Directional shifts in the barber pole illusion: Effects of spatial frequency, spatial adaptation and lateral masking

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Abstract

We report the results of psychophysical experiments with the so-called barber pole stimulus providing new insights on the neuronal processes underlying the analysis of moving features such as terminators or line-endings. In experiment 1, we show that the perceived direction of a barber pole stimulus, induced by line-ending motion, is highly dependent on the spatial frequency and contrast of the grating stimulus: perceived direction is shifted away from the barber pole illusion at high spatial frequency in a contrast dependent way, suggesting that line-ends are not processed at high spatial scales. In subsequent experiments, we use a contrast adaptation paradigm and a masking paradigm in an attempt to assess the spatial structure and location of the receptive fields that process line-endings. We show that the adapting stimulus that weakens most the barber pole illusion is localized within the barber pole stimulus and not at line-endings' locations. Current models of line-endings' motion processing are discussed in the light of these psychophysical results.

Keywords: Motion integration, Neuronal adaptation, Lateral masking, Surround suppression

Introduction

The "aperture problem" (Fennema & Thompson, 1979; Marr & Hildreth, 1980) refers to the impossibility of accurately determining the direction of motion of a straight contour with "motion sensors" whose spatial extent is smaller than the contour itself. Because orientation and direction selective neurons in visual cortex have such limited spatial extent, and thus face the "aperture problem," a large number of studies have been conducted to understand how the visual system overcomes this problem. Among them, many have built on the perception of motion elicited by a grating drifting behind an aperture, also referred to as the "barber pole" stimulus in the literature (Wallach, 1935; Wuerger et al., 1996). Wallach (1935) noticed that the perceived direction of a grating drifting behind a rectangular aperture was always in the direction of the longer side of the aperture, whatever the orientation and direction of the grating itself. His observations led him to suggest that the number of line-endings at aperture borders, larger for the longer aperture side, determined the perceived direction. Although this insight has been confirmed by a number of authors (e.g., Nakayama & Silverman, 1988; Castet et al., 1999; Fisher & Zanker, 2001), the mechanisms by which the motion of line-endings is extracted and used to yield the direction of motion seen in the barber pole illusion remains a matter of debate.

When examining the studies concerned with the processing of line-endings or terminators, two main streams of research emerge. One states that processing line-endings can be accommodated by the responses of simple and complex cells found in primary visual cortex (e.g., DeValois et al., 1982), often modeled as a population of localized linear spatial frequency filters, with no need for specific units selectively processing these features (Majaj et al., 2002). In this view, processing line-endings' direction would not differ from processing any other motion characteristics, and would result from an integration process pooling all responses of a population of motion energy filters at a second stage (e.g., area MT; Adelson & Movshon, 1982; Movshon et al., 1986). A second approach suggests that line-ends are processed by a subpopulation of specialized units, able to determine and constrain global object direction (Nakayama & Silverman, 1988; Shimojo et al., 1989; Lorenceau et al., 1993). Within this latter scheme, several models concerned with the nature of the computation realized by these units have been proposed. Some models consider that some non-linearity, such as the surround suppression expressed by many V1 neurons (Hubel & Wiesel, 1965; Gilbert, 1977; Sillito & Versiani, 1977; Orban, 1991), is relevant to the processing of line-endings' motion. The question is then to design computational models that provide biologically plausible accounts of surround suppression, also referred to as end-stopping[1] (Dobbins et al., 1987; Heitger et al., 1992; Skottun, 1998; Líden & Pack, 1999; Sceniak et al.,

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[1]Hubel & Wiesel (1965) first suggested that end-stopping was a functional property of a specific subclass of V1 neurons, which they called hypercomplex cells. It has been since found that end-stopping was not a property limited to a specific cell type but a very general property of neurons in V1 that exhibit end- or side-inhibition (DeAngelis et al., 1994), and is now referred to as surround suppression. In the following, the terms end-stopping or end-stopped cells will be used to refer to the general mechanism of surround suppression.

1999). Others have designed alternative models aiming at modeling direction selectivity for moving line-ends without reference to end-stopping (Zetsche & Barth, 1990; Löffler & Orbach, 1999; Geisler, 1999).

A second aspect of the debate concerns the spatial scale and the spatial localization of units involved in processing terminators' motion. When considered as geometrical features, line-endings are well localized in visual space and correspond to fine details of a visual scene (e.g., high spatial frequencies). It has consequently been suggested that line-endings must be processed by cells tuned to these high spatial frequencies, which often have small receptive fields—although the size of a receptive field of a neuron and its spatial frequency tuning are independent parameters. However, the Fourier spectrum of line-endings is widespread and contains a broad range of spatial frequency components at different contrasts and orientations such that a large number of units responding at varying degrees to these components are recruited.

The idea that line-endings are more specifically processed by units with small receptive fields tuned to high spatial frequencies is supported by Kooi's experiment (1993) who used barber pole stimuli with indented apertures of varying size, such that the line-endings no longer moved along the longer side of the aperture but in the direction of the drifting grating (also see Power & Moulden, 1992). With this stimulus, Kooi (1993) was able to show that the barber pole illusion was abolished when the indentations were four times smaller than the spatial period of the drifting grating. However, the highest spatial frequency tested in this study was 2.6 cycles per degree.

In the following we present the results of several experiments aiming at characterizing more precisely the processes underlying the analysis of line-endings' motion.

Materials and methods

Experiment 1

Experiment 1 builds upon Kooi's results (1993) and tests the barber pole illusion using straight aperture borders and varying spatial frequencies up to 16 cycles per degree (cpd hereafter). The rationale for this experiment is as follows: if line-endings are processed by units selective to four times the spatial frequency of the nominal grating, as suggested by Kooi's results, the spatial frequency at which line-endings are presumably processed should fall out of the "window of visibility" (Watson, 1983) for high grating frequencies. As a consequence, the barber pole illusion should be abolished or reduced in these conditions. For instance, the line-endings of a 16-cpd drifting grating should be processed by units tuned to 64 cpd (4×16), well above the spatial frequency that can be resolved by the human visual system; line-endings should consequently not be analyzed, and therefore would not contribute to the perceived direction of the barber pole stimulus, which should in turn appear to drift orthogonally to the grating's orientation. In addition, the effect of spatial frequency should depend on the contrast of the nominal grating, given the rapid fall-off of the human contrast sensitivity with increasing spatial frequency (Campbell & Robson, 1968). This should allow determining a contrast dependent cut-off spatial frequency at which the barber pole illusion is abolished. Note that such a test overcomes a limitation of Kooi's experiment, due to the fact that varying the size of the indentations is correlated to the distance traveled by the line-endings along the indentations. Thus, for small indentations, it

is possible that integration along the direction of motion cannot be completed, yielding unreliable motion signals.

A Sony GDM 1950 (refresh rate 60 Hz, resolution $1280 \times 1024 \times 8$ bits/pixel) driven by custom software is used for visual presentation. Stimuli, viewed at a distance of 92 cm, are composed of a sinusoidal 135° oriented grating drifting behind a horizontal parallelepipedic aperture (16×3.3 degrees of visual angle, dva hereafter) such that all line-endings move along the horizontal so as to maximize the illusion. This stimulus, lacking line-endings moving along the shorter side of the aperture (see Fig. 1a), contrasts with the stimuli used in other studies in which a conflict between line-endings moving in different direction may entail an unstable perception of motion (Castet et al., 1999). A red cross is displayed throughout the experiment at the center of the display to help in maintaining fixation.

A trial consists in 2 seconds of rightward motion with a grating spatial frequency chosen at random among 8 possible values (2, 4, 6, 8, 10, 12, 14 and 16 cpd). At the end of motion, the stimulus is replaced by a red arrow anchored at one end on the fixation point and controlled by the computer mouse that observers use to set their perceived direction of motion for that trial. In Experiment 1a, spatial frequency is varied in the range 2–16 cpd, whereas speed (1 dva/s) and Michelson contrast (90%, mean luminance 20 cd/m^2) are kept constant. Experiment 1b is similar except that several contrast levels (5%, 10%, 20%, and 90%) and only 7 spatial frequencies are tested (2–14 cpd). A session consisted of 80 trials in Experiment 1a and 280 trials in Experiment 1b (10 for each spatial frequency and contrast).

Results

The results of Experiment 1a, shown in Fig. 1b, are expressed as the individual and averaged ($n = 5$) perceived directions of motion relative to horizontal ("illusory" direction of the barber pole, noted 0°) as a function of spatial frequency[2]. As it can be seen, spatial frequency has a strong influence on the perceived direction of motion. At grating spatial frequencies below 8 cpd, mean perceived direction of motion is close to horizontal (5.2°), corresponding to line-endings' motion (i.e., the barber pole illusion). As spatial frequency increases above this value, a shift toward perceiving oblique motion builds up (maximum 32°). An ANOVA conducted on this factorial design indicates a significant main effect of spatial frequency ($F(7,28) = 12.26$, $P < 0.001$). Contrasting the 4 low and 4 high spatial frequencies reveals a significant difference in perceived direction ($F(1,4) = 28.27$, $P < 0.01$), whereas paired-differences between the 4 lowest spatial frequencies on the one hand and the 4 highest spatial frequencies on the other are not significant (Post-hoc analysis, Tukey HSD tests), indicating that perceived directions are not significantly different for spatial frequencies above 8 cpd and below 8 cpd . Thus, at a high contrast (90%), a spatial frequency of 8 cpd appears to be the "upper limit" leading to a "switch" in perceived direction.

Repeating this experiment with varying contrasts (5%, 10%, 20%, and 90%, Experiment 1b, $n = 4$) reveals that this limit

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[2]Previous studies using a barber pole stimulus have reported bi-or tri-modal distributions of perceived directions (Castet et al., 1999). We did not observe such multi-modal distributions with the present version of the stimulus in which a single line-endings' direction is present (see Methods). In addition, the duration of motion used herein (2 s) is too short to observe multi-stable percepts (see Hupé & Rubin, 2003). The observation of a uni-modal distribution justifies that an average across motion directions is used as the mean response.

(a)

(b)

(c)
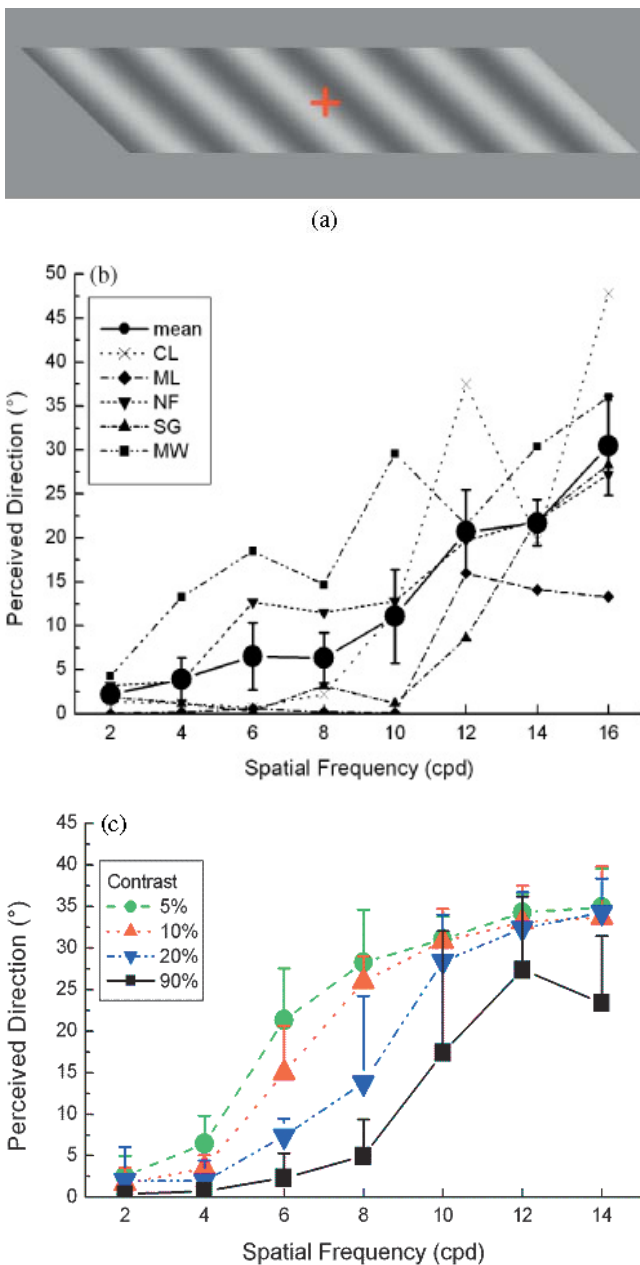
Fig. 1. (a) Barber pole stimulus used in the experiments. A tilted drifting grating is presented behind a parallelepipedic aperture, such that no line-ends move along the shorter sides of the aperture. As all line-ends move along the longest aperture border, this version of the barber pole avoids the issue of a conflict between discrepant direction of line-endings, so as to maximize and stabilize the perception of horizontal motion. (b) Results of Experiment 1a: Directional shifts towards oblique motion (individual responses and mean ± 1 SE), plotted as a function of spatial frequency. (c) Results of Experiment 1b: Directional biases (mean ± 1 SE), plotted as a function of spatial frequency and contrast.

depends upon contrast as shown in Fig. 1c. Decreasing grating's contrast entails oblique biases for progressively lower spatial frequencies, as indicated by a significant interaction between contrast and spatial frequency ($F_{(12, 18)} = 2.93$, $P < 0.01$). Furthermore, the slope of the direction/spatial frequency curves decreases with decreasing contrast: with a contrast of 90%, there is a gradual increase in oblique biases up to a spatial frequency of

12 cpd. A plateau ($\sim 35°$) is also reached at about 10–12 cpd for the three lower contrasts. It is worth noting that the oblique bias at the highest spatial frequency and lowest contrast is $<45°$, the angle to be expected if the barber pole illusion was fully abolished. It must also be noted that keeping the same grating's speed while changing the spatial frequency modifies the drifting temporal frequency. In an additional control experiment, we repeated the same protocol with 3 observers and a subset of conditions with varying drift speeds. Three speeds (2°, 4°, and 6°/s.) combined with 5 spatial frequencies (4, 6, 8, 10, and 12 cpd), were used. Under these conditions (data not shown), the directional biases are small at 4 cpd and increase with increasing spatial frequency, as in the main experiment. These biases are similar at all speeds for a 4-cpd grating and tend to increase with increasing speeds at higher spatial frequencies. Although the effect of spatial frequency is significant ($F_{(4, 8)} = 4.56$, $P < 0.05$), the effect of speed ($F_{(2, 4)} = 0.98$, $P = 0.44$) and the interaction between speed and spatial frequency ($F_{(8, 16)} = 0.55$, $P = 0.80$) are not, suggesting that the factor relevant to account for the directional shifts is the spatial frequency *per se*.

Although these results seem to reveal a strong effect of spatial frequency and contrast on the barber pole illusion which, to our knowledge, has not been documented before (but see Vezzani & Bressan, 1999), potential confounds must be discussed before a conclusion can be drawn. This includes changes in perceived speed with varying contrasts (e.g., Stone & Thompson, 1992) and spatial frequencies (Smith & Edgar, 1990), decreased grating's visibility in eccentric vision at low contrast and high spatial frequency, or residual eye movements.

It seems unlikely that the influence of contrast on perceived speed can account for the data for the following reason: the effect of contrast on perceived speed is found for a range of spatial frequencies, including the lowest spatial frequency used herein (2 cpd). If changes in perceived speed with varying contrasts were to account for the data, one would expect directional shifts for all the spatial frequencies tested. The lack of directional shifts for a 2 cpd grating—at all contrasts tested—argues against this hypothesis and suggests that changes in perceived speed are not the cause of the observed effects. If changes in perceived speed with contrast do not account for the directional shifts, it seems unlikely that changes in perceived speed with varying spatial frequencies do. However, changes in spatial frequency and contrast also modify stimulus visibility at eccentric locations (Kelly, 1979). As the stimulus extends 8° left and right from fixation, the visible part of the stimulus should shrink with increasing spatial frequency and decreasing contrast, such that only the central part of the stimulus would be available to perform a directional judgment. Thus, the observed directional shifts may have resulted from a difficulty to resolve high spatial frequencies in eccentric vision. Although directional shifts are observed at high contrast and moderate to high spatial frequencies, where the stimulus remains fully visible at 8° eccentricity, one cannot exclude that decreased visibility at lower contrasts enhanced the observed directional shifts. Informal testing with smaller stimuli presented in central vision suggests that this effect does not by itself account for the pattern of results observed herein. Finally, despite the fact that observers were asked to fixate the center of the stimulus, residual pursuit eye movements may have had an influence on directional judgments. It is however unclear how and why eye movements would depend on spatial frequency and contrast in order to account for the observed results. It is known that pursuit marginally depends on target contrast (Haegerstrom-Portnoy & Brown, 1979). In addition, the numerous

observations that pursuit is driven by perceived motion (e.g., Stone & Krauzlis, 2003) suggest that, at most, residual pursuit eye movements may have enhanced perceived directional shifts rather than caused them.

Alternately, the effect of spatial frequency and contrast can be accounted for by Kooi's hypothesis (1993) that line-endings are processed by units tuned to 4 times the spatial frequency of the grating and thus fall out of the "visibility window" at high spatial frequency and/or low contrast. However, other interpretations should also be considered. For instance, the Fourier decomposition of the barber pole stimulus indicates that line-endings are characterized by harmonics with different orientations and lower contrasts than the fundamental, such that these harmonics may not be resolved by the visual system when the fundamental has a high spatial frequency and/or a low contrast. Integrating the motion of the harmonics at latter stage (e.g., area MT) in order to determine the overall direction of motion may thus predict the observed pattern of data (Majaj et al., 2002). Finally, these results are also compatible with the view that line-endings' motion is processed by specific units (e.g., end-stopped cells) provided that they have lower contrast sensitivity than units processing the inner part of the grating, a view supported by electrophysiological data (Orban, 1991; Sceniack et al., 1999). An alternative explanation would be that end-stopped cells tuned to high spatial frequencies are either lacking or less numerous, and are unable to fully constrain the global direction.

However, the observation that the directional bias toward perceiving oblique motion does not reach the critical value of 45° (i.e., full orthogonal motion) cannot be used to disentangle these different possibilities. One way to address this question would be to characterize the spatial extent and location of the units underlying line-endings' processing. One paradigm well suited for this purpose is contrast adaptation, in which a selective decrease in contrast sensitivity, correlated to a decrease in neuronal activity (Barlow & Hill, 1963), follows a prolonged inspection of a high contrast pattern. Both Kooi's model and that based on Fourier decomposition suggest that line-ends are processed by units with small receptive fields located at line-endings' position. Selective adaptation at these specific locations should thus entail large directional shifts, because the contribution of these units to the integration process would be lowered after adaptation. In contrast, models based on end-stopping may not suffer much from localized adaptation, as the receptive field structure and spatial extent of such units would not be restricted to line-ends' locations[3]. In an attempt to uncover characteristics of units processing line-ends, and to possibly disentangle the different models described in the Introduction, experiments were designed to examine the effect of adaptation to a variety of "adapters" whose locations and sizes are systematically varied.

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[3]The classical view of the spatial structure of end-stopped cells comprises at least two zones: one corresponds to an excitatory region similar to that of non end-stopped cells—e.g. showing comparable size, orientation and spatial frequency selectivity; the second one is suppressive—side- or end-suppression (whether this zone corresponds to an inhibitory influence is still a matter of debate, see DeAngelis et al., 1994; Skottun, 1998; Sceniak et al., 2001 for discussion)—and possesses similar, although broader, tuning characteristics as their facilitatory counterpart (Sillito & Versiani, 1977; Orban et al., 1979; Orban, 1991). This phenomenological description of end-stopping may correspond to a variety of neuronal circuits. A possibility is that end-stopping results from an inhibitory influence of a cell with an extended receptive field that encompass that of a second excitatory cell (the "Difference of Gaussian" (DOG) model proposed by Sceniak et al., 1999, but see also Dobbins et al., 1987).
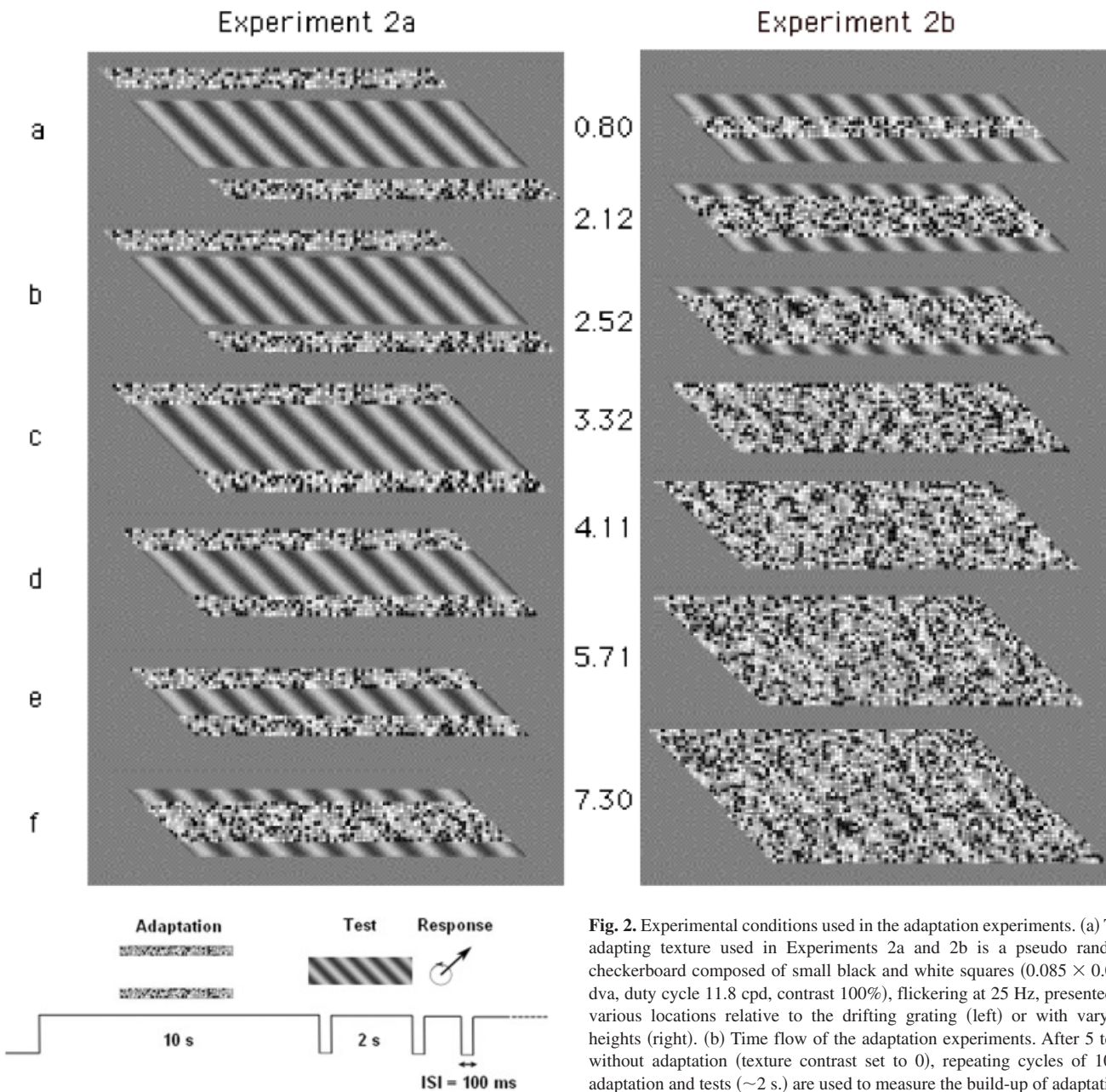
Experiment 2

In this section we describe the results of experiments using a contrast adaptation paradigm with a variety of stimuli, varying in their extent, location, and spatial structure. In Experiment 2a and 2b, a pseudo-random rectangular checkerboard of small black and white squares with varying height and location is used (Fig. 2a). An oriented grating is used in Experiment 2c (see later). In both experiments a "top-up" adaptation procedure, in which an initial 10 s of adaptation is followed by cycles of directional testing (~2 s) and re-adaptation (10 s), is used to determine the build-up and amplitude of adaptation over time. We hypothesized that adaptation may modify the sensitivity of units presumably processing line-endings and thereby induce a departure from the direction perceived in the barber pole (i.e., horizontal motion). Larger perceived directional shifts are expected if the adapting stimulus is more efficient in lowering the efficacy of line-endings' processing and therefore its contribution to global motion computation.

Materials and methods

The barber pole stimulus is similar to that of Experiment 1 except that the spatial frequency (2 cpd), temporal frequency (3.3 Hz) and contrast (90%) are kept the same throughout the experiments. In addition, an initial 10 s period of adaptation to a rectangular black-white checkerboard composed of small white and black squares (0.085 × 0.085 dva; duty cycle 11.8 cpd; contrast 100%) randomly arranged on a grey background of the same luminance as the screen (20 cd/m^2) flickering at 25 Hz, is followed by repetitive cycles of directional tests and adaptation periods (Fig. 2b). Without *a priori* knowledge of the spatio-temporal characteristics of the motion sensitive units that possibly process line-endings, a counterphase flickering stimulus whose spectrum covers a broad range of spatial and temporal frequencies ensures that all types of motion sensitive units may be adapted. These textured patterns are presented at varying positions with respect to the long edges of the test grating shown subsequently (Exp. 2a), or with varying heights (Exp. 2b). Experiment 2a aims at determining the spatial position of the textured patterns that maximizes an oblique directional shift while Experiment 2b aims at optimizing the size of the textured pattern that produces the larger directional shift. In Experiment 2a, two adapting textures (16 × 0.5 dva) are presented at 6 symmetric positions varying with respect to the edges of the grating: The adapting stimulus is either located 1 or 0.5 dva above and below the edges (conditions a and b), abuts on the external grating's edges (condition c), centered on the edges (condition d), abuts on the internal edges (condition e), or covers the inner part of the grating (condition f, see Fig. 2a, left). In this latter condition, the texture pattern is the union of the two patterns used in the other conditions. During each test episode, observers use the computer's mouse to indicate the perceived direction of motion by adjusting a rotating arrow, whose one end is anchored at the center of the screen. Angular responses are recorded and analyzed off-line.

Results

The directional biases build up rapidly with repeating test-adaptation cycles, as shown in the two examples of Fig. 3a. To analyze the data, the last 15 estimated perceived directions were averaged. The resulting data of 3 observers are shown for the six adapting conditions in Fig. 3b. Although large inter-individual

Experiment 2a

Experiment 2b

Fig. 2. Experimental conditions used in the adaptation experiments. (a) The adapting texture used in Experiments 2a and 2b is a pseudo random checkerboard composed of small black and white squares (0.085 × 0.085 dva, duty cycle 11.8 cpd, contrast 100%), flickering at 25 Hz, presented at various locations relative to the drifting grating (left) or with varying heights (right). (b) Time flow of the adaptation experiments. After 5 tests without adaptation (texture contrast set to 0), repeating cycles of 10 s. adaptation and tests (~2 s.) are used to measure the build-up of adaptation.

differences exist, the average deviations from the barber pole illusion strongly depend on the location of the adapting stimulus (Friedman ANOVA, $\chi^2(5) = 12.57$, $P < 0.05$). The effect of adaptation on perceived direction is weak or absent ($<5°$) for conditions a, b, and c (adapting stimulus above or aligned with the grating's edges); it smoothly increases as the adapting stimulus encroaches the grating's edges (conditions d and e) and reaches a maximum (16.3°) when the adapting stimulus is centered in the middle of the grating (condition f).

Because these data indicate that the effect of adaptation is larger when the textured adapting pattern is located at the grating's center as compared to other locations, we sought to determine more precisely the pattern's height that would maximize this effect. In Experiment 2b, the same checkerboard located in the grating center was used, but its height was varied from 0.8–7.3 dva

in 8 steps (see Fig. 2a, right). Because the grating height is 3.3 dva, the textured pattern could thus encompass the whole grating. The first four conditions correspond to an adapting stimulus smaller than the test, whereas the latter four correspond to an adapting stimulus gradually larger than it.

A statistical analysis of the data indicates that directional biases are significantly dependent on the height of the adapting stimulus ($F(8,16) = 4.50$, $P < 0.01$). These biases, plotted as a function of the height of the adapting texture in Fig. 3c, are distributed along an inverted U-shape curve: The averaged perceived direction increasingly deviates from horizontal with increasing adapting heights up to a maximum ($\sim20°$) for a height of 2.52 dva, which is followed by a plateau up to 4.12 dva, and then decreases gradually with larger heights, although a directional bias of 8.4° is still observed for a height of 7.3 dva.
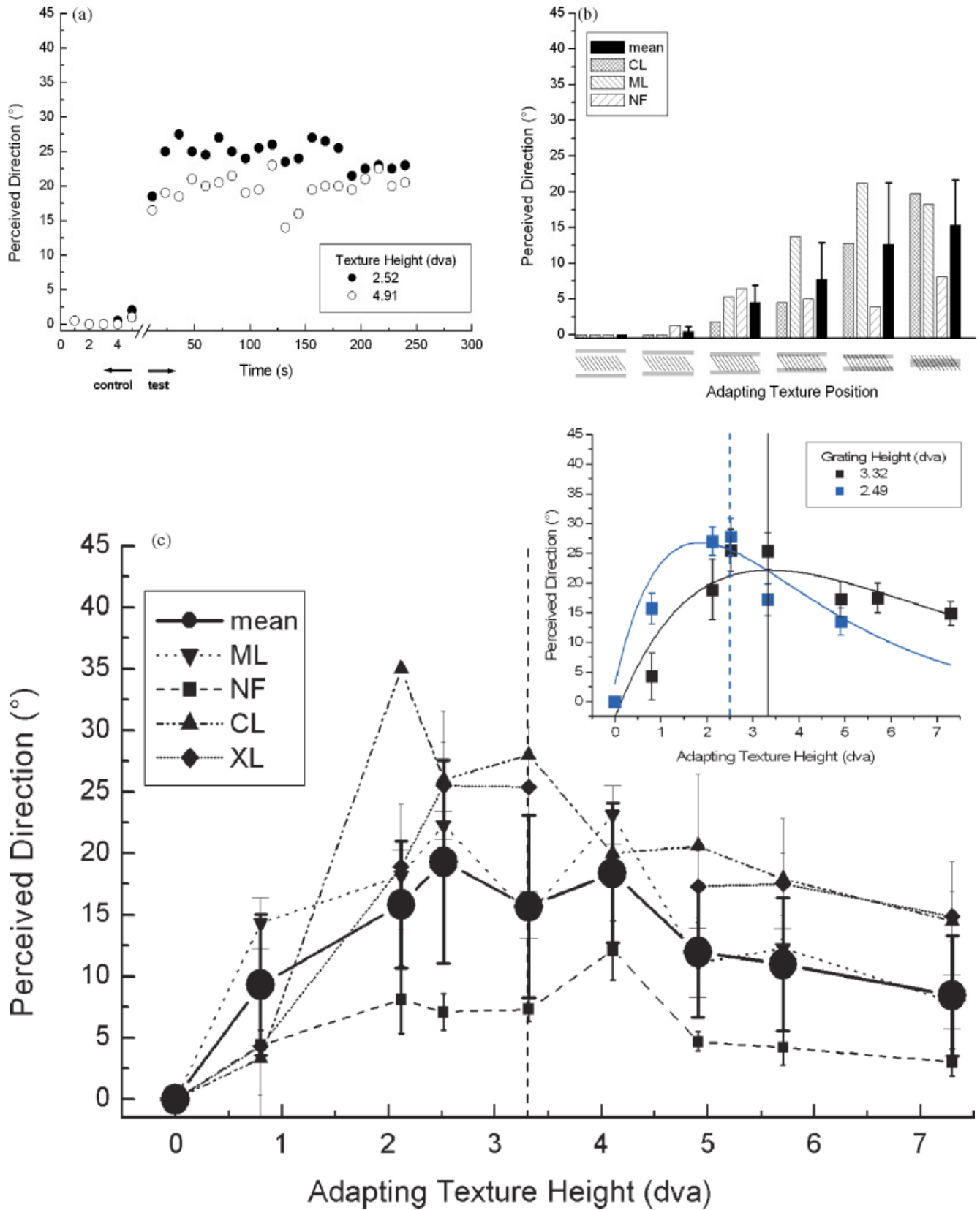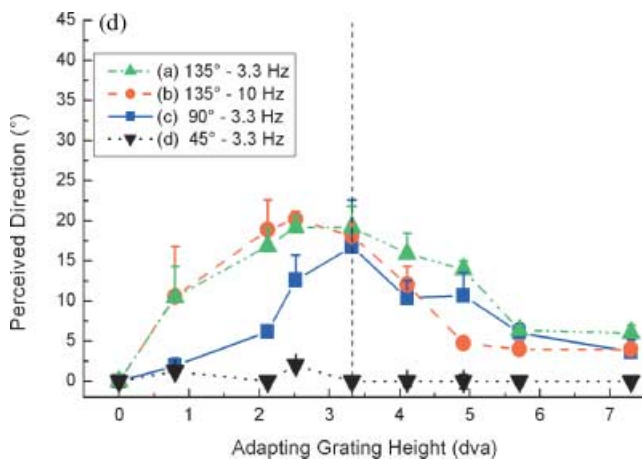
Fig. 3. *Continued on next page.*

Fig. 3. (a) Examples of the build-up of directional shifts with 2 adapter's height for one subject (filled symbols, 2.5 dva; open symbols, 4.9 dva). Directional shifts are plotted as a function of the number of adapting cycles. Five tests without adaptation are followed by repeating cycles of adaptation and tests. The last 15 measures are averaged and used in subsequent analyzes. (b) Results of Experiment 2a: Directional shifts (individual responses and mean $\pm$ 1 SD) for six conditions corresponding to different locations of the texture patterns relative to the grating. From left to right: adapters located 0.5 and 1 dva above and below the grating (conditions a and b in Fig. 2a, left); adapters abutting on the outer grating borders (condition c); adapters covering the grating's borders (condition d); adapters abutting on the inner grating's borders (condition e); adapters at the grating's center (condition f, the adapter is the union of the two texture patterns used in other conditions). Directional shifts following adaptation are maximized when adapters are located at the grating's center. (c) Results of Experiment 2b: Directional shifts (individual responses and mean $\pm$ 1 SE) for eight conditions corresponding to different heights of the texture pattern located at the grating's center. The vertical dashed line represents the test grating's height. (Inset) Similar to previous conditions, except that two grating's heights are used. Smooth curves are quasi-Newton fits to the data. Directional shifts are larger for adapters slightly thinner than the test grating. Vertical solid and dashed lines indicate the two grating's heights (3.3 and 2.5 dva, respectively). (d) Results of Experiment 2c: Effects of adaptation with drifting gratings (2 cpd) at varying orientations (45°, 90°, and 135°) and temporal frequencies (3.3 and 10 Hz) on the perceived direction of the test grating (135°, 3.3 Hz). The observed directional shifts (mean $\pm$ 1 SE) are plotted as a function of the adapter's height (from 0.8–7.3 dva).

To ensure that the duty cycle of the texture pattern, which determines the spectrum's fundamental spatial frequency, was not too high to significantly adapt the neuronal responses, the same experiment has been replicated for a subset of conditions with a checkerboard made of larger black & white squares (0.425 × 0.425 dva, duty cycle 2.4 cpd). This did not change the main effect of adaptation: the directional biases remain small with checkerboards located near line-ends but are large when they are located at the grating's center (data not shown).

In a last experiment (2c), a sinusoidal grating (2 cpd) of varying orientation, height, and temporal frequency is used in place of the checkerboard pattern. In this way, we sought to control for the direction, orientation, and speed selectivity of adaptation. The grating's heights used as adapters varied from 0.8–7.3 dva. For each height, four adaptation conditions are tested: adapter with the same orientation (135°) as the test grating drifting at two temporal frequencies (3.3 & 10 Hz, conditions a and b), vertical (90°), or

orthogonal gratings (45°) drifting at 3.3 Hz (conditions c and d). The results displayed in Fig. 3d show (i) no directional biases for an ortho-oriented grating drifting at 3.3 Hz, (ii) intermediate biases for a vertical grating, with a peak for a height identical to that of the test stimulus, and (iii) large directional biases for an adapting grating with the same orientation as the test, independent of the temporal frequency of the adapter. As expected, these results indicate that the effect of adaptation is larger when the adapting stimulus shares the same spatial characteristics as the test. In this experiment, the directional biases are similar to those observed in the previous experiment (conditions a and b), and always smaller than the value of 45°, expected if the barber pole illusion was fully abolished.

Interestingly, and as found in experiments 2a and 2b, the peak of the effect (i.e., the maximum directional bias) is slightly offset towards an adapting height smaller than that of the test grating. To verify the generality of this finding, we have replicated Experiment 2b with a thinner grating test (2.5 dva), and found that the directional biases followed the same band-pass function but with a maximum now peaking near the grating's height (Fig. 3c, inset). The data were fitted with double exponential functions[4] (R^2 = 0.86 and 0.92 for the large and thin grating, respectively). As can be seen, the maximum of the fitted functions are close to the width of the corresponding test grating, although slightly offset toward smaller values.

Experiment 3

In the previous experiment, the adapting pattern and test grating were temporally offset. Although the build-up of the observed directional biases over time suggest that they result from the adaptation of units recruited by the stimulus, one cannot exclude that the response to the transient stimulus offset also has an effect on perceived direction. One way to avoid this potential confound is to investigate whether the simultaneous presentation of "flankers" together with the test grating produce similar effects. Another limitation of the previous experiment is related to the use of a high contrast checkerboard pattern, which has a broad spatio-temporal spectrum and thus may adapt a large population of units. In the following experiment, we measure the perceived direction of the barber pole stimulus in the presence of spatial frequency "flanking" gratings at different spatial frequencies and contrasts. This design, similar to that used by Líden & Mingolla (1998), extends their approach by using gratings as "flankers" and by varying the distance and contrast between the "flankers" and the test grating.

Materials and methods

Static flanking gratings (16 × 1.2 dva) with different contrast (5%, 10%, 20%, and 90%) were located at varying distances of the grating's line-endings (0, 0.16, 0.33, and 0.5 dva). Flankers at two spatial frequencies were used in different sessions: one with the same spatial frequency as the test (2 cpd), and one at 4 times the test spatial frequency (8 cpd), in keeping with Kooi's results (see Experiment 1). In this experiment, observers ($n = 4$) judged the

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[4]Curve fitting was performed using a quasi-Newton least-squares minimization regression method (Davidon-Fletcher-Powell algorithm, Fletcher & Powell, 1963). Although any single exponential-based function would allow finding a maximum to the fitted data, double exponential functions have been used to take into account the differing slopes for low and high adapting height with respect to the maximum.

direction of the drifting grating after 2 seconds of motion, with the same adjustable arrow as before.

Results

The results (Fig. 4) show that large, contrast dependent, directional shifts are observed in these conditions. These shifts are larger at high contrasts and decrease as the distance to the test grating increase, as confirmed by a significant interaction between these two factors ($F(9,27) = 6.43$, $P < 0.001$). It is worth noting that these shifts are still observed when a gap of 0.5 dva is present between the test grating and the static "flankers." This indicates that the perceived directional shifts are not exclusively because of occlusion cues at aperture borders that only exist when the flankers abut on the test grating and modify the status of line-endings from

Fig. 4. Results of Experiment 3: Directional biases (mean ± 1 SE) plotted as a function of flankers-grating separations (0, 0.16, 0.33, 0.5 dva), contrast (5, 10, 20, 90%) and spatial frequency (2 and 8 cpd). A decrease in directional shifts is observed with decreasing contrast and/or increasing flankers' distance.

intrinsic to extrinsic. Although these shifts are larger with a flanking grating at 8 cpd as compared to 2 cpd, this effect does not reach significance ($F(1,3) = 2.61$, $P = 0.21$). Altogether, these results suggest that stimulating the "remote surrounds" of the grating has a strong influence on the perceived direction of the barber pole.

Discussion

The results of the present experiments indicate that large, although suboptimal, shifts in the perceived direction of the barber pole stimulus occur (i) at a high cut-off contrast dependent spatial frequency (ii) after adaptation to flickering patterns located in the center of the barber pole stimulus, and (iii) when flankers are present in the vicinity of the grating's borders.

Before examining the significance of these results for models of line-end motion processing and global motion computation, possible confounding issues should be first addressed. Although a fixation point was provided to minimize eye movements during the experiments, they have not been recorded. It is thus possible that observers made residual eye movements or involuntary pursued the stimulus. It is however unlikely that the large directional shifts reported here could be explained by such eye movements. In particular, in Experiment 2a and 2b, the adapting stimulus is a flickering checkerboard with no net direction of motion, such that the eyes are unlikely to be involuntary dragged towards a particular direction of motion. The selective effects reported here suggest that adaptation was restricted to specific locations, even if imperfect fixation may have slightly "blurred" the adapted zone. Eye movements that may occur during the test period should not differ across conditions, the drifting test stimulus being identical; however the perceived direction of motion varies greatly. In Experiment 3, which replicates and extends the findings of Líden & Mingolla (1998), the stimuli may induce an opto-kinetic nystagmus. However, there is no obvious reason that eye movements would be different across experimental conditions, yet, the directional shifts were dependent on the experimental conditions, suggesting that they cannot be because of uncontrolled eye movements.

Another potential confound is related to the dynamics of motion integration. Several studies (Lorenceau et al., 1993; Masson et al., 2000; Pack & Born, 2001) have shown that the perceived direction of oblique lines or gratings moving along a horizontal axis evolves within the first 200 ms of motion, shifting from an oblique to a horizontal perceived direction. Is this effect, well correlated to the dynamics of the global motion computation in area MT (Pack & Born, 2001), responsible for the directional shifts found herein? The duration of stimulation (2 s), much longer than the integration time found in these previous studies, the high grating contrast used herein, which entails short integration times (<100 ms; Lorenceau et al., 1993), and the fact that the directional shifts strongly depend on the experimental conditions in Experiment 2 and 3 altogether argue against this possibility. It thus seems unlikely that eye movements or the dynamics of global motion computation can account for the present results.

Going back to the results, we first note that the effect of spatial frequency (Exp. 1) and that of adaptation (Exp. 2) may point toward different interpretations. The observation of contrast dependent directional shifts at high spatial frequency suggest that processing line-endings involve, at least in part, units tuned to spatial frequencies higher than the grating itself, in agreement with Kooi's conclusions. From his results, Kooi (1993) suggests that these units may correspond to the subunits underlying models of
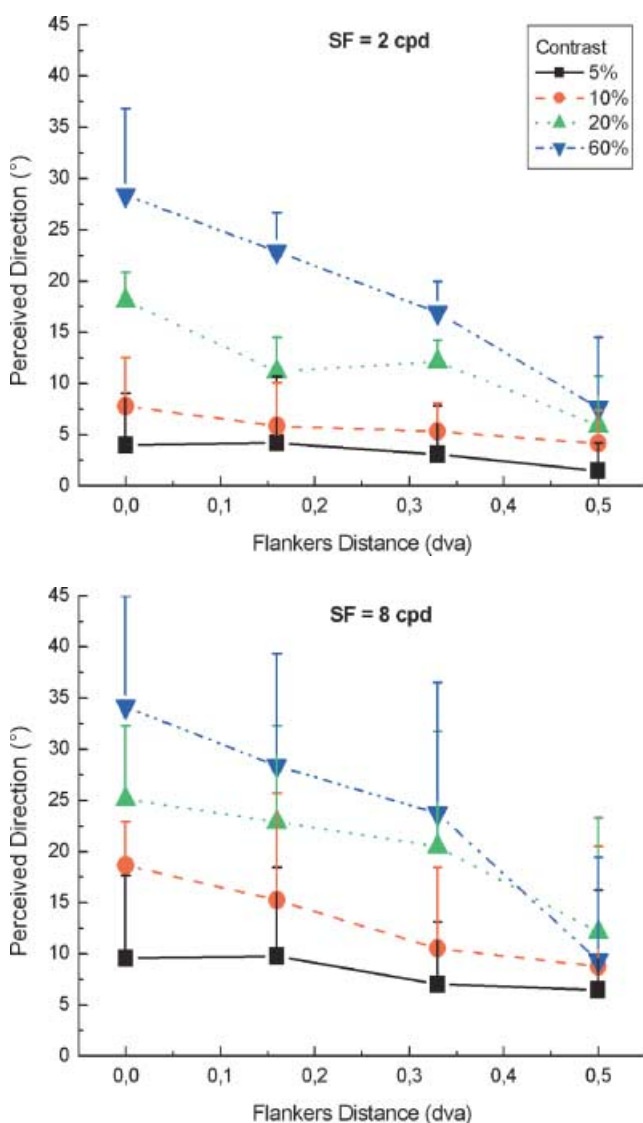
motion processing (Adelson & Bergen, 1985; Watson & Ahumada, 1985; van Santen & Sperling, 1985). According to this view, one may expect, as for other models (e.g., Zetsche & Barth, 1990; Geisler, 1999), that recovering line-end motion requires small receptive fields centered on line-ends' positions. This prediction seems at odd with the results of the adaptation experiments in which adapters restricted to line-end locations have little effect (see Fig. 3b and Fig. 2a, conditions c, d, and e). One explanation of these conflicting interpretations may be related to the adaptation procedure itself: the spatio-temporal structure of the adapting checkerboard patterns may not be well suited to effectively adapt these units (although the duty cycle of the checkerboard patterns, higher than that of the grating, should be well tuned to the (sub)units involved in line-end motion analysis). For instance, simple cells may not respond well to our black and white random texture and thus show little adaptation, or the distribution of temporal frequencies in the energy spectrum may be biased toward too high frequencies, or the adaptation time constants of the underlying units may be long relative to the temporal parameters used in our protocol (Lorenceau, 1987). Although these criticisms could account for the "suboptimal" directional shifts measured here, they cannot explain the effect of adaptation on perceived direction.

One counter intuitive result is that adapting the grating center alone produces large directional shifts (Exp. 2a, condition f). This is unexpected if one considers that adaptation in this case should decrease the responses of units facing the aperture problem. In turn, this should strengthen, rather than weaken, the barber pole illusion, because these units, which only signal a direction orthogonal to grating's orientation, normally contribute to the global motion computation so as to counteract the perception of horizontal motion. An additional intriguing aspect of the data is the "band-pass" effect of adaptation with adapters of increasing height. In Experiment 2b, the directional shifts following adaptation first augment with increasing the height of the adapter, reach a maximum for adapters of similar, although slightly smaller, height as the test grating and then decrease with increasing further adapter's height, which then encompasses the test grating. This effect, reminiscent of the end-stopped responses to stimuli of increasing length, suggests that neurons exhibiting surround suppression or end-stopping are possibly engaged in the computation of the barber pole motion. According to the "classical" view of end-stopping (Hubel & Wiesel, 1965; Sillito & Versiani, 1977; Orban et al., 1979), the excitatory region of an end-stopped neuron optimally activated by a barber pole stimulus would be stimulated by the inner part of the grating, whereas its suppressive end-zone(s) would cover the uniform background and thus be inactive (Fig. 5a).

In Experiment 2a, we have attempted to selectively adapt the suppressive zones with a checkerboard texture located at grating's border (conditions a, b, and c). If adaptation had decreased the response to line-ends, observers should have been biased towards seeing oblique motion. However, the directional shifts measured in these conditions are small suggesting that an adapting stimulus restricted to line-ends location is not very effective in inducing directional shifts (e.g., in reducing the contribution of line-ends to global motion perception). One possible explanation is that adaptation being an activity-dependent process (Sanchez-Vives et al., 2000), the lack of activity of an end-stopped cell during prolonged stimulation of its end-zone(s) may have had no net effect on its response after adaptation. An indirect test of this hypothesis is to stimulate the "end-zones" during the directional test. This was

done in Experiment 3 with lateral "flankers." Large contrast dependent shifts in perceived direction are observed in these conditions. This is compatible with the view that simultaneous stimulation of the end-zones and the center produces large directional shifts. Also note that the flanker effect is not exclusively related to the existence of monocular occlusion cues, as directional shifts also occur when there is a gap between the test grating and the "flankers."

In the "classical" model of end-stopping, an end-zone is spatially offset from its excitatory counterpart. Other models of end-stopping with a different architecture (Dobbins et al., 1987; Sceniak et al., 1999) may shed light on the effects of adaptation. In Dobbins et al's model, two coextensive simple cells with receptive fields of different spatial extent converge onto a neuron (Fig. 5, b). The cell with a large receptive field inhibits its target neuron, whereas the cell with a smaller receptive field has an excitatory influence on the target neuron that thus exhibits end-stopping behavior. The "Difference of Gaussian" (DOG) model of Sceniak et al. (1999) has a similar architecture: the contributions of a large inhibitory surround and a smaller excitatory center shape the receptive fields of V1 neurons in a contrast dependent way. This model nicely fits the electrophysiological responses of V1 macaque neurons, which are mostly end-stopped in layer 4B, layer from which MT mainly receives its inputs. With these models, adaptation at line-ends locations may marginally decrease the end-stopped response because only small regions of the larger inhibitory region would be stimulated. In contrast, adaptation at the grating center would significantly reduce the inhibitory and the excitatory activities and consequently the end-stopped response. As a consequence, the response to line-endings would be decreased and directional shifts would occur. Although speculative, this scheme could account for the effects of adaptation found here, with the assumption that the weights of these end-stopped responses to the global motion computation is larger than the weight of non end-stopped cells, a view supported by electrophysiological evidence (Pack et al., 2004).

This interpretation of the results privileges the role of surround suppression in line-end processing. The observation that the directional shifts found here do not exceed 20° to 30° suggests that adaptation or lateral masking of line-ends' motion did not fully suppress their contribution to global motion perception. Other models should therefore be taken into consideration. Different models proposed to explain how line-ends might be processed are schematically depicted in Fig. 5. In this figure, models that rely on surround suppression are shown on the left (a, b), whereas models that do not are shown on the right hand of the figure (c, d, e). All models explicitly or implicitly propose that the computation of the barber pole motion is realized in area MT (d, e) either through the pooling of the responses of the recruited cells (Majaj et al., 2002) or through a weighted average of the different inputs to MT neurons (Castet et al., 1993; Löffler & Orbach, 1999; Pack et al., 2004).

Löffler and Orbach's model (1999) proposes that the response of a non-Fourier pathway, combining rectified inputs of V1 units in area V2, and the response of a Fourier pathway are pooled at the MT level in order to account for the perceived barber pole direction. As described in Löffler and Orbach (1999), the receptive field of V2 units is much larger than its V1 counterpart and should therefore be tuned to low spatial frequencies relative to that of the barber pole grating. These two features of the model—the spatially localized response and frequency selectivity—seem difficult to reconcile with the present data, because the effect of adapting the
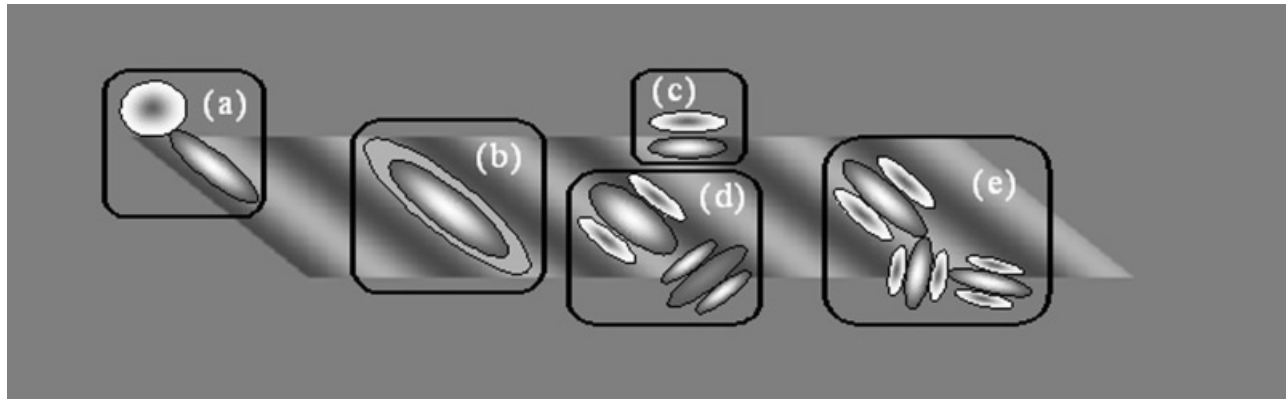
Fig. 5. Schematic illustration of five models of line-end processing. (a) Classical end-stopped neuron with one inhibitory end-zone. (b) Dobbins et al.'s model (1987) based on the joint activity of 2 simple cells. The neuron with the more elongated receptive field inhibits its target neuron while the neuron with the shorter receptive field excites the target neuron, which in turn exhibits end-stopping behavior. (c) Illustration of Geisler's model (1999). Selectivity to line-end direction is achieved by multiplying the responses of a direction selective and an orientation selective cell. (d) Löffler & Orbach's model (1999) involves Fourier (light grey) and non-Fourier (dark grey) units. The Fourier unit projects directly to area MT, whereas the non-Fourier response resulting from the combination of rectified inputs of two V1 units into area V2, projects to area MT. (e) Majaj & al's model (2002). The Fourier decomposition of a line-end, schematically depicted here, results in a broad range of spatial frequency components at different orientations and contrasts. The responses of direction, orientation, and spatial frequency units tuned to these components are pooled at the MT level. See text for details.

center of the barber pole stimulus would presumably have little influence on the responses of these units. Geisler's model (1999), based on the combination of the responses of a direction and an orientation selective cell (see also Zetsche & Barth, 1990), also assumes that the receptive field of units responding to line-ends' motion are located in the vicinity of the grating's borders. Moreover, the modeled units require fast speeds (above 8°/s), because a reliable response of the orientation selective unit needs the integration of line-ends' motion across its receptive field in a short period of time. Again, these features are at odds with the present behavioral results. It remains possible, however, that the adaptation protocol used here was unable to uncover the contribution of these hypothetical units to motion computation.

Similarly, the different schemes based on the responses of a population of neurons to the broad spatial frequency spectrum characteristics of line-endings assume that the receptive fields of neurons contributing to the analysis of line-ends' motion are located in the line-ends' neighborhood. It is unclear how these cells would be significantly adapted by a texture pattern in the grating's center, so as to account for the observed directional shifts. More generally, models assuming that units processing line-ends have receptive fields covering these spatially well-localized features would have difficulties to account for the "remote" effect of adaptation described herein. Several electrophysiological studies have outlined the influence of stimulation outside the classical receptive field on neuronal responses to the barber pole (e.g., Duncan et al., 2000; Pack et al., 2004), and there is direct evidence that end-stopped cells are able to selectively respond to the direction of moving line-endings in area V1 (Pack et al., 2003). Whether the responses of these neuronal populations are sufficient to account for the present results, or whether functionally different units in area V1—or distributed along the dorsal motion pathway— conjointly contribute to the perception of global motion of the barber pole illusion require additional electrophysiological experiments and modeling.

Although simplicity remains a desirable feature of models of motion perception, it is possible that different functional neuronal

properties have developed over time to more selectively process different traits of a moving retinal image (e.g., second order motion, junctions) and that these different units, although they may not always be optimally stimulated, or adapted, by a moving stimulus, still provide responses that contribute to varying degrees to the computation of global object motion.

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