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The oblique plaid effect

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Abstract

Plaids are ambiguous stimuli that can be perceived either as a coherent pattern moving rigidly or as two gratings sliding over each other. Here we report a new factor that affects the relative strength of coherency versus transparency: the global direction of motion of the plaid. Plaids moving in oblique directions are perceived as sliding more frequently than plaids moving in cardinal directions. We term this the *oblique plaid effect*. There is also a difference between the two cardinal directions: for most observers, plaids moving in horizontal directions cohere more than plaids moving in vertical directions. Two measures were used to quantify the relative strength of coherency vs. transparency: $C/[C+T]$ and RTtransp. Those measures were derived from dynamics data obtained in long-duration trials (>1 min) where observers continually indicated their percept. The perception of plaids is bi-stable: over time it alternates between coherency and transparency, and the dynamics data reveal the relative strength of the two interpretations [Vision Research 43 (2003) 531]. $C/[C+T]$ is the relative cumulative time spent perceiving coherency; RTtransp is the time between stimulus onset and the first report of transparency. The dynamics-based measures quantify the relative strength of coherency over a wider range of parameters than brief-presentation 2AFC methods, and exposed an oblique plaid effect in the entire range tested. There was no interaction between the effect of the global direction of motion and the effect of gratings' orientations. Thus, the oblique plaid effect is due to anisotropies inherent to motion mechanisms, not a bi-product of orientation anisotropies. The strong effect of a plaid's global direction on its tendency to cohere imposes new and important constraints on models of motion integration and transparency. Models that rely solely on *relative* differences in directions and/or orientations in the stimulus cannot predict our results. Instead, models should take into account anisotropies in the neuronal populations that represent the coherent percept (integrated motion) and those that represent the transparent percept (segmented motion). Furthermore, the oblique plaid effect could be used to test whether neuronal populations supposed to be involved in plaid perception display tuning biases in favor of cardinal directions.

Keywords: Perceptual anisotropy; Oblique effect; Motion segmentation; Motion integration

1. Introduction

Our perceptual world is not isotropic: objects can look quite differently when we tilt our head, and psychophysical measures such as detection thresholds can change as a function of the global orientation of the stimulus. Perceptual anisotropies are more than curiosities. They can tag the underlying processes, making it possible to identify their neural substrates. One notable example is the *oblique effect*, the greater sensitivity of the visual system to horizontal and vertical contours than to oblique ones (Appelle, 1972), which has been related to orientation selective V1 neurons: it was argued that the oblique effect was due to the observed predominance of V1 neurons coding cardinal orientations (e.g., Furmanski & Engel, 2000; Mansfield, 1974, but see Finlay, Schiller, & Volman, 1976). The correspondence between this neuronal coding bias and the perceptual anisotropy can be taken as an argument in favor of V1 being an important substrate of orientation perception.

Anisotropies were also described for motion perception. However, some studies found anisotropies (Ball & Sekuler, 1980, 1982), while others did not (Ball & Sekuler, 1979; Levinson & Sekuler, 1980). The apparent discrepancy is resolved by noticing that anisotropies are found for motion discrimination, but not for motion detection tasks (see Gros, Blake, & Hiris, 1998 for a

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comprehensive review). Detection and discrimination tasks are not the only ways to unveil perceptual anisotropies. Ambiguous stimuli can also be used, by revealing preferences for perceiving interpretations associated with certain directions. For example, the direction of lines or gratings moving behind an aperture is formally ambiguous, but when there is the choice between perceiving cardinal or oblique motion, the cardinal motion interpretation is often preferred (Wallach, 1935, English translation in Wuerger, Shapley, & Rubin, 1996; Castet & Zanker, 1999; Shapley & Rubin, 1996; Wuerger et al., 1996). These studies, however, did not attempt to disentangle the effect of direction of motion from that of contour orientation: cardinally oriented contours were present in the stimuli used in these experiments. Indeed, it has been suggested by Andrews and Schluppeck (2000) that the preference for cardinal motion they observed was related to the oblique effect for orientation, i.e. that there might be no need to invoke another hypothesized bias, for direction of motion. In the study presented here we report a preference for perceiving cardinal motion for another ambiguous stimulus, the plaid, for which it is possible to manipulate independently the direction of motion and the orientation of the contours.

A plaid is a pattern composed of two superimposed gratings of different orientations. When set in motion, the plaid can be seen as a single pattern moving rigidly, but it can also separate into two gratings which slide over each other in different directions (Wallach, 1935/1996). This ambiguous stimulus was used extensively in the modern literature to study the mechanisms of motion integration (which give rise to the plaid, or "coherent" motion) and motion segmentation (which give rise to the gratings', or "transparent" motion) (Adelson & Movshon, 1982; Kim & Wilson, 1993; Krauskopf & Farell, 1990; Movshon, Adelson, Gizzi, & Newsome, 1985; Smith, 1992; Stoner, Albright, & Ramachandran, 1990; Trueswell & Hayhoe, 1993; Vallortigara & Bressan, 1991). However, most studies used plaids moving only along cardinal directions, overlooking possible directional anisotropies. When direction was manipulated, it was always the direction of the gratings relative to each other (the angle alpha between the grating's directions of motion, Adelson & Movshon, 1982; Kim & Wilson, 1993), never the global direction of the whole stimulus. (Heeley & Buchanan-Smith, 1992, compared performances for plaids moving in oblique and cardinal directions, but the task was to discriminate directions of motion, not to report whether coherency or transparency was experienced; the plaids were assumed to be always perceived as coherent.)

We found that the transparent percept was much more likely to be reported when the global direction of the plaid was oblique than when it was cardinal. The effect is strong enough so that it can be experienced in informal demos (available at http://cns.nyu.edu/home/hupe/arvo01demo). Tilting the head by 45° when viewing a plaid moving horizontally is also often sufficient to trigger the transparent percept. We term this the *oblique plaid effect:* the tendency for plaids moving in oblique directions to slide more readily than plaids moving in cardinal direction. We report here the effects of systematic manipulation of plaid parameters performed to assess the generality and the characteristics of the oblique plaid effect. An important purpose of this study was to characterize anisotropies for motion perception and their relation (or lack of) to anisotropies for orientation perception.

To evaluate the relative strength of the coherent and transparent percepts, we used the dynamics approach that we have recently developed (Hupé & Rubin, 2003). This approach uses the fact that plaids, like many other ambiguous stimuli, lead to bi-stable perceptual alternations: with prolonged viewing, the perception switches back and forth between transparency and coherency. We showed that the cumulative time spent perceiving the coherent percept over long observation durations, $C/[C+T]$, was a sensitive and reliable measure of plaid coherency. A second dynamics-based measure, the time between stimulus onset and the first report of transparency, which we term RTtransp ("response time to see transparency"), was highly correlated with $C/[C+T]$ and thus offered a method which was as accurate, but more efficient than $C/[C+T]$. We also showed that, compared with short presentation 2-AFC methods, dynamics methods permit measuring the probability of coherency and transparency in much wider parametric regimes, since they are less susceptible to floor and ceiling effects (Hupé & Rubin, 2003).

2. Methods

2.1. Apparatus

Stimuli were generated on a Silicon Graphics™ Indigo II workstation and displayed on a 19-in. monitor (45 cm viewable screen size) at a frame rate of 76 Hz. The screen resolution was 1280×1024 pixels. The SGI Graphics Library (GL) was used to generate the stimuli.

2.2. Stimuli

Plaids composed of rectangular-wave gratings were presented through a circular aperture, 13° in diameter. The luminance of the background outside the aperture was 10 cd/m^2 in Experiment I and 18 cd/m^2 in Experiment II. The gratings were comprised of dark stripes (20 cd/m^2 in Experiment I, 24 cd/m^2 in Experiment II) on a light background (30 cd/m^2 in Experiment I, 47 cd/m^2 in Experiment II). The dark regions appeared as "figure" because the duty cycle, defined as [(width of dark bar)/(total cycle)], was always less than 0.5, i.e., the dark stripes were thinner. The luminance of the intersection regions was 17.5 cd/m^2 in Experiment I and 19 cd/m^2 in Experiment II, putting the plaid in the transparent regime (Stoner et al., 1990; Stoner & Albright, 1996). The two gratings had the same spatial frequency (0.6 cycle/° in Experiment I, 0.3 cycle/° in Experiment II), duty cycle (33% in Experiment I) and speed, and the plaids were therefore completely symmetric. The image was refreshed every other frame to allow enough time for drawing the stimuli (see Hupé & Rubin, 2003). A colored fixation point was overlaid on a homogeneous circular patch that covered the center of the plaid, to minimize OKN eye-movements (2.5° diameter, same luminance as the background outside the aperture). Observers were instructed to maintain fixation during the whole duration of stimulus presentation. The stimuli were viewed from a distance of 57 cm in a darkened room.

2.3. Observers

Observers were the two authors (designated O1 and O2, or NR and JMH; these codes are the same as the one used in Hupé & Rubin, 2003), five colleagues and five undergraduate students from New York University. The colleagues and students were naïve about the purpose of the experiments. The students were paid for their participation. All participants had normal or corrected-to-normal vision. Three naive observers (O10–O12) with no previous exposure to plaids and one of the authors (JMH) participated in Experiment I. The two authors and seven naïve observers participated in Experiment II. Four of these observers had been previously exposed to plaid stimuli (observers O1, O2, O5 and O9).

2.4. Procedure

In Experiment I, observers were asked to continually indicate when they perceived coherency and transparency by holding down a mouse button for each of the two interpretations, or to not press any button when they were unsure of their percept. For the stimuli used in this experiment, the first reported percept was coherency in all trials, for all observers. The stimulus remained on the screen for 1 min after the first report of transparency unless transparency was not reported within 1 min in which case the trial was terminated. In Experiment II observers were asked to press a mouse button as soon as they saw the plaid separating into two transparent gratings, after which the trial ended.

2.5. Design

The experiments were set up as full factorial designs: all combinations of the different values of the independent variables were used. There were one (Experiment I and third group of observers in Experiment II) or two (first two groups in Experiment II) repetitions of the complete set of parameters in a randomized order. The pattern could move in eight possible directions, four cardinal (right, left, up, down), the other four oblique (45° from a cardinal axis). Two other plaid parameters were manipulated: the angle alpha between the gratings' directions of motion and the gratings' speed. In Experiment I, the values for alpha were 110° and 140°, and speed was either 2.1°/s or 4.2°/s. In Experiment II, the duty cycle was also manipulated, and three groups of observers were tested with slightly different values of alpha, speed and duty cycle. The exact values of alpha used for each group are given in figures 6 and the other parameters were detailed in another study using the same set of data for analyses that are not related to the oblique plaid effect (Hupé & Rubin, 2003; see Table II).

2.6. Data analysis

We used two dynamics measures of the strength of the coherent percept, $C/[C+T]$ in Experiment I and RTtransp in Experiment II. C and T were the cumulative times spent reporting coherency and transparency, respectively, during the 1 min stimulus presentation starting at the first report of transparency (i.e., C did not include the first, coherent, percept). $C/[C+T]$ was therefore the relative time seeing coherency, or the probability of the coherent percept at "steady state" (Hupé & Rubin, 2003). If the transparent percept was not reported within the 1 min limit, $C/[C+T]$ was set to 1 (100% coherency, 5 cases out of 122). RTtransp was defined as the time from stimulus onset to the first report of transparency. The independent variables were categories—the plaid global direction of motion and observer identity (random factor)—and continuous predictors (or covariates)—alpha, speed and duty cycle. In order to test interactions, alpha (Section 3.3), speed and duty cycle (Section 3.4) were treated as categories. Data were run through an analysis of covariance (ANCOVA; Statistica, StatSoft^{TM}), with either $C/[C+T]$ (Experiment I) or RTtransp (Experiment II) as the dependent variable. RTtransp values were transformed to their natural logarithm (Hupé & Rubin, 2003; ln(RTtransp) is linearly related to $C/[C+T]$). A condition of validity of these analyses is that the noise in the data be normally distributed. This condition was satisfied for $C/[C+T]$ and ln(RTtransp) (Experiment I, Kolmogorov–Smirnov test, $d = 0.115$, $N = 122$, $p < 0.1$; Experiment II [1]: K–S, $d = 0.016$, $N = 7279$, $p < 0.1$). Another condition of validity is that the variances be homogeneously distributed. To test this, the

[1] See Fig. 3 in Hupé & Rubin, 2003.

standardized residual values were plotted as a function of the ANCOVA-predicted values, and these scatter-plots were visually inspected for each analysis. The variances were judged to be homogeneously distributed for $C/[C+T]$ in Experiment I but not for ln(RTtransp) in Experiment II. In this case, smaller predicted values had a smaller variance. We explained previously that this resulted from a floor effect of RTtransp, which happens when the probability of the transparent percept reaches a ceiling of 100% (Hupé & Rubin, 2003). The transparent percept then tends to be the first percept, and parametric manipulations have little effect on either the probability of the coherent percept or RTtransp. We showed that we could overcome this floor effect by selecting data of observers with on average longer response times to see transparency (Section 3.3). More detailed evidence of the relationship between floor effect and inhomogeneity of variances is available at http://cns.nyu.edu/home/hupe/plaid_demo/suppl.htm. The analysis of residuals was also used to remove outlier values (when z-score were too low or too high: 6 outlier values out of 128 in Experiment I, 25 out of 7304 in Experiment II).

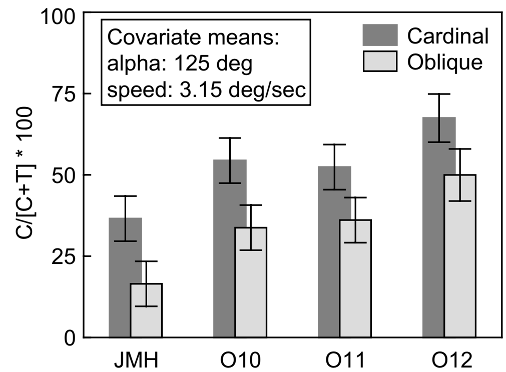

Fig. 1. The probability of perceiving the coherent percept is higher for plaids moving in cardinal directions. This *oblique plaid effect* exists for every observer. $C/[C+T]$ was measured for 1 min after the first report of the transparent percept. Least square means of $(C/[C+T]\times 100)$ were computed for covariates at their means (See inset. Effects of these parameters were factored out in the ANCOVA. We verified that there was no interaction between the oblique plaid effect and the effects of alpha and speed) as a function of the global direction of plaid. Here and in all the other graphs, error bars denote 0.95 confidence intervals for the means.

3. Results

3.1. Experiment I: $C/[C+T]$

Plaids were presented for (RTtransp + 1 min) to four observers who continuously reported whether they experienced the transparent or the coherent percept. The probability of coherency was compared for plaids moving in an oblique direction (four directions) and plaids moving in a cardinal one (four directions). For all observers, the probability of coherency was significantly higher for cardinal directions (Fig. 1), indicating a preference to see coherent motion in cardinal directions. Put differently, the probability of the transparent percept is higher for oblique directions; this is what we call the oblique plaid effect. On average, the probability of perceiving the coherent percept was about 25% higher for plaids moving in cardinal directions. Fig. 2 shows the probability of coherency for each of the eight directions tested, averaged across observers. The probability of coherency was higher for each of the four cardinal directions. Another difference appears between vertical and horizontal directions, which we examine further in the next experiment.

3.2. Experiment II: RTtransp

We previously demonstrated that ln(RTtransp) was linearly related to $C/[C+T]$, the steady-state probability of coherency (see Figs. 5 and 6 in Hupé & Rubin, 2003). Consequently, the effects of parametric manipulations were the same when tested with the two measures. In order to study the oblique plaid effect further, we therefore turned to using the RTtransp measure, which is far more efficient in terms of data yield.

The first step was to replicate the oblique plaid effect using RTtransp. We presented plaids with different parametric values (Section 2) to nine observers and asked them to press a mouse button as soon as they perceived the transparent percept. Fig. 3 presents the RTtransp responses grouped by whether the plaid was moving in an oblique direction or a cardinal one (i.e., all other parameters were pooled). For all observers, RTtransp values were on average significantly longer for cardinal directions, confirming the preference to see coherent motion in cardinal directions. The effect of cardinality on ln(RTtransp) was strong ($F(1,9.39) = 154$, $p < 10^{-6}$). Despite large differences of average response times between the nine observers ($F(8,8.05) = 60$, $p < 10^{-5}$), the interaction between the cardinality effect and observer identity was small on a relative scale ($F(8,7258) = 8$, $p < 10^{-10}$), as indicated by the much smaller F value. The strength of the oblique plaid effect was therefore slightly different for different observers (note that it was not correlated with mean response time, Fig. 3).

In order to examine further the effect of the global direction, we looked at the average response times for each of the eight global directions (Fig. 4). RTtransp was clearly longer for the four cardinal directions. But it is also clear that horizontal directions produced longer RTtransp than vertical directions. In order to find out which directions could be grouped together without any *a priori* assumption, we computed a second ANCOVA

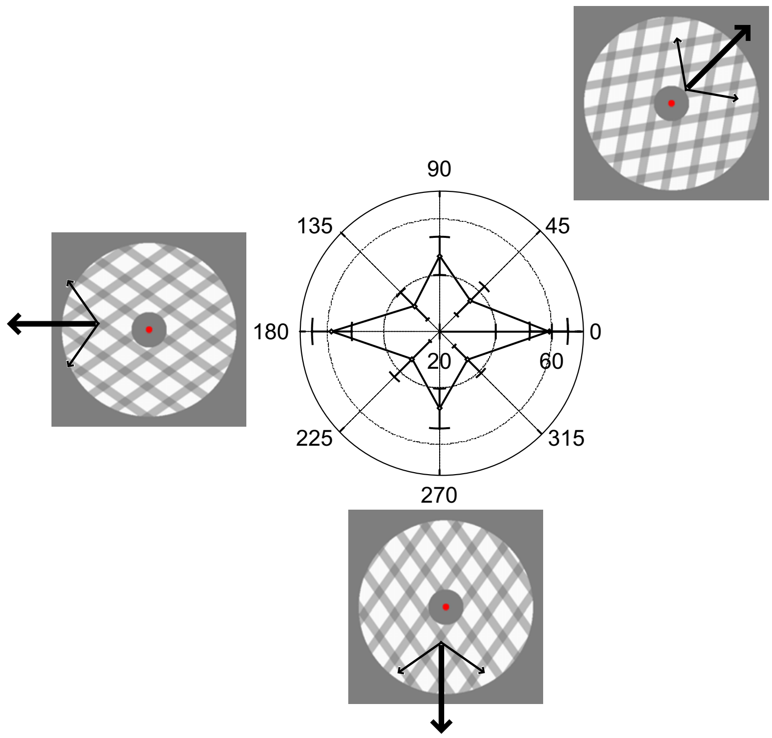

Fig. 2. Polar plot of the effect of the plaid global direction on the probability of coherency, as measured by ($C/[C+T]\times 100$). Icons depict examples of plaids (with alpha = 110°) moving in an oblique (45°), horizontal (180°) or vertical (270°) direction (large arrows). Small arrows: grating directions. Values for each direction were averaged over the four observers and different values of alpha and speed (same means of covariates as in Fig. 1).

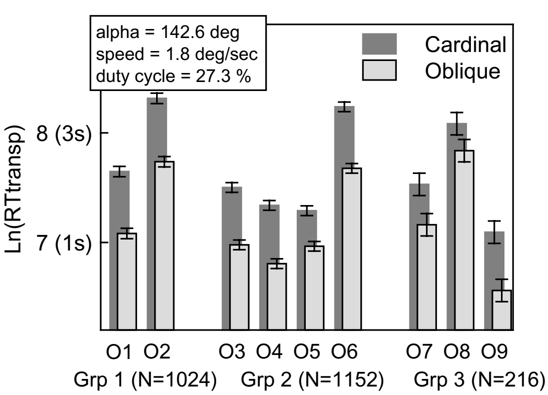

Fig. 3. The oblique plaid effect as revealed by the RTtransp method: Response times to report transparency are longer for plaids moving in cardinal directions. RTtransp was measured in ms, so a natural log value of 7 corresponds to ~1 s (1097 ms exactly; see approximate values in parentheses on the ordinate axis).

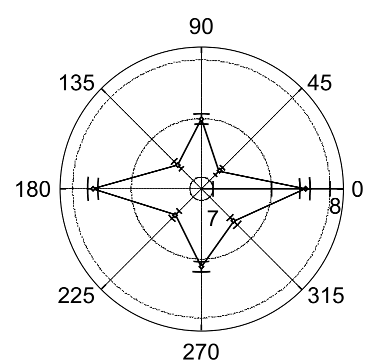

Fig. 4. Polar plot of the effect of the plaid global direction on ln(RTtransp). The data were averaged across the nine observers. Same means of covariates as in Fig. 3.

with the 'global direction' variable having 8 values instead of 2, and we performed post-hoc tests of the effect of global direction. [2]

RTtransp values for plaids moving to the right (0°) and to the left (180°) were not significantly different from each other but were significantly different from RTtransp values for plaids moving in all the other directions. The two vertical directions also grouped. RTtransp values for the four oblique directions were not significantly different from each other, except for 45° and 315°. This ANCOVA also revealed a significant interaction between the effects of global direction and observer identity ($F_{56,7204} = 7.7$, $p < 10^{-17}$). Fig. 5 shows the effects of global direction for four naive observers, whose results

[2] As mentioned in Section 2, the variances were not homogeneously distributed: precise results as such as those given by post-hoc analysis should therefore be taken with caution. We chose the Scheffé test, which is a very conservative post-hoc test (Day & Quinn, 1989; Ludbrook, 1991), with a significance threshold of 0.01, in order to be sure that the differences that we observed were robust (but possibly overlooking minor differences).

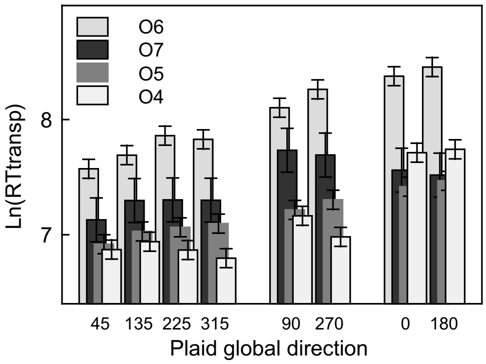

Fig. 5. Average response times to see transparency for four naive observers and for the eight directions of motion. Same conventions as in previous figures.

span the range of individual differences. For most observers RTtransp values for vertical directions were approximately halfway between the values for oblique and horizontal directions. This was observed whether the mean response times were long (O6) or short (O5). For other observers, like O4, the difference between vertical and horizontal directions was stronger than the difference between vertical and oblique directions. Only one observer (O7) had equivalent response times for vertical and horizontal global directions. We did not observe any systematic difference among subjects between the response times for oblique directions 45° and 315° (see the response times of O4 for example), even though 45° produced generally shorter RTtransp than the other oblique directions. In summary, post-hoc tests and observation of individual data indicate that the two horizontal and the two vertical directions should be considered as two distinct groups. The differences in RTtransp values for the four oblique directions were relatively small and not consistent between observers, and were therefore grouped together for further analyses.

3.3. The role of the gratings' orientations in the oblique plaid effect

Until now, we have described the oblique plaid effect in terms of the global direction of the plaid, our manipulation being a global rotation of the display. But each time the global direction changes, the gratings' directions (and orientations) also change (see the stimulus icons in Fig. 2). It is therefore not possible to know *a priori* whether the oblique plaid effect is due to anisotropies in the global direction of motion or anisotropies in the gratings' orientations or their directions of motion (or both). The lower probability of coherency when the plaid's global direction is oblique may be rephrased as a higher probability of the gratings to slide for specific gratings' directions. In the icons of Fig. 2, for example, where alpha = 110°, the gratings' directions are closer to cardinal directions for the oblique global direction (top right, 10° away) than for the cardinal plaid directions (35° away). This question can be empirically tested by manipulating alpha, the angle between the gratings' directions of motion, since it is possible to test different gratings' orientations for a given global direction of motion. Specifically, if the gratings' directions are involved in the oblique plaid effect, we should expect to observe an interaction between the effects of the global rotation of the display and of the manipulation of alpha. For example, we might expect that the oblique plaid effect should be less significant (or even vanish) when alpha = 135°, since in that case each grating is always exactly 22.5° away from the closest cardinal axis, irrespective of the plaid global direction.

To test for interactions between alpha and global direction, we performed a new ANCOVA with alpha considered as a category. [3] (The three groups of observers were tested with slightly different values of alpha, so separate ANCOVAs were done for each group.) There was a significant interaction between the effects of alpha and plaid direction (three categories: oblique, vertical and horizontal) for all three groups of observers. Inspection of Fig. 6 indicates, however, that the oblique plaid effect was present and significant for the entire range of alpha values tested (and in particular did not vanish for 135°). This means that the global direction of the plaid, and not specific orientations/directions of the gratings, is responsible for the oblique plaid effect.

Closer inspection of the data revealed that the interactions were due to a tendency for the effect to be smaller for larger values of alpha. Since RTtransp values themselves were also smaller for these large alpha values, we suspected that the interactions could be due to a floor effect (see Hupé & Rubin, 2003). We therefore reanalyzed the data to look for interactions in individual observers who had shorter and longer average response times. Fig. 7 presents results for six individual observers (two from each group; "fast" observers on left, "slow" on right). Observers with long RTs (O2, O6, O7) displayed very little interaction between alpha and global direction (contrast with observers with short response times, O1, O4, O9). The distribution of the residuals confirmed that there was a floor effect for "slow" observers but not for "fast" observers (analysis not shown; details available at http://cns.nyu.edu/home/hupe/plaid_demo/suppl.htm). In other words, the only interaction between alpha and the oblique plaid effect is that as alpha grows, RTtransp values hit a "floor" for some (fast) observers, decreasing the size of the effect. This, in turn, means that the gratings' orientations are not inherently involved in the oblique plaid effect.

[3] The main effects of alpha, speed and duty cycle were analyzed in details in a previous paper (Hupé & Rubin, 2003).

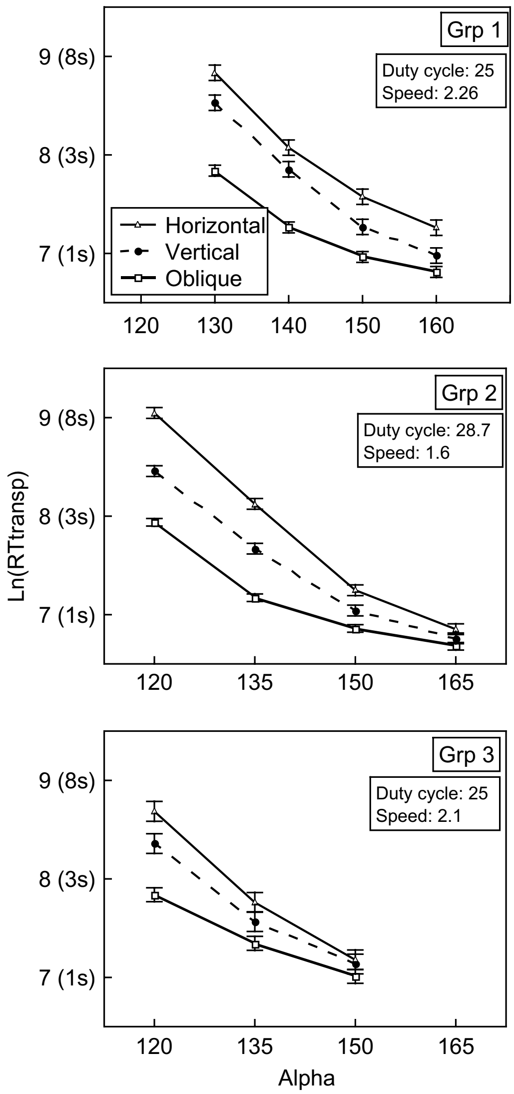

Fig. 6. Plots of ln(RTtransp) as a function of alpha for the horizontal, vertical and oblique directions separately show an interaction between the oblique plaid effect and alpha: the differences in RTtransp between cardinal and oblique directions diminish for large alpha values. (Separate plots for the three groups of observers, see Section 2; insets show covariate means of speed and duty cycle for each group.)

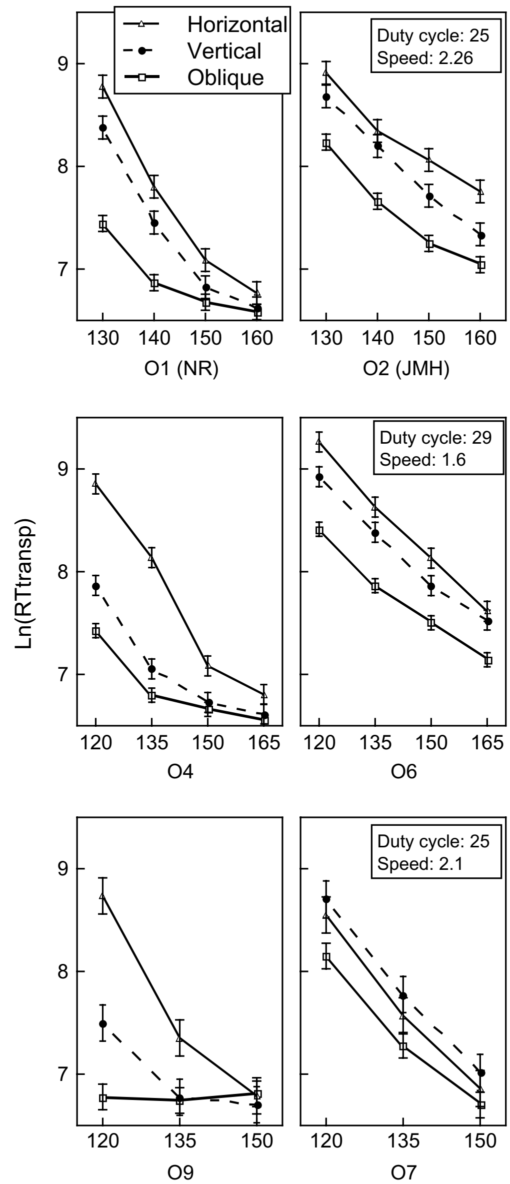

Fig. 7. The interaction between alpha and the oblique plaid effect is caused by a "floor effect" in some observers. Observers who are on average faster to experience the transparent percept (left plots) show strong interactions between the effects of alpha and global direction. There is no interaction for observers with long RTtransp (right plots): the effect of alpha on RTtransp is linear whatever the global direction, and the three curves are roughly parallel.

To inspect the effect of gratings' orientations further, one of the "slow" observers (JMH) performed an additional experiment covering the full range of possible alpha values. [4] The results are shown in Fig. 8, and indicate that the oblique plaid effect is present for the full range of alpha, with no significant interaction with this parameter (*Homogeneity of slopes* model, $F(2,82) = 0.34$, $p = 0.71$; For alpha between 40° and 140°, $F(2,50) = 0.05$, $p = 0.96$ and the R^2 *values* of the linear fitting for oblique, vertical, and horizontal were respectively 0.84, 0.93 and 0.96). These data again confirm that the oblique plaid effect results from anisotropies specific to motion mechanisms, since gratings' orientation do not play a role in it.

3.4. Interactions between oblique plaid effect and other parameters

We tested the generality of the oblique plaid effect for different values of speed and duty cycle. [3] Response

[4] Duty cycle was 25% and speed was 3.1°/s in all the trials. If no button was pressed, the trial ended after 2 min; otherwise, the stimulus was displayed for 40 s after RTtransp.

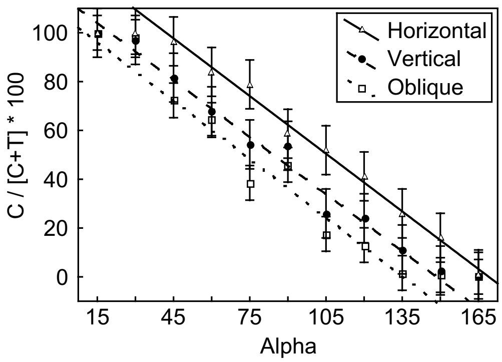

Fig. 8. $C/[C+T]$ values show significant separation for the horizontal, vertical and oblique global directions of motion for the entire range of possible alpha values (one observer, JMH). The best-fit linear curves for the three conditions are parallel, indicating no interaction between alpha and the oblique plaid effect. (To prevent ceiling and floor values from biasing the fits, the best-fit linear curves were computed based on the 40–180° data for the horizontal direction and 40–140° for the vertical and oblique directions.)

times to report transparency were systematically longer for cardinal directions for all values of speed (0.65–3.2°/s) or duty cycle (10–47.5%) tested. Considering speed as a category, we measured the interaction between speed and global direction. The interaction was significant but small in comparison with the effects of speed and direction. Careful analysis of the data for each subject revealed that only JMH had a significant interaction between speed and global direction (due to the decrease of the difference between RTtransp for vertical and horizontal directions at slow speeds; data and analysis not shown). Nevertheless, the possibility of an interaction between speed and global plaid direction should be noted for further studies. Considering duty cycle as a category, we did not detect an interaction effect between duty cycle and global direction in any of the three groups of observers. The analysis of the data of observers with long response times (and no floor effect) confirmed this lack of interaction for speed (except for JMH) as well as for duty cycle.

The oblique plaid effect was observed in several other parametric regimes that we have tested—in fact, in all the cases we have tested. For example, JMH performed an additional experiment with gratings at a higher spatial frequency (0.9 cycles/°) and a duty cycle of 10%. The bars of the gratings were then only 4 pixels (~0.11°) wide, and the display looked therefore like crossed lines, not like crossed bars anymore. The oblique plaid effect was exactly as strong in these conditions. [5] A robust oblique plaid effects was observed also when we changed the luminance profile of the constituent gratings. Many studies of plaids used sinusoidal gratings (e.g., Adelson & Movshon, 1982; Kim & Wilson, 1993; Movshon et al., 1985; Smith, 1992). In a previous study we showed that the effects of several parametric manipulations were quantitatively similar for rectangular and sinusoidal plaids (Hupé & Rubin, 2003). In one of the experiments described there, two observers (JMH and NR) were tested with sinusoidal plaids. These plaids were moving either along vertical or horizontal directions. The preference to see coherent motion for horizontal direction (average: 61%; JMH: 56%) over vertical directions (average: 46% JMH: 45%) was identical to what we observed with rectangular plaids (Experiment I, JMH: 41% vs. 32%; see also footnote 5). In summary, our results indicate that the oblique plaid effect is a general property of the perception of plaids, whatever specific parameters are used.

[5] This experiment used the $C/[C+T]$ protocol. The probability of coherency were 20%, 37% and 47% for the oblique, vertical and horizontal directions respectively.

4. Discussion

4.1. The oblique plaid effect

The oblique plaid effect, the greater tendency for transparency for plaids moving in oblique directions compared with cardinally moving plaids, is a highly reliable finding. Every observer tested showed it (twelve observers in this study), whatever the other plaid parameters (alpha, speed, duty cycle, spatial frequency, rectangular and sinusoidal waveform). The effect is strong: changing the global direction from oblique to horizontal corresponds to a change of probability of the coherent percept by 25%. One can get a sense of the effect by simply tilting one's head (http://cns.nyu.edu/home/hupe/arvo01demo). We also found that vertical and horizontal directions were not equivalent: the coherent percept was stronger for horizontal directions. On average, the probability of sliding for plaids moving in vertical directions was halfway between the probabilities for oblique and horizontal directions (only one out of twelve observers showed no significant difference between horizontal and vertical directions). The preference for horizontal motion over vertical motion had been observed for other ambiguous stimuli (Castet, Charton, & Dufour, 1999; Shapley & Rubin, 1996; Wallach, 1935, 1996).

The oblique plaid effect was not reported in previous studies. This might be due to the use of brief-presentation methods, which have limited dynamic range. In large parametric regimes, plaids may be perceived in brief presentations as transparent 100% of the trials, and similarly as coherent 100% of the trials in other regimes. However, we previously showed that when data from long observation periods are taken, the dynamics-based measures ($C/[C+T]$ and RTtransp) show gradual, near-linear variation with parametric manipulations within those regimes (see, e.g., the effect of alpha, the angle between the gratings' direction of motion; Hupé & Rubin, 2003). Thus, the dynamics approach permits to uncover the true underlying relation between transparency and coherency, which is masked by "floor" and "ceiling" effects when brief-presentations methods are used. Similarly here, the dynamics-based measures uncovered the effect of the global direction of motion of the plaid in parametric regimes which would appear to be saturatingly "coherent" (or transparent) using brief-presentation methods. Another reason why the oblique plaid effect was not found previously may be that most studies used only a few directions of motion (typically one or two vertical directions), and this prevented an opportunity for the oblique plaid effect to be discovered. In one study that used the four cardinal directions (Lindsey & Todd, 1996), the authors compared the average probability of sliding in blocks of trials where only one vertical, two vertical, or the four cardinal directions were presented. They found that the probability of sliding was different between blocks: it was higher in blocks of trials using only one or two (vertical) directions. They concluded that adaptation was responsible for this result. However, our results indicate that the effect of adding the two horizontal directions (see their Figs. 2 and 3) was at least partly due to the greater tendency to see coherent motion in horizontal directions. This hypothesis could be tested by tallying the data from the four directions separately.

4.2. Direction and orientation anisotropies

Motion direction anisotropies have been reported previously for direction discrimination (but not for motion detection tasks: see Gros et al., 1998, for a review) as well as for ambiguous motion stimuli (Andrews & Schluppeck, 2000; Castet & Zanker, 1999; Shapley & Rubin, 1996; Wallach, 1935, 1996). While it is not clear how the same mechanisms might be responsible for direction discrimination anisotropies and preferences for cardinal directions of motion in ambiguous stimuli, the results obtained with both protocols bring up the same question: do they originate from motion-specific anisotropies, or can they be explained by the well documented orientation oblique effect? Learning studies showed that orientation discrimination improved after direction discrimination, but not the reverse (Matthews, Liu, Geesaman, & Qian, 1999). So even if there is a "partial overlap between the sensory responses constraining these two visual tasks" (Matthews et al., 1999), it is unlikely that orientation anisotropies alone are the source of anisotropies in motion discrimination. Similarly, our experiments with ambiguous motion stimuli revealed preferences to see motion in cardinal directions independently of orientation anisotropies, since the effect was present over the whole range of gratings' orientations, including when there were no cardinally oriented contours.

Evidence for a motion-specific oblique effect (independent of an orientation oblique effect) was scarce until now, since cardinal contours were also present in most previous studies that reported a preference for cardinal motion in ambiguous stimuli (e.g., Shapley & Rubin, 1996; Castet & Zanker, 1999; either the orientation of the moving stimuli was cardinal or the contours of the aperture behind which they moved had cardinal orientations). For example, Andrews and Schluppeck (2000) reported a strong preference to see motion along cardinal directions for their ambiguous stimuli composed of three drifting gratings which orientations were 60° apart (one cardinal and two oblique orientations). Their observers perceived most of the time the cardinal grating to move independently and the two oblique gratings to cohere and move as a pattern (plaid) in the opposite (cardinal) direction. The alternative percepts, with motion along the two oblique axes, were almost never reported. Andrews and Schluppeck (2000) interpreted their result to mean that the (orientation) oblique effect could be responsible for a preference to see cardinal contours, whether they were stationary or moving, and was therefore sufficient to explain the observed motion anisotropy. Our results indicate, however, that the oblique plaid effect is sufficient to explain the anisotropies described by Andrews and Schluppeck (2000), and therefore there is no need to invoke the preference to see cardinal contours.

To our knowledge, only one example of a preference for cardinal motion independent of orientation was reported so far, by Wallach (1935, 1996, p. 1332), using ambiguous displays. Wallach showed it by having a single oblique line moving behind a triangle aperture. In most of the cases, the perceived direction depended on the edges (the line was perceived to move in the direction midway between the aperture edges, or between its terminators' trajectories). However, for some configurations of orientation of the line and of the triangle, the motion was perceived as horizontal or vertical, away from both the direction orthogonal to the line orientation and the direction of the bisector.

Where might motion direction anisotropies come from? In the orientation domain, it was proposed that the oblique effect is related to the predominance of cardinal contours in the visual environment (Annis & Frost, 1973), suggesting that the visual system "matches" the environment. It is not obvious whether cardinal motion is more present than oblique motion in the world. However, it seems likely that our perceptual world be dominated by cardinal motion, due to the predominance of eye movements in cardinal directions (especially horizontal directions in reading).

4.3. The oblique plaid effect and models of plaid perception

Existing models of plaid perception (or, more generally, of motion integration/segmentation) take into account only the *difference* of directions of the gratings relative to each other (alpha; e.g., Kim & Wilson, 1993), while the absolute direction of the plaid (or, equivalently, of its constituent gratings) does not play a role in the computation. The oblique plaid effect indicates that this needs revision, since absolute directions of motion have an effect on whether motion signals of differing directions are integrated into a single "global" motion signal (plaid) or segmented to different surfaces (transparent gratings).

Most models of plaid perception assume a two-stage process (e.g., Adelson & Movshon, 1982; Movshon et al., 1985; Wilson, Ferrera, & Yo, 1992; Wilson & Kim, 1994). The first stage is responsible for recovering of the motion of the gratings (one-dimensional, local motion cues), the second stage combines the output of the first stage to extract the global direction. Since we showed that the oblique plaid effect depends only on the global direction of motion, not on the grating orientations, this suggests that in two-stage models the anisotropies should arise at the second stage, independently of the input from the first stage (see Heeley & Buchanan-Smith, 1992, for a similar interpretation). While this is certainly possible, it is not obvious or intuitive how or why such anisotropies should emerge only at the second stage. In contrast, models which extract the global direction of motion from the stimulus at a first stage, such as in feature based models (e.g., Alais, van der Smagt, Verstraten, & van de Grind, 1996), or in models which incorporate a "second-order" pathway (Wilson et al., 1992; Wilson & Kim, 1994), are more straightforward to modify such that they would exhibit preference for cardinally moving plaids as we found experimentally. A model with broad-band orientation mechanisms involved in the perception of coherency (Scott-Samuel & Hess, 2002) should also be able to account for the oblique plaid effect with minor adjustments (e.g., these mechanisms should be even broader-band for cardinal directions).

Recently, we proposed a different approach to understand the perception of plaids, which parallels well-accepted views of the mechanisms underlying other bi-stable phenomena (primarily binocular rivalry). According to this view, the decision between integration (coherency) and segmentation (transparency) is not done in a "feedforward" way, but rather the neural representations of the 'coherent' and 'transparent' interpretations of the stimulus continually compete for dominance, e.g., via mutually inhibitory connections (Hupé & Rubin, 2001, 2002, 2003; Rubin & Hupé, 2002). In such a neurally-based model motion anisotropies would follow naturally from biases in the distribution of direction selective neurons. We therefore summarize below what is known from physiological studies about such biases.

4.4. Neurophysiology and the oblique plaid effect

Area MT is the natural candidate area to look for a neural basis of the oblique plaid effect, since part of the neurons in monkey's MT code the global direction of the plaid (Movshon et al., 1985; Pack, Berezovskii, & Born, 2001; Rodman & Albright, 1989; Stoner & Albright, 1992). Pattern responses have also been found in monkey area V3 (Gegenfurtner, Kiper, & Levitt, 1997), but fMRI signals show the strongest selectivity for pattern motion in human MT (Huk & Heeger, 2002). Where the transparent percept is coded is more questionable, but MT might also be involved (Castelo-Branco et al., 2002), since another population of MT neurons code the component directions independently of the plaid global direction of motion (Movshon et al., 1985; Rodman & Albright, 1989; Stoner & Albright, 1992), and the responses of MT neurons are well correlated with the perception of moving surfaces (e.g., Newsome, Britten, & Movshon, 1989). In the neurally based model we proposed in the previous section, the populations of neurons coding the transparent and the coherent percepts are in continual competition. The oblique plaid effect means that there is an advantage to the population of neurons coding the coherent percept for cardinal directions. This advantage could be obtained by having a higher proportion of MT neurons (and more specifically "pattern" neurons) coding the cardinal directions.

Such bias was not reported so far in published studies (Albright, Desimone, & Gross, 1984; Churchland, Gardner, Chou, Priebe, & Lisberger, 2003; Maunsell & van Essen, 1983). However, the neurons were not selected in a systematic way, leading to potential sampling bias problems. Such sampling issues were well illustrated by the search for orientation anisotropies in V1: when Finlay et al. (1976) looked at the distribution of orientation preferences of a huge sample of hundreds of neurons recorded in monkey V1 over many experiments, they did not find any orientational bias. Mansfield (1974), on the other hand, addressed the question of orientation anisotropies systematically, by recording only one neuron per penetration, and mapping a large extent of V1 with one penetration every 500 microns. He found a much larger number of neurons coding the cardinal orientations. The stronger neuronal signals for cardinal orientations were confirmed by intracortical VEPs in monkey V1 (Mansfield & Ronner, 1978) and by optical imaging in the ferret (Chapman & Bonhoeffer, 1998; Coppola, White, Fitzpatrick, & Purves, 1998; Muller et al., 2000; but not in the cat, Muller et al., 2000). An fMRI study also measured stronger signals in human V1 for cardinal orientations (Furmanski & Engel, 2000). Transferring what was learned from the quest for orientation anisotropies in V1, this means that a systematic mapping of the direction selectivities of MT neurons might still reveal direction anisotropies. fMRI of MT might also reveal stronger signals for plaids moving in cardinal directions (Schluppeck & Engel, 2003; these authors showed preliminary evidence that the MT+ region was more activated for plaids moving in vertical directions compared to plaids moving in oblique directions). Alternatively, the lack of evidence for directional anisotropies found so far in MT might indicate that area MT does not play such a determinant role in plaid perception.

4.5. A few words about the phenomenology of plaids

When two superimposed gratings are perceived as sliding over each other, an implicit assumption in the literature seems to be that each grating is perceived to move in the direction orthogonal to its orientation, as if each grating was presented alone (e.g., Adelson & Movshon, 1982; Stoner et al., 1990). However, phenomenological observations indicate that this was not always the case: for example, when the pattern direction of motion is upwards, the two gratings are sometimes perceived to move to the right and the left, i.e., along opponent cardinal directions, not along the oblique directions perpendicular to their orientation. (Not all observers experienced this percept, when asked about it after an experiment, but many did, including naive and inexperienced observers. The reader may refer to the demo on the web page to see whether s/he experiences this kind of opponent motion of the gratings during transparency.) Interestingly—and this relates to the oblique plaid effect—the opponent gratings motion occurs preferentially for cardinal directions of motions: for plaids moving in oblique directions, the gratings are typically perceived as moving orthogonally to their orientation (when the transparent percept is experienced). This oblique effect for motion opponency is probably a consequence of the oblique plaid effect (and not a cause), since the oblique plaid effect was present for all observers whereas not all observers experienced motion opponency. Nevertheless, it may be important to take these phenomenological observations into account (and to further document and quantify them) in theories that attempt to provide explanations of the mechanisms leading to motion segmentation and integration in plaid stimuli.

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