The isodifference contours were then obtained by linear interpolation of the "smoothed" data. Adjacent iso-difference contour lines are separated by 0.5 dB. The dotted area in Fig. 7 is intended to show, given the rather large standard deviation of the sensitivity differences and the smoothing of the actual sensitivity curves, the approximate spatio-temporal region where movements of opposite directions are supposed to be processed independently (6 dB sensitivity

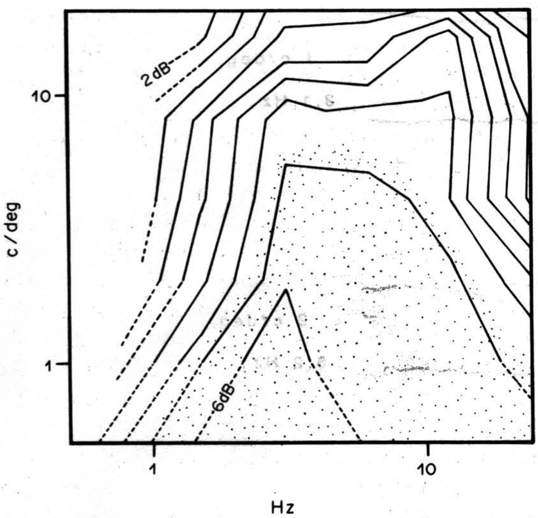

Fig. 7. Iso-sensitivity difference contour lines in the spatio-temporal frequency plane obtained by subtracting movement thresholds from counterphase thresholds. Each contour line refers to a constant sensitivity difference (in dB). Adjacent contour lines are separated by 0.5 dB sensitivity differences. Dashed lines refer to extrapolations within the frequency region where raw data were not available. Given some considerations on the standard deviation of the sensitivity differences and on the interpolation procedure (see text), the dotted area refers to the approximate spatio-temporal range of maximum sensitivity difference.

difference). This region only partly overlaps with the "transient" area of Fig. 6 and it certainly does not coincide with the maximum movement perception area of Fig. 5.

Eye movements

Saccades and eye pursuits have been analysed for the last 50 sec of inspection and for observer A.G. only. The analysis included all the experimental conditions except those at 16 c/deg and 25 Hz. Saccades and eye pursuits of less than about 7 min arc and 10 min arc/sec, respectively, have been excluded. We develop below four sets of arguments suggesting that eye movements did not determine the phenomenal experience of motion perception.

(i) The first consideration refers to the direction of both saccades and eye pursuits, on one hand, and the direction of reported motion experience, on the other. Admitting that the initiation of either a saccade or an eye-drift will elicit a given motion experience, it can be expected that the reported direction of the latter would strongly depend on the direction of the former. This was not the case. Leftward and rightward motion reports were equally probable (50%) whereas more than 90% of the eye pursuits and less than 20% of the saccades were directed to the right. Consequently, the direction of the motion experience cannot be accounted for in terms of the direction of either pursuit or saccadic behaviour.

(ii) Although the analysis of eye pursuits cannot specify in any way whether they are the cause or the effect of a motion experience*, one would expect to find, in the first case, a positive correlation between their frequency and the frequency of motion experiences. This correlation (as all the correlations to be discussed below) was computed across the 12 experimental conditions (4 spatial and 3 temporal frequencies). It is negative and not significant ($r = -0.182$, $P > 0.1$, Pearson correlation). One other consideration related to the eye pursuits concerns the relation between their accuracy and the percentage of motion perception. It can be indeed hypothesized that, if motion perception is dependent on the pursuit behaviour of the eye, higher accuracies will be observed in those experimental conditions that elicit strong movement perception. The accuracy was defined as the ratio between the recorded velocity of the eye pursuits and the actual velocity of the drifting components of the compound stimulus (a ratio of 1 indicating perfect accuracy). The computed Pearson correlation between accuracy and percentage of motion perception was not significant ($r = 0.041$). On the other hand, the correlation between the recorded velocity of the eye and the actual velocity of the stimulus was highly significant ($r = 0.88$, $P < 0.005$). Nevertheless, our data indicate that percentage of motion perception is independent of stimulus velocity. It can be thus concluded that eye pursuits are strongly dependent on the physical velocity of the stimuli, but independent of the motion experience of the subject.

(iii) Considering now that the initiation of a saccade (irrespective of its direction) may elicit a motion percept, we looked for an eventual correlation between their frequency and the frequency of motion reports. The Pearson correlation computed across the 12 experimental conditions was negative and not significant ($r = -0.2$, $P > 0.1$). Consequently, the saccadic behaviour cannot account for the phenomenal experience of the observer.

(iv) Perhaps the most powerful test excluding an explanation of our results in terms of the eye-movement behaviour consisted in looking at the counterphase modulated gratings through an image-stabilisation device. These observations have been made possible due to the kind assistance of Dr C. Burbeck at SRI International, in California. Both C. Burbeck and the first author did report alternative motion percepts within the spatio-temporal range where they were visible without stabilization. Inter-

*One possible way to answer this question would have been to analyse the correspondance between the initiation of each eye pursuit and the contingent phenomenal direction shift. This was however impossible because the manual reaction time of the observer was typically very variable and there was no way to make sure that a given response was contingent to the first recorded drift or to the preceding one. Moreover, the recorded manual responses were not labeled in terms of rightward motion, leftward motion and flicker experience.

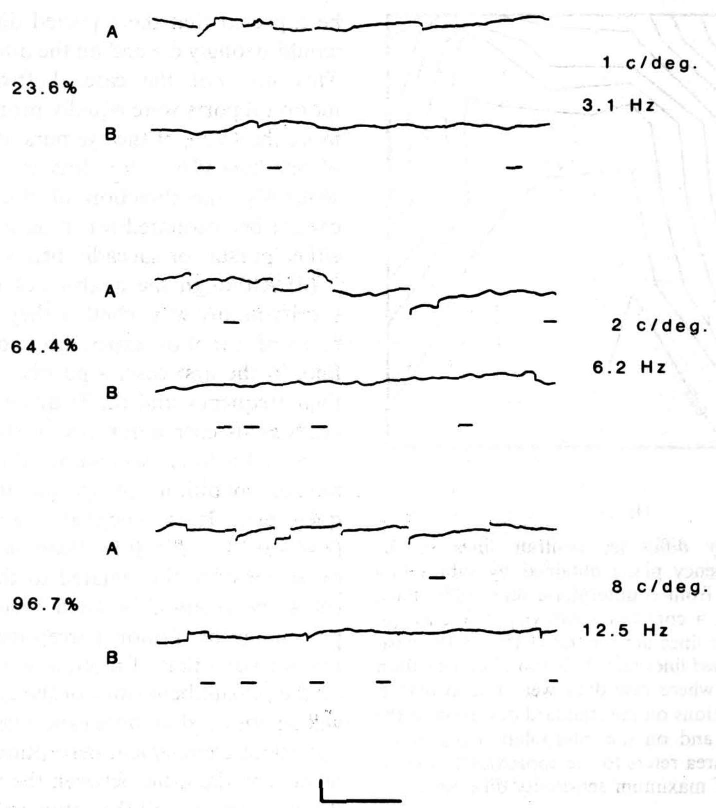

Fig. 8. Eye movements recordings for three experimental conditions as indicated on the right of the Figure. The experimental conditions were chosen to illustrate low, medium and high percentages of motion perception, as indicated on the left of the Figure. Each recording is a 5 sec sample. For each experimental condition two samples have been chosen in order to illustrate "strong" oculomotor activity with no or very few phenomenal shifts (upper traces) and "weak" oculomotor activity associated with a relatively high frequency of phenomenal shifts (lower traces). Phenomenal shifts are indicated by dashes at the bottom of each eye movement recording. The horizontal and vertical bars at the bottom of the Figure indicate time (1 sec) and space (1 deg) calibrations, respectively (observer A.G.).

estingly, motion was perceived only with small (2–3 deg) inspection fields and was ambiguous or absent with larger (10 deg) ones. Moreover, this was partially true even without stabilization, although motion could be eventually triggered in this case by voluntary eye movements. Nevertheless, large fields have not been used in our main experiment and therefore no quantitative description of the bistability phenomenon under these conditions is available. One possible explanation of this field-size effect could be the spatial inhomogeneity of the instantaneous balance between motion and flicker percepts: while flicker can be experienced at a given retinal locus, motion might be perceived at another locus. Obviously, overall motion perception is difficult, or at least ambiguous in these conditions. This interpretation, although purely speculative, is consistent with the idea of local motion mechanisms (e.g. Marr and Ullman, 1981; McKee, 1981) with internal noise (partly) correlated such that the correlation decreases with their spatial separation. According to this interpretation, our experiments with a 2.5 deg field thus had the advantage of isolating a retinal area with a homogenous response to motion.

Figure 8 displays 5-sec eye recording samples for three experimental conditions eliciting low, medium and high percentages of motion experience (observer A.G.). Manual responses (indicating a phenomenal shift) are shown at the bottom of each panel. For each condition two samples have been chosen such as to illustrate "strong" oculomotor activity with no, or very few phenomenal shifts (upper traces) and "weak" oculomotor activity corresponding to a relative high frequency of phenomenal shifts (bottom traces). The choice of these samples is not representative of the overall correspondence between oculomotor behaviour and phenomenal shifts, but simply intended to illustrate significant departures from the hypothesis according to which the oculomotor behaviour could have been an important factor in eliciting the motion experience of the observer.

Given the eye movements analysis discussed in this section, it can be concluded that the perceptual bistability phenomenon is strongly (if not entirely) dependent on the genuine visual processing of an ambiguous stimulus such as a counterphase modulated grating.

DISCUSSION

A counterphase suprathreshold grating can be seen either to drift or to flicker. This perceptual experience does not seem to be strongly dependent on the eye movement behaviour of the observer, but it appears to depend on the size of the inspection field. This latter effect might reflect spatial inhomogeneities in the instantaneous balance between flicker and motion perceptions.

The alternation in time between the two perceptual experiences depends on the spatio-temporal characteristics of the stimulus. For spatial frequencies below about 1 c/deg the counterphase grating elicits only flicker perception, independently of the temporal frequency. The same is true for temporal frequencies below about 2 Hz, whatever the spatial frequency. Beyond these limits motion perception increases and attains a maximum (about 97%) for 8 c/deg, 12 Hz gratings. The data do not show any evidence that motion perception is velocity dependent.

It was argued in the Introduction that the two perceptual experiences cannot be entirely accounted for in terms of the interactions between two sets of directional selective mechanisms. The data displayed in Figs 3 and 4 supported this assertion. It was indeed shown that flicker and movement perceptions follow (at least for observer A.G.) different time courses (Fig. 3). More particularly, flicker perception for this observer showed strong adapting effects, while motion perception did not. Moreover, the data shown in Fig. 4 indicated that, for both observers, the average perception time of the individual flicker experiences was strongly dependent on the spatio-temporal characteristics of the stimulus, whereas the average perception time of the individual motion experiences was not.

The difference between the spatio-temporal maps for motion sensitivity (Figs 6 and 7) and for motion experience (Fig. 5) should be interpreted with caution. Although it has been shown that, within a particular theoretical framework, a unique quantitative model can account for the behaviour of the visual system at both threshold and suprathreshold levels (e.g. Wilson, 1980), this is obviously not of general validity. The "uniqueness" of the stimulated mechanisms is even more problematic when the threshold and suprathreshold measures are as different as they were in the present experiments. Thus, we do not know whether the threshold and suprathreshold experiments addressed the same motion (and flicker) mechanisms. Nevertheless, sensitivity data have been frequently used to interpret suprathreshold phenomena (see for example Marr, 1982) and such a comparative discussion is, we think, worthwhile in the present case.

When compared with the sensitivity data (Figs 6 and 7) our suprathreshold experiments (Fig. 5) show a shift of the spatio-temporal range for optimum motion experience toward spatial frequencies beyond the range of optimum "transient" activation. At suprathreshold levels everything happens as if motion perception was mediated by both transient and sustained mechanisms. This interpretation is consistent with recent evoked potential recordings showing that suprathreshold gratings "effectively stimulate both types of channels" (Vassilev, Manahilov and Mitov, 1983). That motion sensitivity necessitates the combined activity of the two mechanisms is not a new idea. Marr and Ullman (1979), for example, proposed a general model where directional sensitivity is obtained by the coupling of at least two X (sustained) and one Y (transient) units. More recently, Murray *et al.* (1983) also suggested that sustained mechanisms can signal motion. These authors argued for the existence, at the detection threshold, of two distinct motion mechanisms, i.e. a "fast" and a "slow" one. It is not clear why the "slow" motion mechanism, preferentially activated by high spatial and low temporal frequencies was not revealed by the "factor of 2" experiment (Fig. 7). One possibility might be that, given the limitation to 16 c/deg of the spatial frequencies used in the present study, the spatial frequency range where these mechanisms are effectively stimulated (above 18 c/deg) was simply neglected. This would imply that the "factor of 2" sensitivity surface of Fig. 7 should have been bimodal (rather than unimodal as it appears), had we have measured it over a larger spatial frequency range. Whatever the underlying mechanisms accounting for the suprathreshold motion experience, it remains true that, within the spatio-temporal range used in this study, the interpretation of the sensitivity data presented in Figs 6 and 7 in terms of a transient-sustained dichotomy does not account for our suprathreshold recordings. Moreover, the lack of any motion experience in the spatio-temporal range where the "transient" mechanisms are supposed to be fully activated at the detection threshold (spatial frequencies below 1 c/deg and medium temporal frequencies) strongly argues against such an interpretation. Note that the spatio-temporal map for motion experience (Fig. 5) cannot be entirely accounted for in terms of the short-range process proposed by Braddick (1974) either. Indeed, although the optimum motion perception is within Braddick's spatio-temporal limits (i.e. 15 min arc and 100 msec), motion experience decreases for spatial and temporal frequencies above 8 c/deg and 12.5 Hz, respectively. This is not consistent with the short-range process whose upper spatio-temporal limits are exclusively determined by the resolution power of the visual system. More recently, Petersik, Pufahl and Krasnoff (1983) showed that the spatio-temporal limits of the short-range process are relative rather than absolute. The main finding of these authors was that the spatio-temporal range confining the "end-to-end" motion percept, initially described by Pantle and Picciano (1976) and Petersik and Pantle (1979) and identified by these authors with the short-range process, are dependent on the size of the stimuli (i.e. two temporal frames each of which contains three equidistant vertical bars whose arrangement is such that two bars in each frame are spatially overlapping). Moreover, in order to keep the strength of the end-to-end motion percept constant, an increase of the temporal interval between the two frames must be compensated by an increase in stimulus displacement. No such spatio-temporal trade-off can be observed in the data displayed in Fig. 5. Motion perception elicited by suprathreshold counterphase gratings cannot thus be entirely specified as a form of apparent motion.

Throughout this study the perception of motion was defined by opposition to the perception of flicker. This distinction was purely perceptual. By no means do our data imply an underlying functional dichotomy accounting for these phenomenal differences. It is nevertheless important to note that while flicker perception is not necessarily related to the stimulation of distinct "flicker" mechanisms, the failure to perceive motion in a moving stimulus must be related to an impairment in the activity of the directional selective mechanisms. Whether such an impairment is due to a loss in their overall sensitivity relative to the activation of a different mechanism, or to a specific drop in their directional selectivity, remains to be assessed. We argue below in favour of this last hypothesis.

It has already been proposed that flicker and motion are serially processed (Green, 1981) and thus strongly interacting at the detection threshold (Gorea, 1981; Green, 1981). This line of thinking is consistent with the idea that flicker sensation might be the phenomenal outcome of an "impairment" in the activation of directional selective mechanisms (Gorea, 1979). Suppose a population of movement responsive units presenting a wide range of spatio-temporal tuning characteristics. When presented with a drifting grating some of them will not be optimally activated because of their particular tuning properties. Units with receptive fields significantly smaller than the size required to integrate the spatial structure of the stimulus will not be able to extract any of its directional information and still respond to its temporal modulation. Such units, though directionally selective, will convey a "flicker" response. Depending on the spatio-temporal characteristics of the stimulus and on the distribution of the spatio-temporal tuning properties of the directional-selectivity units, the balance between optimally and nonoptimally stimulated detectors may vary in such a way that either flicker or movement responses will be elicited. Although we do not know of any systematic investigation of this phenomenal instability elicited by drifting stimuli, the literature frequently mentions conditions under which moving gratings are seen to flicker rather than to drift (e.g. Burr and Ross, 1982).

Obviously, flicker sensation is strongly increased by the addition of a second stimulus drifting in the opposite direction. Although the inhibitory interactions between the two stimuli (e.g. Levinson and Sekuler, 1975b) may partially explain this phenomenon, we have already argued that they cannot account for the dependence of the flicker-motion balance on the spatio-temporal characterics of the stimuli. Another possibility might be that most of the flicker perception obtained with a counterphase modulated stimulus is due to the improper stimulation of a "higher order" detector whose function is to signal coherent or incoherent two-dimensional motion depending on the inputs it receives from a family of one-dimensional, "lower order" motion detectors (Adler and Movshon, 1982). The balance between flicker and motion could thus be accounted for in terms of the competition between lower, properly stimulated and higher order, improperly stimulated motion detectors. In this case the motion surface of Fig. 5 may be interpreted to show the spatio-temporal range of optimum stimulation of the lower order motion mechanisms.

The preceding discussion is highly speculative. We therefore believe that further investigation of the bistability phenomenon described in this study may provide more information on the effectiveness of the activation of motion sensitive mechanisms under their full range of operation and its phenomenal consequences.

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