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Interocular interactions reveal the opponent structure of motion mechanisms

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Abstract

Interactions between motion sensors tuned to the same and to opposite directions were probed by means of measuring summation indexes for sensitivities (d') to contrast increments and/or decrements applied to drifting gratings presented in binocular and in dichoptic vision. The data confirm a phenomenon described by Stromeyer, Kronauer, Madsen & Klein (1984, J. Opt. Soc. Am. A 1, 876–884), whereby opposite polarity contrast changes applied to binocular gratings drifting in opposite directions yield sensitivities significantly higher than same sign changes for which performance complies with probability summation (PS). The effect disappears in dichoptic vision where opposite sign contrast changes yield a performance close to, or below PS, whether they are applied to same or to opposite direction stimuli. Same sign changes in dichoptic drifting stimuli yield a performance higher than PS independently of their relative directions and close to the performances obtained when these same sign changes are applied to dichoptic, static $\pm 45°$ gratings. Opposite sign changes applied to such static gratings yield PS. The data support the view according to which: (i) motion direction is extracted at the monocular site; (ii) motion sensors exhibit mutual inhibition within each eye when tuned to opposite directions; and (iii) binocular summation when tuned to the same direction. The data also suggest that (iv) independently of their directional tuning, all motion sensors converge on a binocular, motion non-specific ('flicker') unit; and that (v) signals carried by ON and OFF pathways are slightly inhibitory to each other.
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1. Introduction

Stromeyer, Kronauer, Madsen, and Klein (1984) reported that changes in the contrast of each of two superimposed gratings drifting in opposite directions (counterphase modulation) are easier to detect when one change is an increment and the other is a decrement, relative to conditions where both are increments or decrements. This observation, hereafter referred to as the SKMK effect, was taken as evidence that the detection mechanism operates on the output of units that compute the difference between the activation of motion sensors tuned to opposite directions of motion, as in the standard opponent Reichardt motion sensor (Reichardt, 1961; van Santen & Sperling, 1984, 1985; Adelson & Bergen, 1985; Georgeson & Scott-Samuel, 1999). However, the SKMK effect could also result from the operation of motion sensors tuned to opposite directions with separate outputs (Levinson & Sekuler, 1975a; Watson, Thompson, Murphy, & Nachmias, 1980; Doorn & van Koenderink, 1983; Watson & Ahumada, 1985; Heeger, Boynton, Demb, Seidemann, & Newsome, 1999) but mutually inhibitory (Levinson & Sekuler, 1975b; Emerson, Bergen, & Adelson, 1992; Qian & Anderson, 1994; Qian, Anderson, & Adelson, 1994a,b;Heeger et al., 1999). Besides accounting for the SKMK effect, this mutual inhibition scheme can also explain the impossibility of seeing opposite motions at the same time and place within the same spatial fre-

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quency band (Adelson & Bergen, 1985; Qian & Anderson, 1994; Qian, Anderson, & Adelson, 1994a) and the motion aftereffect (see Mather & Harris, 1998). By means of probing the SKMK effect under conditions where each of the two gratings drifting in opposite directions is seen by only one eye (a 'dichoptic' condition not previously tested), we intend to reveal the connectivity of the motion sensors across eyes and indirectly test the mutual inhibitory scheme against the standard Reichardt opponency. Because the literature strongly supports the view according to which directional information is extracted at a monocular site in the visual pathway (Braddick, 1974; Arditi, Anderson, & Movshon, 1981; Green & Blake, 1981; Lu & Sperling, 1995), a failure to observe the SKMK effect under dichoptic stimulation would imply that the connectivity of the monocular motion sensors tuned to opposite directions is different within and across eyes.

To assay the specificity of the results obtained with pedestals moving in opposite directions, the SKMK paradigm was also applied to gratings drifting in the same direction and to static orthogonal gratings (a standard stimulus in binocular rivalry experiments; see Blake, Sloane, & Fox, 1981; Lee & Blake, 1999). The comparison of the SKMK effects across these conditions was expected to provide further indications on the functional connections between motion sensors.

2. Methods

2.1. Stimuli

Sinusoidal gratings (1 c deg^{-1}, 40% contrast) were generated electronically on a color video monitor (Sony Trinitron Multiscan 15SX screen; 28×21 cm; 75 Hz frame-rate) under the control of a Power PC using Matlab in conjunction with the Psychophysics Toolbox (Brainard, 1997). The mean luminance of the gratings and the $40° \times 30°$ surrounding field was 25 cd m^{-2}. In the motion conditions, the gratings appeared within a $9° \times 9°$ square area; they were horizontally oriented, and drifted upward and/or downward at 20° s^{-1}. When presented simultaneously, the two directions of motion were either physically superimposed (counterphase stimulation; binocular vision), or shown separately to each eye (dichoptic presentation). (The use of horizontal gratings produces vivid rivalry with dichoptic stimulation; in contrast, vertically oriented gratings drifting in opposite directions create continuously changing disparity and, consequently, the gratings fuse and move in depth.) When static, the gratings were oriented $\pm 45°$, subtended a $4° \times 4°$ diamond-shaped area and were always presented in dichoptic vision with one of the two orientations in each eye (the smaller angular subtense of the static gratings minimized the incidence of piecemeal rivalry; Blake, O'Shea, & Mueller, 1992). In all the dichoptic conditions, the left- and right-eye gratings were presented 9° to the left and to the right of the center of the monitor, and they were viewed through a mirror stereoscope. Stable binocular alignment was achieved by adding strong fusion contours around the borders of the two half-images and by including a black, $1° \times 1°$ fixation cross in the center of each grating. A 200 ms contrast increment or decrement ($\pm \Delta C$) was applied to either one of the two gratings, or to both of them. Unless specified otherwise, ΔC was 4% for observer AG and 5% for observer TC (values yielding approximately equal d' values for the two observers). Viewing distance was 40 cm.

2.2. Observers

The first two authors served in all but one experimental condition. Observer TC had intensive training in rivalry experiments where she typically showed significantly less rivalry than any of the many observers tested in the lab (including observer AG).

2.3. General procedure

Sensitivity (d') for detection of increments and/or decrements against a pedestal was measured using a standard Yes/No procedure with a signal rate of 50%. At the start of each session, the observer carefully adjusted the mirrors of the stereoscope to achieve stable binocular alignment of the outline and fixation cross. Fifty milliseconds after a key-press (see below) the 'signal' (a contrast increment and/or decrement) was presented with a probability of 0.5. Depending on the session, it was applied to either the dominant or to the suppressed stimulus or to both of them. The observer pressed the 'left' or 'right' arrow-key to indicate the presence/absence of the signal. Auditory feedback was provided for incorrect responses (misses and false alarms).

Detection performance was measured under five different stimulus conditions:

1. *Counterphase binocular* — both eyes viewed the same grating.
2. '*Counterphase*' *dichoptic* — the upward-drifting grating was viewed by one eye and the downward drifting grating by the other (direction was counterbalanced over eyes).
3. *Static dichoptic* — the diagonal-left grating was viewed by one eye and the diagonal-right grating by the other (orientation was counterbalanced over eyes).
4. *Same direction binocular* — both eyes viewed a single horizontal grating drifting upward or drifting downward (direction counterbalanced over sessions).

5. *Same direction dichoptic* — horizontal gratings drifting in the same direction presented separately to the two eyes, making it possible to introduce an increment to one eye's grating and a decrement to the other eye's grating.

Because conventional (i.e. monocular or binocular) counterphase gratings produce perceptual alternations in dominance between their two grating components (Gorea & Lorenceau, 1984) similar to those observed when the two drifting components are presented dichoptically (Blake, Yu, Fukuda, & Lokey, 1998), performance under Conditions 1–3[2], was measured when the observer initiated presentations: (a) contingent on the rivalry state that he or she signaled by pressing the 'up' or 'down' keys on the keyboard (tracking); and (b) independently of the rivalry state, always pressing the 'up' key (non-tracking). Thus, there were eight experimental conditions altogether. Within each condition, one experimental session was characterized by the pattern of the contrast increments and decrements as they were applied to one (Single sessions) or to the two pedestals (Dual conditions). In the non-tracking state, there were five such contrast changes: 2 Single (with an increment or a decrement applied randomly across trials to one of the two gratings) and 3 Dual (increments/decrements applied to both pedestals, or an increment and a decrement applied to each of the two pedestals). In the tracking state, there were eight contrast changes combinations because increments and/or decrements could be applied to either the dominant or the suppressed stimulus/eye (i.e. 4 in the Single sessions and 4 in the Dual sessions). The tracking/non-tracking states were blocked over 100 trials (one session) with the contrast increment/decrement combinations randomized over trials. The session sequence was randomized over repeats and observers. Each datum point (d') was computed out of at least 400 trials (four repeats). Because the SKMK effect (or its absence) did not depend on the observer's tracking state (see the Results section), performance was eventually averaged over tracking and non-tracking conditions yielding at least 800 trials per datum point in Conditions 1–3.

3. Results

When trials were initiated based on the perceptual state during binocular rivalry, performance was generally worse when increments/decrements were presented during suppression compared to when they were presented during dominance. This finding merely replicates the well-established loss in sensitivity accompanying suppression periods of binocular rivalry (e.g. Westendorf, Blake, Sloane, & Chambers, 1982). Interestingly, performance did not depend on the perceptual state in the counterphase binocular condition, i.e. with both eyes viewing the same gratings, although the two drifting components fluctuate in perceptual dominance (Gorea & Lorenceau, 1984) as they do under dichoptic stimulation. This suggests that stimulus rivalry within one eye presents a different substrate than interocular stimulus/eye rivalry (Cogan, 1987; Cogan, Clarke, Chan, & Rossi, 1990; Blake, 1989).

When averaged over the dominant and suppressed states, performance of the two observers while tracking rivalry was practically indistinguishable from that obtained without tracking. Thus, the data presented below were pooled over the tracking and non-tracking sessions. Because, overall, contrast increments and decrements yielded about equal performances, they were also pooled to yield three final cases for each Condition and observer: the Single case (one increment or decrement), the Dual Same Sign case (two increments or decrements) and the Dual Opposite Signs case (one increment and one decrement).

The data from all five Conditions are shown in Fig. 1a–e under the same format. Values of d' obtained for the two observers (left- and right-hand panels) are shown for Single, Same Sign and Opposite Signs conditions (thick bars) together with probability summation (PS) predictions (open circles) for the latter two conditions. Thin vertical lines are $+1$ SE. PS predictions were computed according to the general formula $d'_{[\mathrm{Dual}]} = \sqrt{d'^2_{[\mathrm{Single\ 1}]} + d'^2_{[\mathrm{Single\ 2}]}}$. The $d'_{[\mathrm{Single}]}$ used in this equation depended on the increment/decrement combination used in the Dual condition.

3.1. Condition 1: counterphase binocular (Fig. 1a)

This condition replicated the SKMK effect (where observers view physically superimposed gratings drifting in opposite directions): whereas performance for the Dual Same Sign case is, overall, close to the PS predictions (a factor of 1.11, geometric mean), performance obtained for the Dual Opposite Signs case is significantly higher than PS (by a factor of 2.52 and 1.44 for observers AG and TC, respectively). For the Same Sign condition, observer AG shows facilitation (his sensitivity is 1.41 times the PS prediction), whereas observer TC's performance is slightly below PS ($0.88\times$). In principle, the transient increments and/or decrements applied to the two drifting components could have activated, in addition to the motion sensors, some generic 'flicker' units (Gorea, 1979) whose contribution should have boosted performance beyond probability summation even in the Same Sign condition. However, because of the continuous change in the relative phase of the two opposite drifting components, these dual increments and/or decrements sum, in average, to only

[2] Perceptual state tracking was meaningless under Conditions 4 and 5 since the two stimulus components were identical.

one increment and/or decrement. As a consequence, the probability summation observed under these dual same conditions must be attributed to the motion units alone and suggests that such units tuned to opposite directions yield separate outputs.

3.2. Condition 2: 'counterphase' dichoptic (Fig. 1b)

In this condition the two gratings drifting in opposite directions were presented to separate eyes so that they did not yield a counterphase stimulus in the conventional sense. With this exception, Conditions 2 and 1 were identical. Nonetheless, the SKMK effect disappears: the Opposite Signs case yields an average performance below PS (the measured vs. PS ratios are 1.15 and 0.72 for AG and TC). Evidently, the substrate of the SKMK effect (whether accounted for in terms of 'Reichardt opponency' or mutual inhibition) is monocular. On the other hand, Same Sign configurations yield a performance 2.56 × and 1.53 × higher than the Single configurations (factors of 1.82 × and 1.08 × with respect to PS, for observers AG and TC, respectively). Facilitation of this magnitude has been frequently observed (Blake et al., 1981; Green & Blake, 1981; Westendorf et al., 1982) and is within the range of Legge's (1984b) quadratic summation rule. It may also be contributed to by the activation of binocular flicker detectors integrating contrast changes across the eyes; because these changes are applied to physically non-overlapping stimuli, they do not cancel out (as in the binocular condition above). The absence of such a facilitation for the Opposite Signs case suggests that these binocular flicker detectors are sign sensitive.

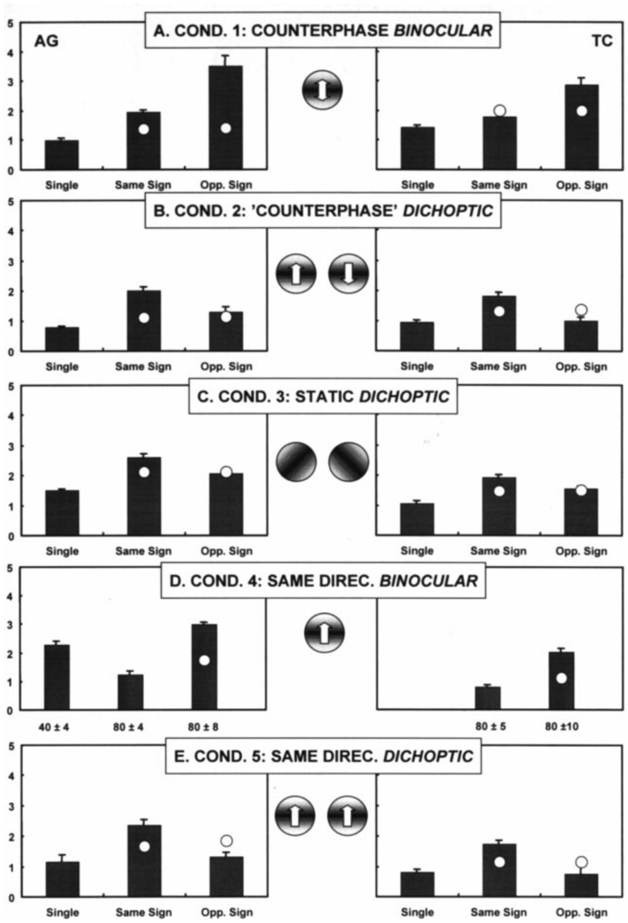

Fig. 1. (a) Condition 1: d' for contrast discrimination (bars) for single and dual (same and opposite signs) contrast changes and for the two observers. Open circles show probability summation predictions for the dual conditions. Vertical lines show $+1$ SE. All measurements are for gratings drifting in opposite directions and presented binocularly (i.e. counterphase gratings). (b) Condition 2: Same as (a) but with dichoptically presented gratings. (c) Condition 3: Same as (b) but with static $\pm 45°$ gratings. (d) Condition 4: Same as (a) but with the two gratings drifting in phase in the same direction. This configuration yields one single binocular pedestal (see text). The digits on the abscissa denote the contrast of the pedestal (40 or 80%) and of the increment/decrement (4 and 8% for observer AG and 5 and 10% for TC). (e) Condition 5: Same as (b) but with the two gratings drifting in phase in the same direction. Insets for each Condition illustrate the stimulus configuration with arrows showing the direction of the gratings; one and two disks are for binocular and dichoptic presentations respectively.

3.3. Condition 3: static dichoptic gratings (Fig. 1c)

This experiment serves as a reference for the previous one. Indeed, most studies having assessed sensitivity under binocular rivalry have used static stimuli (see for reviews Grossberg & Kelly, 1999; Lee & Blake, 1999). It is of interest to know whether the effects obtained with rivalrous moving stimuli also apply to rivalrous $\pm 45°$ static gratings. Overall, the data provide a positive answer. Opposite Signs contrast changes yield performances practically identical to PS predictions, whereas Same Sign ones show some facilitation (measured/PS ratios of 1.23 and 1.31 for AG and TC). Binocular summation with rivalrous stimuli seems thus to be stimulus non-specific (e.g. Westendorf et al., 1982).

To this point, the results indicate that the neural connectivity between opposite motion detectors accounting for the SKMK effect is absent across eyes. They also show that, for dichoptic stimulation, monocular channels tuned to opposite directions of motion or to orthogonal orientations yield binocular summation if activated with same sign contrast changes and a weak inhibition (for observer TC) or no interaction at all if stimulated with opposite sign contrast changes. The latter observation bears out previous data suggesting inhibitory interactions between ON and OFF processing channels (Cohn & Lasley, 1976; Cohn, Leong, & Lasley, 1981).

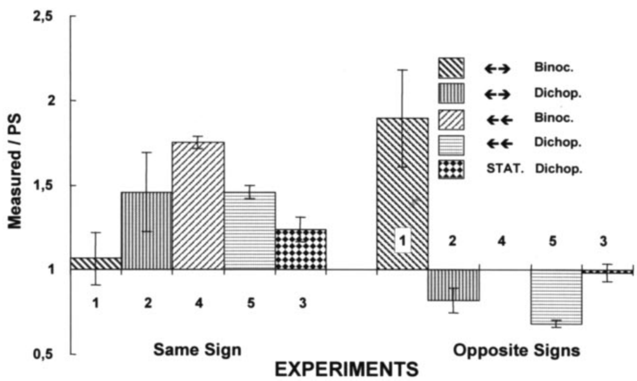

Fig. 2. Measured d'/PS ratios for all dual contrast changes conditions. Each bar is for a different Condition as numbered along the abscissa for Same Sign (left) and Opposite Signs contrast changes. Ratios larger and smaller than one indicate effective summation and inhibition, respectively. Vertical lines show ± 1 SE.

3.4. Conditions 4 and 5: same direction binocular (Fig. 1d) and dichoptic (Fig. 1e)

The comparisons between Conditions 4 and 1, on the one hand, and 5 and 2, on the other hand, are meant to reveal the influence on contrast discrimination of the relative direction factor under binocular and dichoptic conditions, respectively. The comparison between Conditions 4 and 5 should reveal the influence of the stimulus presentation factor (binocular vs. dichoptic) on contrast discrimination within motion processors tuned to the same direction.

In Condition 4, the physical superposition of two identical gratings drifting in phase in the same direction simply yields one single pedestal grating twice the contrast of its 'components'. It is the standard configuration for measuring contrast discrimination performance. Under the format of Condition 4 the Single and Same Sign configurations of Condition 1 correspond to $\pm \Delta C/C$ Weber fractions of $\pm 4/80$ (or $\pm 5/80$, for observer TC) and $\pm 8/80$ (or 10/80), respectively. Here, the denominator C is the sum of the two identical gratings of 40% contrast each. Observer AG was also tested with a Weber ratio of 4/40, a condition without correspondence in the preceding experiments. The Opposite Signs cases under this format is meaningless since simultaneous contrast increments and decrements cancel out.

In Condition 4, doubling the contrast increment (or decrement) yields more than a twofold increase in d′ (2.4 × and 2.6 × for observers AG and TC, respectively). This increase is 1.7 × (AG) and 1.8 × (TC) larger than predicted by PS and significantly greater than the equivalent increase obtained in Condition 1 (an average factor of 1.11). Halving the pedestal contrast (compare conditions 80 ± 4 and 40 ± 4 for observer AG) yields a 1.8 × increase in d'. Both effects match closely data published by Legge (1981, 1984a)[3].

Same Sign configurations yield comparable summation indexes in Conditions 2 and 5 (opposite vs. same direction in dichoptic vision; Fig. 1b and Fig. 1e) and comply with Legge's (1984b) quadratic summation rule[4] (average measured/PS ratios close to 1.4). Thus, summation of same sign contrast changes across eyes is independent of whether they are applied to pedestals moving in the same or in opposite directions. As for the Opposite Signs configuration, Conditions 2 and 5 yield measured/PS ratios (geometric means) of 0.9 and 0.7, respectively. Thus opposite sign contrast changes applied to drifting stimuli presented in dichoptic vision entail some sort of inhibition irrespectively of the relative directions of the pedestals. No such inhibition is observed with the static gratings (Condition 3, Fig. 1c).

4. Discussion

With both binocular and dichoptic viewing, the two opposite directions of motion compete for perceptual dominance. However, only with dichoptic viewing do the dominant and suppressed states yield differences in discrimination sensitivity. This implies that the neural concomitants of eye suppression (Lee & Blake 1999) may be different from those underlying stimulus suppression (Logothetis, Leopold, & Sheinberg, 1996).

[3] Eq. (1) in Legge (1984a) provides a fair fit of his measured discrimination d' as a function of ΔC: $d' = (\Delta C/\Delta C')^n$, with $\Delta C'$ a threshold parameter representing the contrast change yielding a d' of 1 and with n indicating the steepness of the psychometric function. Using this equation to fit AG's and TC's data for the 80% pedestal yields $\Delta C'$ values of, respectively, 3.4 and 6% and n values of 1.27 and 1.37. The equivalent n values obtained for Legge's three observers (for 25% pedestals and binocular vision) range from 0.62 to 1.12.

For the 40% pedestal (obs. AG, $\Delta C = 4\%$, $d' = 2.26$) this same eq. yields $\Delta C' = 2.1\%$. Using now Legges (1981) equation accounting for the contrast discrimination threshold as a function of the pedestal contrast, i.e. $\Delta C = kC^{n'}$ (with $n' = 0.6$, the average exponent found in that study), one can derive k (= 0.29) for the 80% pedestal condition at the actually measured performance level of $d' = 1.23$ (obs. AG, $\Delta C = 4\%$) and predict the ΔC at this same performance level but for the 40% pedestal condition (predicted $\Delta C = 2.6\%$). Using now $\Delta C'$ (= 2.1%) derived from the actual 40%-pedestal data for a $d' = 1.23$ in Legge's (1984a) eq. (1) should bear out the same prediction of ΔC if the pedestal effect on discrimination was the same in his and in the present study; this is indeed the case since the newly predicted $\Delta C = 2.5\%$.

[4] Legge's (1984b) quadratic summation rule was derived from experiments where the pedestal was present in only one eye under monocular conditions and in the two eyes under binocular ones. Under such conditions, the quadratic summation rule bears no advantage for binocular vision when the pedestals are highly suprathreshold.

Fig. 2 summarizes the ensemble of the data; it displays measured/PS ratios in the same and opposite sign cases for each of the five Conditions. In this format, ratios larger and smaller than 1 indicate facilitation and inhibition, respectively (across stimuli and/or eyes). Because tracking or not the dominant perceptual state (in Conditions 1–3) did not yield any significant binocular summation difference, the ratios in Fig. 2 are pooled over the two conditions. The overall pattern of the data is as follows:

1. Contrast changes applied to gratings moving in opposite directions and presented binocularly (Condition 1) sum probabilistically if they are of the same polarity but yield strong facilitation if they are of opposite signs (the SKMK effect). Because under the binocular condition increments/decrements applied to each of the drifting components sum across trials to only one increment/decrement, the summation observed in the same polarity case cannot be attributed to the response of a flicker detector. It suggests instead that motion channels tuned to opposite directions display separate outputs (see also Arditi et al., 1981): if they converged on a unique differentiating output, the Single and Same Sign cases should have yielded equal performance (i.e. less than PS). When taken together, the two sets of data suggest that the SKMK effect results from the mutual inhibition between motion sensors tuned to opposite directions rather than from the convergence of these units upon a unique 'differentiator' (i.e. 'Reichardt opponency').
2. The SKMK effect disappears under dichoptic conditions (Condition 2), implying that monocular motion sensors tuned to opposite directions do not interact across eyes. It is tempting to speculate that the absence of interocular connections between opposite directions of motion accounts, at least in part, for data showing that stereomotion (toward or away from the observer) yields lower sensitivities than lateral, monocular motion (for a discussion of the topic, see Harris, McKee, & Watamaniuk, 1998).
3. The weak inhibition observed for opposite signs under dichoptic vision with stimuli drifting in opposite directions (Condition 2) is also observed for dichoptic stimuli moving in the same direction (Condition 5), but not for the static dichoptic gratings (Condition 3; see also Green & Blake, 1981). Note that the observed inhibition is not accounted for by Legge's (1984b) binocular energy-detector.
4. In all the dichoptic conditions, the summation of the same sign contrast changes yields performance higher than PS. This facilitation observed with both rivalrous (opposite directions and static $\pm 45°$ gratings) and non-rivalrous stimuli (Blake et al., 1981; Westendorf et al., 1982; Legge's, 1984b; Grossberg & Kelly, 1999; Papathomas, Kovács, Fehér, & Julesz, 1999) is globally compatible with a quadratic summation rule (less than the full summation exemplified here by Condition 4). It may also be contributed to by direction insensitive, binocular flicker detectors (Gorea, 1979; Green & Blake, 1981). The stronger facilitation obtained with moving than with static gratings would then suggest that the activity of such units is boosted by the drifting pedestals (relatively to the static ones). Observation 3 above suggests that these flicker detectors are sign-specific and slightly inhibitory to each other (Cohn & Lasley, 1976; Cohn et al., 1981).

The present results suggest that the SKMK effect is due to the mutual inhibition between motion sensors tuned to opposite directions within one eye rather than to 'Reichardt opponency'. In the remainder, we recapitulate how this effect may come about and use this same inhibitory scheme to account for both the classical monocular (or binocular; Mather & Harris, 1998; Niedeggen & Wist, 1998) and dichoptic motion aftereffect (see Moulden, Patterson, & Swanston, 1998.

4.1. The SKMK effect

A counterphase grating (monocular or binocular) activates motion sensors tuned to the two directions of its oppositely drifting components (here upward and downward). These 'U' and 'D' units are mutually inhibitory within the Left and Right eye ($L_U \Theta L_D$, $R_U \Theta R_D$) but not across eyes. Because linear inhibition will yield a negative response from a non-activated unit when the opponent unit is activated, one may pose that their outputs are half-way rectified. Divisive inhibition would yield an equivalent outcome. The monocular U and D units converge on binocular motion sensors tuned to opposite directions of motion, B_U and B_D. This convergence displays less than full summation (e.g. quadratic summation). In the monocular (or binocular) counterphase stimulating case, incrementing the contrast of, say, the U component will enhance the response of the corresponding monocular L_U and/or R_U unit(s) by an amount more than that expected based on the physical increment itself: inhibition from these units will silence the L_D and/or R_D unit(s) so that desinhibition will boost the activity of the former. Accordingly, a contrast increment in one motion component accompanied by a contrast decrement in the oppositely drifting component will yield an even larger response increment in the unit tuned to the former than the increment produced in the absence of a decrement in the latter. This is the SKMK effect. (Note that the binocular stage per se is not needed to account for this effect.) Because monocular, opposite direction sensors are not connected across eyes, the SKMK effect should not be observed under dichoptic stimulation.

4.2. The motion aftereffect

Prolonged activation of the monocular L_U (or R_U) unit will decrease its own responsiveness as well as the responsiveness of the corresponding binocular B_U unit (adaptation). Inhibition of L_D (or of R_D) will progressively decrease. Upon disappearance of the adapting stimulus, inhibition will cease abruptly and the monocular unit L_D (or R_D) will 'bounce' into spontaneous activity. Because these units converge on the binocular unit B_D, this 'bouncing', presumably yielding the motion aftereffect, will be observed under either monocular, binocular or dichoptic adaptation, with binocular adaptation yielding stronger motion aftereffects than either monocular or dichoptic stimulation (e.g. Moulden et al., 1998). This interpretation is kin to standard models bearing on the opponent nature of the motion sensor (Mather & Harris, 1998).

In conclusion, we have shown that the SKMK effect is present in binocular vision and absent in dichoptic vision. The data suggest that the binocular SKMK effect is due to the mutual inhibition between monocular motion units tuned to opposite directions within each eye and that these units do not interact across eyes. This scheme also accounts for the interocular motion aftereffect and, in conjunction with a putative binocular flicker detector, for a variety of binocular summation effects obtained with stimuli moving in the same and in opposite directions.

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