



Orientation dependent modulation of apparent speed: psychophysical evidence

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Abstract

We report several experiments showing that a Gabor patch moving in apparent motion sequences appears much faster when its orientation is aligned with the motion path than when it is at an angle to it. This effect is very large and peaks at high speeds (64°/s), decreases for higher and lower speeds and disappears at low speeds (4°/s). This speed bias decreases as the angle between the motion axis and the orientation of the Gabor patch increases, but remains high for curvilinear paths, provided that element orientation is kept tangential to the motion trajectory. It is not accounted for by decision strategies relying on the overall length and duration of the motion sequence or the gap size (or spatial jump) between successive frames. We propose a simple explanation, thoroughly developed as a computational model in a companion paper (Seriès, Georges, Lorenceau, & Frégnac: “Orientation dependent modulation of apparent speed: a model based on the dynamics of feedforward and horizontal connectivity in V1 cortex”, *Vision Research*, 42, 2757), according to which long-range horizontal connections in V1 elicit differential latency modulations in response to apparent motion sequences, whose read-out at an MT stage results in a perceptual speed bias. The consequences of these findings are discussed.

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1. Introduction

Processing the speed of moving objects or animals is an ecological necessity in vision: catching prey or a ball, predicting a collision, avoiding obstacles, require that speed can be accurately estimated. In line with these behavioral needs, psychophysical experiments in the laboratory have shown that human observers can discriminate the speed of two stimuli even when their difference is as low as 5% (McKee, 1981), although this value tends to increase for speeds higher than 30°/s or lower than 2°/s and for short duration of motion (Orban, De Wolf, & Maes, 1984). However, in his seminal study, Brown (1931) reported that the size, length and

orientation of simple moving shapes influence their perceived speed. These initial observations have been confirmed and extended over the past twenty years: it was found that form (including size, orientation, spatial frequency, spatial layout; Diener, Wist, Dichgans, & Brandt, 1976; Campbell & Maffei, 1981; Castet, Lorenceau, Schiffman, & Bonnet, 1993; Verghese & Stone, 1997), contrast (Stone & Thompson, 1992; Thompson, 1982), or the presence of a background against which objects move (Blakemore & Snowden, 2000) all modulate perceived speed.

In this study, we focus on the influence of stimulus orientation on perceived speed for the following reasons. First, most direction selective neurons respond to bars or gratings moving in a direction orthogonal to their preferred orientation, pointing to a fundamental relationship between orientation and motion processing. One theoretical reason of this link has been formulated as the “aperture problem”, which stresses that any motion unit with a receptive field of a limited spatial extent has only access to the motion component normal

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to the orientation of a moving contour that encompasses its limits (Fennema & Thompson, 1979; Henry, Bishop, & Dreher, 1974). There are, however, several electrophysiological reports that some V1 cells respond to motion along an axis collinear to their preferred orientation (Crook, Wörgötter, & Eysel, 1994; Geisler, Albrecht, Crane, & Stern, 2001; Wörgötter & Eysel, 1989). Similarly, some neurons in area MT also selectively respond to motion in a direction parallel to their preferred orientation (Albright, 1984). Studying the effect of stimulus orientation on perceived speed may therefore provide insights into the underlying mechanisms. Second, a number of studies report that the “strength” or the detectability of motion is enhanced along the direction of motion (Alais & Lorenceau, 2002; Anstis & Ramachandran, 1987; Vergheze, McKee, & Grzywacz, 2000; Watamaniuk, McKee, & Grzywacz, 1995; Werkhoven, Snippe, & Koenderink, 1990). To our knowledge, few studies examined whether these findings extend to perceived speed. Third, psychophysical (Löffler & Orbach, 2001; Lorenceau, Shiffrar, Wells, & Castet, 1993), behavioural (Masson, Rybarczyk, Castet, & Mestre, 2000) and physiological (Pack & Born, 2001) evidence indicate that the perceived direction of moving lines depends on their inclination relative to the motion axis and that lines tilted relative to the motion axis appear to move more slowly than lines perpendicular to it (Castet et al., 1993; Scott-Brown & Heeley, 2001). This slowing down reaches a maximum for lines aligned with the motion axis. As only slow speeds (2–4°/s) were tested in these studies, it is not known whether these effects also hold at high speeds.

A general framework that accounts for the processing of velocity (direction and speed) was initially proposed by Reichardt (1961) and later elaborated in several models (Adelson & Bergen, 1985; Simoncelli & Heeger, 1998; van Santen & Sperling, 1985; Watson & Ahumada, 1985). These models are based on the convergence (additive or multiplicative) of the outputs of two non-direction selective subunits onto a third target cell. The key feature is that a delay (e.g. low temporal filtering) imposed on the output of one sub-unit confers a direction and speed tuning to the target motion selective (MS) cell.¹ It has been shown that the properties of direction selective simple cells in V1 are well described by these types of models (Emerson, 1997). One consequence of this architecture is that whether the response latency of one of the two sub-units is lengthened, or shortened, (e.g. by using different polarity, luminance or

contrast levels), the velocity tuning of the MS cell should shift toward higher or slower speed and its sign may even be reversed (Anstis & Rogers, 1975).

Recent electrophysiological data demonstrate that stimuli flashed outside the classical discharge field of a V1 neuron elicit a subthreshold modulation of its membrane potential (excitatory or inhibitory) with a delay that increases linearly with the distance from the receptive field centre (Bringuier, Chavane, Glaeser, & Frégnac, 1999; Chavane et al., 2000). This raises the intriguing possibility that stimulation in the “silent” surround of a cell’s receptive field also modulates the cell’s response latency to incoming stimuli flashed in the discharge field. If so, and assuming that such cell is one of the input sub-units that projects onto MS units, its contribution to motion processing could shift the population response of MS cells, and presumably bias the perceived stimulus velocity (Churchland & Lisberger, 2001; Mikami, Newsome, & Wurtz, 1986; Newsome, Britten, & Movshon, 1989). To be effective, such latency modulation requires the cooperative activation of a network that links neighboring cells whose receptive fields span the motion axis. As a matter of fact, such a network has been described in area V1, as neurons selective to the same orientation that interact through long-range horizontal connections are often co-aligned (Gilbert & Wiesel, 1989; Sincich & Blasdel, 2001; Ts’o, Gilbert, & Wiesel, 1986). These horizontal connections are thought to facilitate the response of cells with similar orientation preference, and to reduce their response otherwise (Kapadia, Ito, Gilbert, & Westheimer, 1995; Kapadia, Westheimer, & Gilbert, 2000; Nelson & Frost, 1985). In this context, we hypothesized that the perception of speed could be differentially modulated by motion sequences of oriented stimuli collinear and aligned to the motion axis or at an angle to it.

In the following, we present the results of psychophysical experiments that aim at testing the influence of orientation relative to the motion axis on perceived speed. Observers were asked to discriminate the speed of apparent motion sequences composed of an oriented Gabor patch moving either along the motion axis or at an angle to it. In contrast with previous results (Castet et al., 1993), we observed a “speedup” illusion: a Gabor patch moving along its orientation appears much faster than a Gabor patch at an angle to the motion axis. This effect is quite large at high speeds, decreases at intermediate speeds and disappears at low speeds. Our hypothesis that the speedup found at high speeds is related to the dynamics of activity within the plexus of long-range horizontal connections is supported both by a computational model (Seriès, Georges, Lorenceau, & Frégnac, this issue) and by electrophysiological intracellular recordings done in cat primary visual cortex for the same stimulus configurations (Baudot et al., 2000; Lorenceau et al., 2001).

¹ In elaborated versions of the Reichardt model, subunits are non-direction selective cells with simple receptive fields in phase quadrature and feed two motion units tuned to opposite directions, whose outputs are added (Watson & Ahumada, 1985) or multiplied (Adelson & Bergen, 1985). However, these different architectures do not change the main argument developed here.

2. General method

2.1. Apparatus and display

All stimuli were displayed on a 60 Hz monitor (Sony Trinitron GDM 1950, 19 inches, 1280 × 1024) driven by a graphics card (Adage PG 90/10, 8 bits, gamma corrected). The display consisted of a Gabor patch (sinusoidal spatial luminance profile weighted by a Gaussian function) sequentially flashed for very brief duration (16.66 ms, one frame) in different locations along a vertical axis, thus eliciting the perception of an apparent motion, either upward or downward. The Gabor patch had a spatial frequency of 1.5 cpd ($\lambda = 0.67^\circ$, Michelson contrast 51%), the standard deviation of the Gaussian envelop, σ , was 0.4° (30 pixels) and the mean luminance was 50 cd/m². Observers viewed the stimuli binocularly from 114 cm, with their head maintained in a chinrest. They were requested to fixate the center of the screen and to discriminate the speed of two apparent motion sequences. Speed discrimination was measured using a two interval forced choice design (ISI of 500 ms between each interval) associated with a method of constant stimuli. To minimize the possibility that observers used the length or total duration of the motion sequence to perform this task, the number of frames (from 3 to 5) in each sequence were randomly varied. Since each motion sequence lasted 50, 66.7 or 83.4 ms, it is unlikely that observers could initiate pursuit eye movements or “express” saccades. However, as motion was often undetectable at a slow speed (4°/s) with these short sequences, motion duration was increased to 8–10 frames (133.4–166.7 ms) for this particular speed.

In the first experiment, a reference speed consisting of a vertical Gabor patch moving up or down along a vertical axis—“collinear sequence” thereafter—was compared to an apparent motion sequence that was in all respects the same, except that the Gabor patch was orthogonal to the motion axis—“parallel sequence” thereafter—(see Fig. 1). Six reference speeds (4°/s, 12°/s, 24°/s, 40°/s, 64°/s and 96°/s) were tested in separate, counter-balanced, blocks of trials. Each reference speed was compared to seven comparison speeds ranging from -60% to +60% of the reference speed by 20% steps. Different reference and comparison speeds were obtained by varying the spatial jump between successive patches (see Table 1). Observers ($n = 6$, 4 naives and two authors SG, JL), with normal or corrected to normal vision, were asked to indicate which temporal interval contained the fastest motion (Fig. 1). Before each new session, observers were trained in a practice block of typically 42 trials.

3. Experiment 1

In this first experiment, the speed of a Gabor patch collinear and aligned to the motion axis was compared

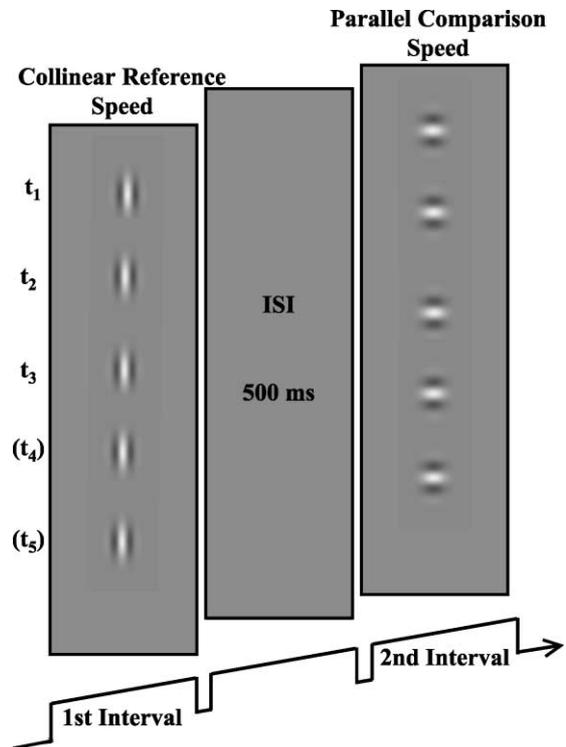


Fig. 1. Schematic representation of a trial. Two apparent motion sequences—a reference or a comparison speed—are presented in succession with an inter-stimulus interval of 500 ms. Six reference speeds—obtained by varying the spatial jump between frames—are used in Experiment 1 (4°/s, 12°/s, 24°/s, 40°/s, 64°/s and 96°/s). Each sequence lasts 50, 66.6 or 83.4 ms (inter frame interval of 16.67 ms, i.e. 3–5 frames), except for 4°/s where 8–10 frames were used. The comparison speeds range from -60% to +60% of the reference speed. The direction of motion—up or down—and number of frames are chosen at random for each motion sequence.

to the speed of a Gabor patch orthogonal to it, as a function of the speed of brief apparent motion sequences. If the orientation of the Gabor patch had no influence on perceived speed, reference and comparison sequences having the same physical speed should appear as equally fast and the point of subjective equality (PSE) should lie around 1. On the contrary, if the orientation of the Gabor patch influenced perceived speed, reference and comparison sequences with the same physical speed should yield different estimates and the PSEs should be greater or smaller than 1.

3.1. Results

Fig. 2 represents the percentage of the trials in which the reference “collinear” sequence appears faster than the comparison “parallel” sequence as a function of the relative speed of the parallel sequence, for six reference speeds and three of the six observers. The right bottom panel shows the data averaged across 6 observers. Several features of the results are worth noting. At a slow reference speed (4°/s), the orientation of the Gabor

Table 1

Center to center distances—i.e. spatial jump—between successive position of a Gabor patch during an apparent motion sequence in degree of visual angle and λ units, for six reference speeds and for the minimum and maximum speeds of the comparison sequences. The right columns indicates whether two successive Gabor patch overlap during a sequence

Reference speed (°/s)		Spatial distance (°)	Spatial distance (λ units)	Overlap
4		0.07	0.10	Y
12		0.20	0.30	Y
24		0.40	0.60	Y
40		0.67	1.00	Y
64		1.07	1.60	N
96		1.61	2.40	N
	<u>Min. comp. speed (°/s)</u>			
4	1.6	0.03	0.04	Y
12	4.8	0.08	0.12	Y
24	9.6	0.16	0.24	Y
40	16	0.27	0.40	Y
64	25.6	0.43	0.64	Y
96	38.4	0.64	0.96	Y
	<u>Max. comp. speed (°/s)</u>			
4	6.4	0.11	0.16	Y
12	19.2	0.32	0.48	Y
24	38.4	0.64	0.96	Y
40	64	1.07	1.60	N
64	102.4	1.72	2.56	N
96	153.6	2.57	3.84	N

patch relative to the motion axis has no influence on performance: comparison speeds higher (respectively slower) than the reference speed are correctly judged as faster (respectively slower). The slopes of the psychometric curves are shallow, however, and speed discrimination thresholds are large (22% on average), indicating that the task was difficult at the short duration used, consistent with previous results (McKee, 1981; McKee & Welch, 1985; Orban et al., 1984). As the reference speed increases, the psychometric curves progressively flatten, but speed discrimination is far from chance level performance (50%): collinear sequences are consistently perceived as being faster than parallel sequences. At intermediate speeds (12–24°/s), collinear sequences are judged as slightly faster than parallel sequences. This effect becomes surprisingly large at high speeds: collinear sequences moving at 40°/s, 64°/s and 96°/s are still perceived as being faster than parallel sequences moving at 64°/s, 102.4°/s and 153.6°/s in respectively 52%, 64% and 60% of the trials. This effect is maximum for a speed of 64°/s, such that a collinear sequence appears faster than a parallel sequence moving at the same physical speed in 81.25% of the trials.

An ANOVA confirms that this speed bias increases with increasing reference speeds, resulting in a significant interaction between the parallel comparison sequence speeds and the collinear reference sequence speeds ($F_{(30,150)} = 6.37, p < 0.001$). Comparing the lower (4°/s, 12°/s and 24°/s) and higher speeds (40°/s, 64°/s and 96°/s) also results in a significant effect ($F_{(1,5)} = 57.25, p < 0.001$). Planned comparisons further indicate that

the speed bias is larger for 64°/s as compared to 40°/s and 96°/s ($F_{(1,5)} = 46.26, p < 0.001$).

Weibull functions were fitted to the averaged data and used to estimate the PSEs (Fig. 3). At slow speeds, the PSE is close to 1, in keeping with our observation that the orientation of the Gabor patch relative to the direction axis has no effect in this case. PSEs increase up to a maximum for higher speeds (2.07°/s for 64°/s) and decrease for the highest speed used (1.66°/s for 96°/s). Although this pattern of results suggests that the speed bias is band-pass along the speed dimension, this conclusion should be considered with caution as it relies on the decrease of the PSE at 96°/s. However, such band pass behavior is strongly supported by our model (Seriès et al., this issue).

To rule out the possibility that the observed speed bias depends on whether the collinear or the parallel sequence is used as a reference, we conducted a control experiment in which parallel sequences were used as the reference speed, whereas collinear sequences were used as comparison sequences. Under these new conditions the results remained qualitatively the same² (data not shown). In another control experiment, we verified that observers did base their judgments on speed, rather than

² Note that this experimental design does not allow direct comparisons between this control and the main experiment. Indeed, the comparison speed being a fraction of the reference speed, the pairs of parallel/collinear speeds are not the same, except for physically identical speeds.

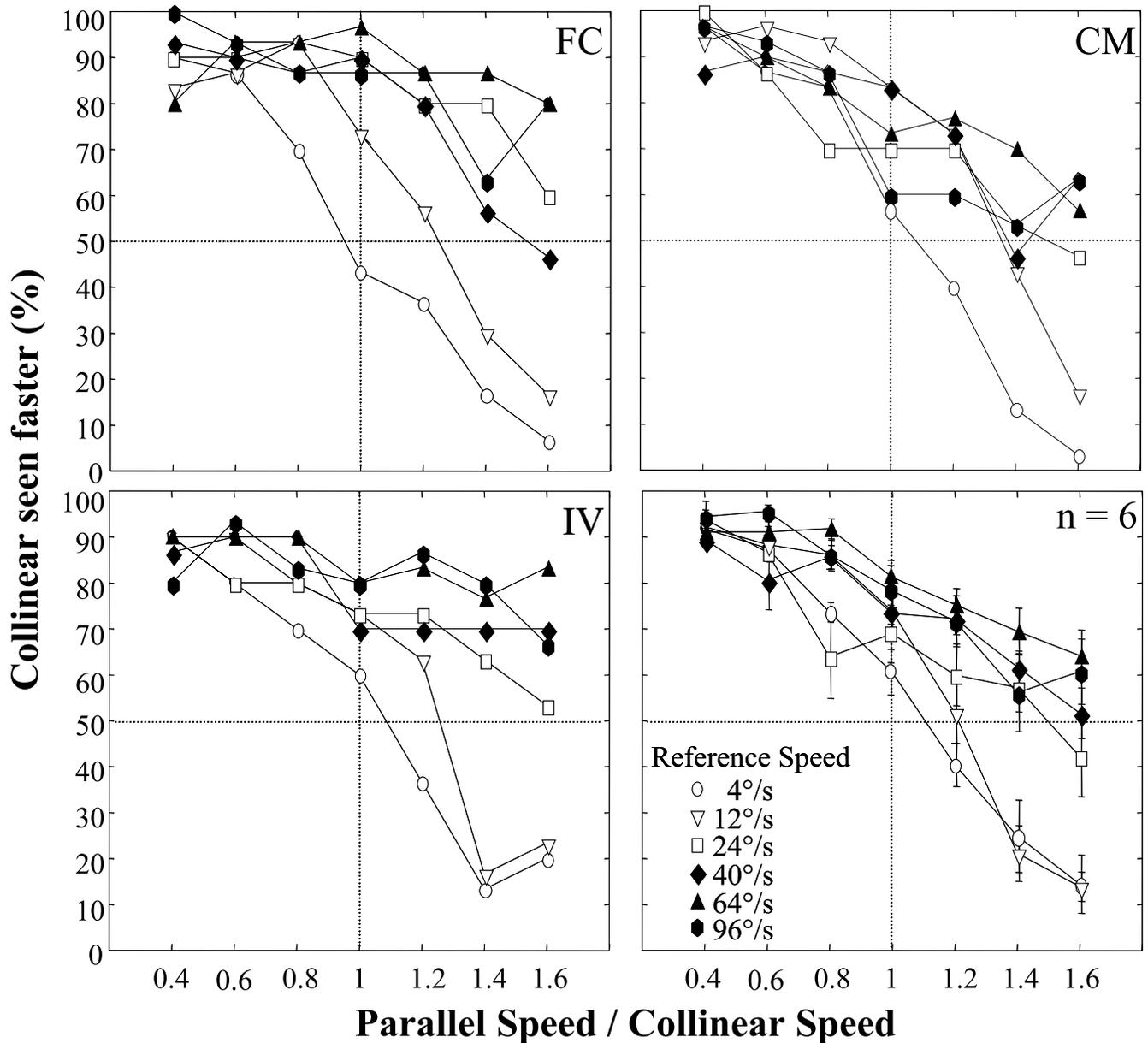


Fig. 2. Results of Experiment 1: percentage of the trials in which a collinear reference sequence is judged as faster than the parallel comparison sequence, as a function of the ratio between the comparison and reference speed for six different reference speeds: 4°/s (○), 12°/s (△), 24°/s (□), 40°/s (◆), 64°/s (▲) and of 96°/s (●). Three panels represent the individual data for three observers. Each point corresponds to 40 trials. The right bottom panel shows the results averaged across six observers (240 trials per point). The errors bars represent ± 1 SEM.

on the jump size or on the overall sequence length or duration, by using exactly the same experimental design but a different task. Observers were now instructed to indicate which of the two motion sequences contains the largest jump between successive Gabor patches. The results (data not shown) indicate that large jumps, corresponding to high speeds, are discriminated more accurately than small jumps, corresponding to slow speeds. This indicates that observers did not use this spatial cue to perform the speed discrimination task in the main experiment. Furthermore, given that the length, duration and direction of motion were ran-

domized across the two intervals of a trial, using these cues would have yielded incoherent results. We therefore feel confident that our data reflect a genuine and compelling speedup illusion.

4. Experiment 2

We then estimated the sensitivity of this effect to orientation anisotropy in a second experiment using stimuli whose orientational content was gradually varied. A strong sensitivity of the speed bias to a small

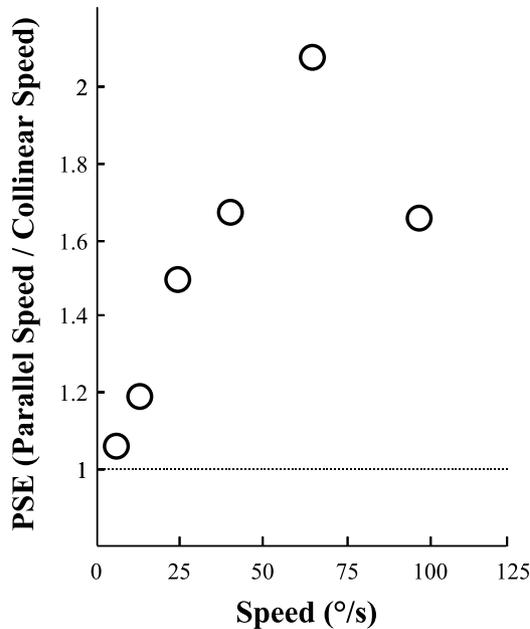


Fig. 3. Points of Subjective Equality (PSEs) as a function of the physical speed of the reference collinear sequence, calculated by fitting the data with a Weibull function.

orientation anisotropy would suggest that mechanisms highly selective to orientation are involved in this speedup effect.

4.1. Method

We used the same design as for Experiment 1 except for the following changes: The stimuli were Gaussian blobs with different width/length aspect ratios. Five aspect ratios (4/9, 5/7, 1, 7/5 and 9/4) were chosen to generate vertical, circular and horizontal elongated Gaussian blobs with the same mean luminance (Fig. 4a). Gaussian blobs with complementary aspect ratios were used for comparison and reference sequences in different blocks (e.g. a blob with an aspect ratio of 5/7 was compared to a Gaussian blob with an aspect ratio of 7/5). Only three speeds (40°/s, 64°/s, and 96°/s) were used in this experiment. As before, the comparison speeds ranged from –60% to +60% of the reference speed by steps of 20%. The combination of aspect ratios and speed resulted in 15 different blocks (280 trials each) that were randomly intermingled across sessions for each observer. Four observers with normal or corrected to normal vision were instructed to indicate which of two intervals contains the fastest motion. Only one observer (SG) had also participated in the first experiment.

4.2. Results

The percentage of the trials, averaged across 4 observers, in which the reference sequence appeared faster

than the comparison sequence is plotted in Fig. 4b as a function of the relative speed of comparison sequences for three reference speeds. Whatever the speed of the reference, speed discrimination is accurate when both the reference and comparison sequences are composed of circular Gaussian blobs. For the 3 speeds that were tested, the points of subjective equality (PSEs) derived from the experimental data are close to the point of physical equality (1.00, 0.97 and 0.95, for 40°/s, 64°/s and 96°/s respectively). Weber fractions are large (0.27, 0.28 and 0.24 for 40°/s, 64°/s and 96°/s respectively) and consistent with previous results (McKee, 1981; Orban et al., 1984), indicating that the speedup found in Experiment 1 did not result from an inability to perform the task at high speeds.

Whenever the aspect ratio of the Gaussian blobs differs from 1, a speed bias similar to that observed in Experiment 1 occurs. Elongated Gaussian blobs aligned with the motion axis are judged as faster than Gaussian blobs orthogonal to it. When the reference is a horizontal Gaussian blob, the PSEs are shifted to the left of the point of physical equality. Conversely, when the reference is a vertical Gaussian blob, the PSEs are shifted to the right of the point of physical equality. Statistical comparisons confirm the significant effect of aspect ratio ($F_{(4,12)} = 15.78$, $p < 0.001$). However, the differences between aspect ratios of 9/4 and 5/7 ($F_{(1,3)} = 0.94$, ns) and 4/9 and 5/7 ($F_{(1,3)} = 1.21$, ns) are not significant. In addition, the results obtained for the three reference speeds are not significantly different ($F_{(2,6)} = 3.46$, ns).

These results suggest that the speedup illusion observed in Experiment 1 is highly sensitive to the orientation of the elements of a motion sequence. It is worth noting that the effect is already strong for aspect ratios as small as 5/7 and 7/5, where the Gaussian blobs are only slightly elongated. This may partly result from our choice to compare vertical and horizontal Gaussian blobs. Although further experiments should be done to determine the smallest orientation anisotropy necessary to induce a speed bias, our data nevertheless suggests that the mechanisms underlying this effect must be highly sensitive to small orientation differences. In this respect, neurons in area V1 or area V2 are plausible candidates, as they are highly selective to stimulus orientation.

5. Experiment 3

In the two first experiments, only vertical and horizontal orientations were used together with a single vertical motion axis. This does not allow to measure the effect of the relative angle between element orientation and the motion axis. This could be done in two ways: first, the motion axis could remain the same, while the orientation of the moving elements would progressively

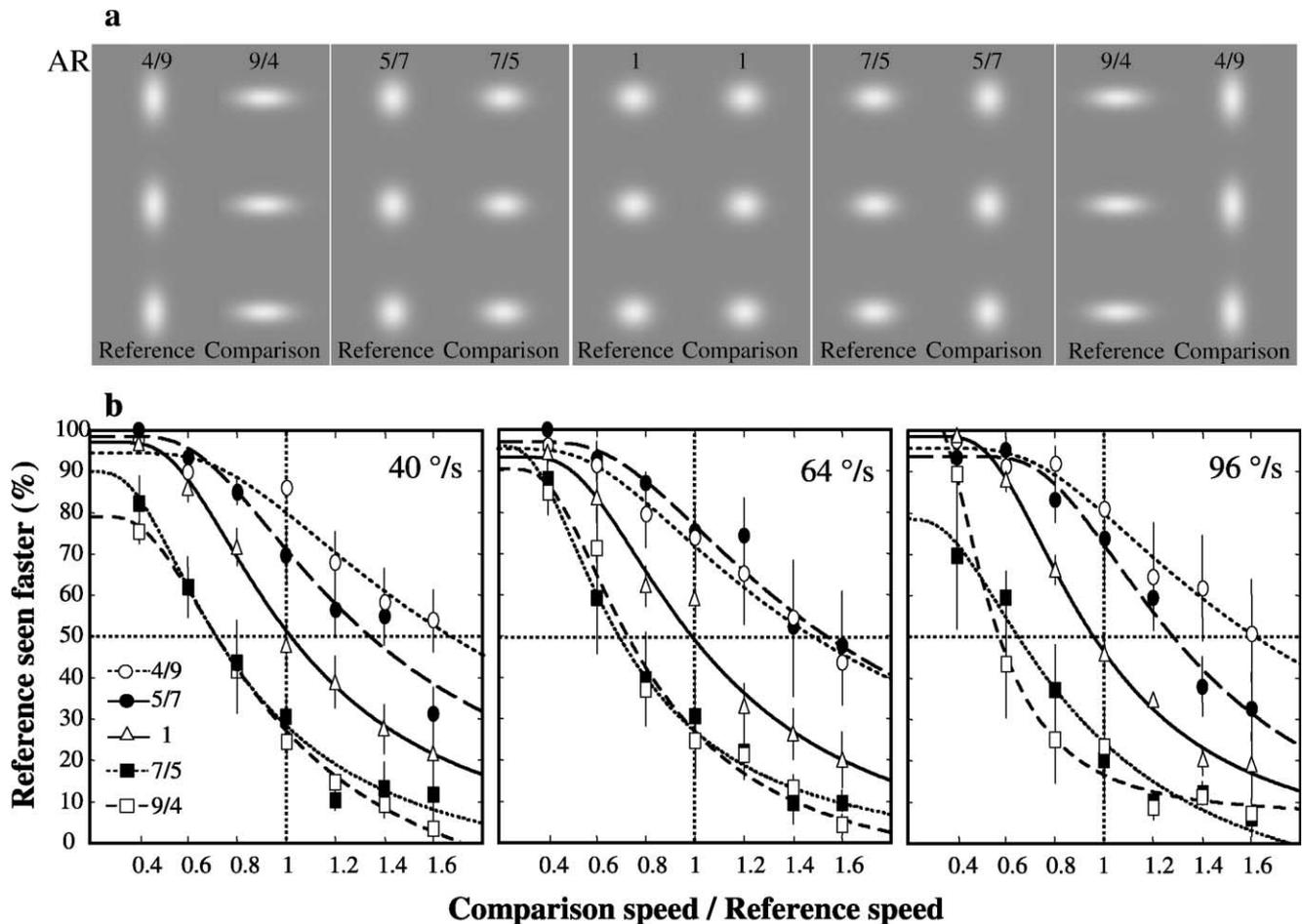


Fig. 4. (a) Stimuli used in the Experiment 2. The left column of each panel shows the elongated Gaussian blobs used as a reference sequence whereas right columns shows the elongated Gaussian blobs used as comparison sequences. Complementary aspect ratios are used for the reference and comparison sequences. Three reference speeds (40°/s, 64°/s and 96°/s) are used. See text for details. (b) Results of Experiment 2: percentage, averaged across four observers, of the trials in which the reference sequence is judged as faster than the comparison sequences, as a function of the ratio between comparison and reference speeds. Each point is the average of 160 trials. Errors bars are ± 1 SEM. Symbols correspond to different aspect ratios: 4/9 (\circ), 5/7 (\bullet), 1 (\triangle), 7/5 (\blacksquare), 9/4 (\square). Solid curves shows the fits of the averaged data by a Weibull function (R^2 range between 0.93 and 0.99).

vary. One possible drawback of this design is that the sensitivity of the visual system is not homogeneous across different orientations (the “oblique effect”, Appelle, 1972). Another possibility is to vary the direction of motion, while keeping the orientation of each element constant. Although a slight “oblique” effect has also been described for moving stimuli (together with an heterogeneity in the visual field, van de Grind, Koenderink, van Doorn, Milders, & Voerman, 1993), it is of a lesser amplitude than that found for orientation (but see Löffler & Orbach, 2001). Therefore, we chose the second solution to determine the influence of the orientation of a Gabor patch relative to the motion axis, and restricted our investigation to the lower left quadrant of the visual field (see Fig. 5a and method below). In Experiments 1 and 2, comparison speeds were systematically varied by changing the jump size. Although we checked that observers did not use this spatial cue to perform the task,

we reasoned that the speed bias should still occur if a single spatial jump was used together with varying motion axes. Therefore, we used a single physical speed (i.e. a single jump size) for both the reference and the comparison sequences, that differed only by their relative direction of motion. In this way, we could vary the relative angle between the moving elements and the motion axis, thus degrading progressively the spatio-temporal alignment between successive frames of the motion sequence, while using the same spatial jump in all sequences. This design thus permits to estimate the orientation tuning of the speed bias, for both collinear and parallel sequences.

5.1. Method

We used the same design as before, except for the following changes: we used a single speed of 64°/s for

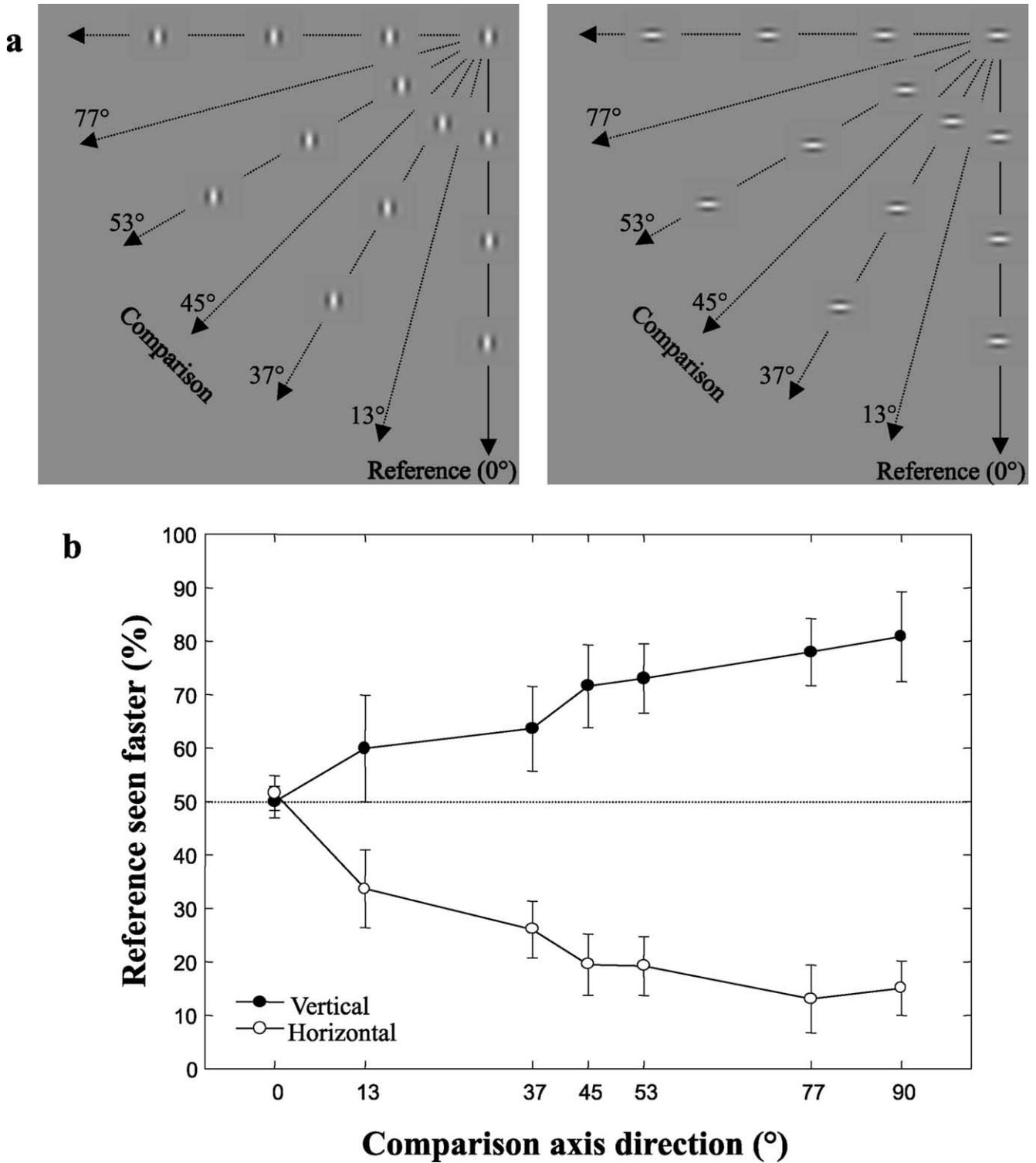


Fig. 5. (a) Example of the stimuli used in Experiment 3. The reference sequence is vertical (0°) or horizontal (90°). Comparison sequences move at the same physical speed as the reference (64°/s) along different motion axes (0°, 13°, 37°, 45°, 53°, 77° and 90°). A vertical (left panel) and a horizontal (right panel) Gabor patch are used as reference. (b) Results of Experiment 3: percentage, averaged across 9 observers, of the trials in which the reference sequence is judged as faster than the comparison sequences as a function of the direction of motion. The results for a vertical Gabor patch (●) and a horizontal Gabor patch (○) are shown. Error bars represents ±1 SEM.

which the effect was at a maximum in Experiment 1. A reference sequence moving either along a horizontal

(90°) or a vertical (0°) axis was compared to seven comparison sequences moving along different axes (0°,

13°, 37°, 45°, 53°, 77° and 90°, Fig. 5a). In one block of trials, the reference consisted either in a vertical or a horizontal Gabor patch resulting in 28 different conditions. Eight naive observers and one author (SG), with normal or corrected to normal vision, performed 4 blocks of 336 trials each.

5.2. Results

The results, averaged across 9 observers, are plotted in Fig. 5b. The percentage of the trials in which the reference sequence is judged as being faster than the comparison is shown for the two Gabor orientations as a function of the direction of the comparison sequences. As expected, observers responded at random (50%) when the comparison and the reference sequences having the same physical speed both move along the same motion axis. As the relative angle between the reference and comparison sequences increases a speed bias builds up gradually. When compared to a “collinear” reference sequence, comparison sequences are judged as moving more slowly, whereas the reverse is true for “parallel” reference sequences.

It is worth noting that the apparent speed of collinear sequences appears higher than comparison sequences despite the physical speed being the same in all pairs of reference and comparison sequences. This suggests that the speed bias is intrinsically related to the orientation of the moving elements relative to the motion axis, and provides additional evidence that observers did not rely on the length, jump size or duration of motion in the previous experiments.

6. Experiment 4

Up to now, it is not clear whether the speed bias found in the previous experiments results from an overestimation of speed for collinear sequences or from an underestimation of speed for parallel sequences, as both were directly compared. Answering this question may help to determine whether the speed bias results from a facilitation for collinear sequences or a suppression for parallel sequences, but requires a “neutral” sequence, whose speed would be “veridically” perceived. Although this may never be the case, it remains possible to estimate the speedup effect relative to stimuli devoid of orientation anisotropy. Two stimuli meet this requirement: a circular Gaussian blob and a circular grating patch weighted by a Gaussian. In two distinct experiments, we therefore asked observers to estimate the speed of those two stimuli, relative to horizontal and vertical moving Gabor patches. We first describe the results obtained with circular Gaussian blobs, and then briefly discuss the results obtained with circular gratings.

6.1. Method

We used exactly the same experimental design as in Experiment 1 except for the following changes. The reference speed was composed of either a horizontal or a vertical Gabor patch while the comparison sequences were composed of white circular Gaussian blobs, whose envelope was identical to that of the oriented Gabor patches. Since the speed bias was found to be larger at high speeds, only the three highest reference speeds of Experiment 1 (40°/s, 64°/s, 96°/s) were used. Two observers and one author (SG), with normal or corrected to normal vision, participated in these experiments.

6.2. Results

In Fig. 6, the percentage of the trials in which the reference speed is perceived as faster than the comparison speeds is plotted for the three reference speeds as a function of the comparison speeds. For the three reference speeds used, observers overestimated the speed of the collinear sequence relative to that of a circular Gaussian blob. Conversely, they underestimated the speed of the parallel sequence relative to the same circular Gaussian blob. Not surprisingly, the main effect of Gabor orientation is significant ($F_{(1,3)} = 32.92$, $p = 0.011$). Consequently, the PSEs are shifted to the right with a vertical Gabor patch (1.18, 1.50 and 1.23 for 40°/s, 64°/s and 96°/s respectively) and to the left with a horizontal Gabor patch (0.68, 0.60 and 0.60 for 40°/s, 64°/s and 96°/s). Although the maximal difference between horizontal and vertical oriented Gabor patches is observed for a reference speed of 64°/s, the effect of speed is not significant ($F_{(2,6)} = 0.74$, ns) in this experiment, maybe because of the limited number of observers.

To ensure that the lack of luminance modulation in Gaussian blobs does not account for the observed pattern of results, we performed an additional experiment using a circular sinusoidal grating patch weighted by a Gaussian. The spatial parameters—nominal spatial frequency and overall size—and contrast of this stimulus (51%), which lacks a predominant orientation, were equated to those of the Gabor patches used as reference sequences. Only a speed of 64°/s was used. The results are shown in the middle panel of Fig. 6 with filled symbols. As before, we found that the speed of non-oriented comparison sequences was underestimated relative to that of collinear sequences and overestimated relative to the speed of parallel sequences (PSEs of 1.30 and 0.72 respectively). These results are qualitatively similar to those obtained with circular Gaussian blobs.

Under the assumption that the comparison sequences used in these experiments are indeed “neutral” in the orientation domain, these results suggest that the speedup bias involves a relative facilitation for collinear

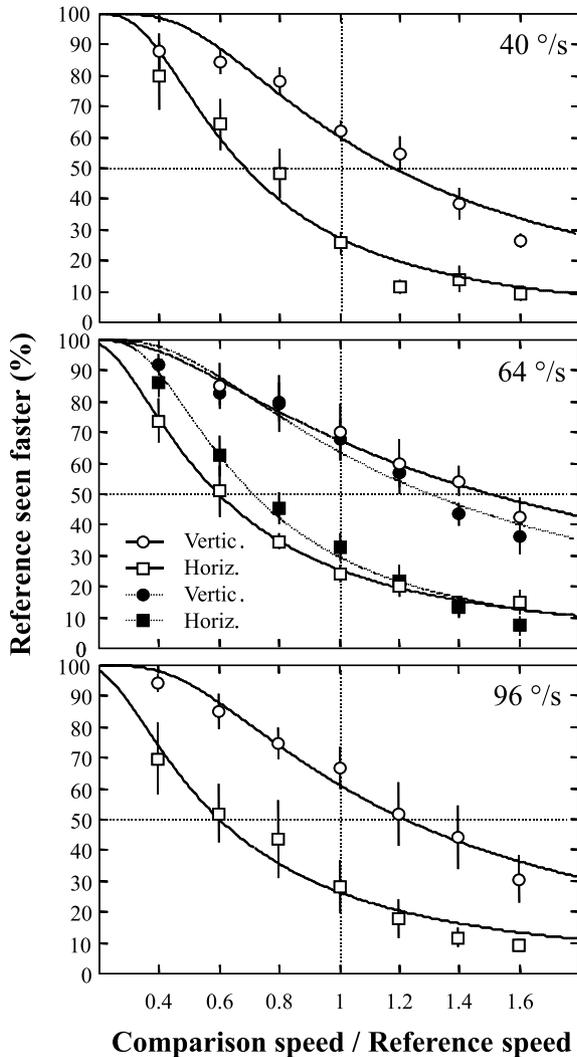


Fig. 6. Results of Experiment 4: percentage, averaged across 4 observers, of the trials in which the reference sequence (either the collinear or parallel sequence) is judged as faster than the comparison as a function of the ratio between the comparison and reference speeds, for the three reference speeds. Each point is the average of 180 trials. Errors bars represent ± 1 SEM. Open symbols represent the results for a circular Gaussian blob. Solid symbols represent the results for a circular grating patch. Circles correspond to a vertical Gabor patch, and squares correspond to a horizontal Gabor patch. Solid curves represent the fits of averaged data by Weibull function. (R^2 range between 0.92 and 0.99).

sequences and a relative suppression for parallel sequences. This point will be discussed further in the general discussion.

7. Experiment 5

One potential explanation of the speed bias would be that elongated receptive fields could behave as spatio-temporal “collector” units. The existence of such “collector” units has been hypothesized on the basis of psychophysical experiments using static displays (Mor-

gan & Baldassi, 1997; Morgan & Hotopf, 1989; Moulden, 1994). The neural substrate of these units may lie in layer 6 of primary visual cortex where some neurons have very elongated receptive fields (Bolz & Gilbert, 1986; Gilbert, 1977). Such view requires a number of assumptions however: these units should collect synaptic inputs along their receptive field with integration time constants compatible with those required to process the high speed sequences used here. Moreover, they should possess some form of direction and speed selectivity along their preferred orientation in order to respond differentially to directional apparent motion and to random stimulation in different receptive field locations. Whether these “collector” units have these properties is yet unknown. However, since these units presumably have straight elongated receptive fields, they should not be capable of processing curvilinear trajectories. Indeed, the assumption of collector units tuned to all possible motion paths leads to a problem of combinatorial explosion, whereby the visual cortex would need an infinitely large number of neurons to cover all possible trajectories. Based upon this line of thinking, we performed experiments using curvilinear motion trajectories. We reasoned that if collector units account for the observed speed bias, it should disappear, or at least diminish, for curvilinear motion paths. Several types of trajectories—circular, wiggled and S-shaped—were tested in different experiments. For simplicity and because the results are similar, we analyze the results obtained with a circular path in a single section below.

7.1. Method

The only way to build a motion sequence with a fixed curvilinear path while changing its speed is to change the temporal interval between successive frames (inter frame interval, IFI). With the 60 Hz refresh rate used in our experiments, the IFI can only be changed by steps of 16.6 ms, such that the speed dimension can only be coarsely explored. However, this manipulation is interesting as it is complementary to that used in our previous experiments where only the spatial jump size was varied to yield different speeds, allowing to test whether our results hold under this fixed jump condition.

In a first experiment, elongated Gaussian blobs (with aspect ratio of 4/9) were sequentially flashed along a circular path (radius = 0.68° , Fig. 7a). As before, a 2IFC design was used to measure speed discrimination. In one interval the orientation of Gaussian blobs was tangential to the motion path while it was orthogonal to it in the other interval. Three different speed ratios (2/3, 1, 3/2) were obtained by combining two different speeds (31°/s and 47°/s) obtained by using IFIs of 2 and 3 frames. Five observers with normal or corrected to normal vision were instructed to indicate which of the two successive motion sequences appears as being faster.

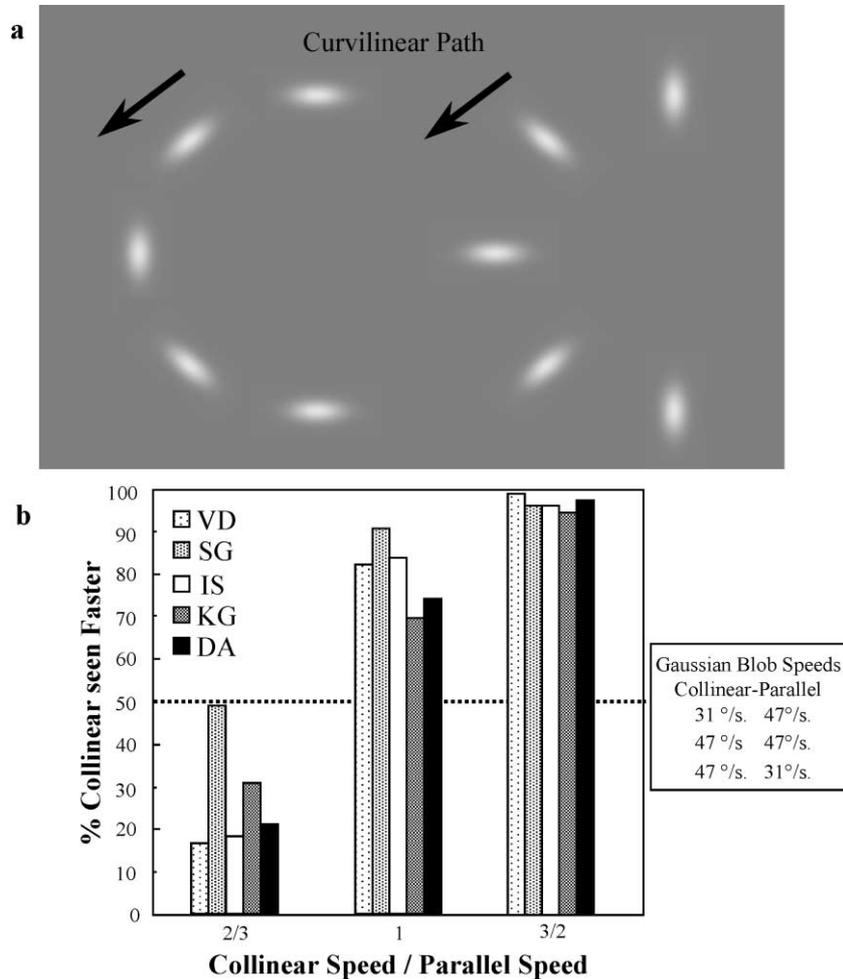


Fig. 7. (a) Stimuli used in Experiment 5: Elongated Gaussian blobs in apparent motion are either tangential to a circular motion path (curvature radius = 0.68°) or orthogonal to it (collinear and parallel sequence, respectively). Two different speeds ($31^\circ/\text{s}$ and $47^\circ/\text{s}$), obtained by changing the inter frame interval (IFI of 2 or 3 frames) are combined to yield 3 speed ratios ($2/3$, 1, $3/2$). (b) Percentage of the trials in which the collinear sequence is judged as faster than the parallel sequence as a function of the speed ratio. Individual results of 5 observers.

7.2. Results

The percentage of the trials in which observers perceived the collinear configuration as faster than the parallel is plotted for 5 observers in Fig. 7b for different speed ratios. The results clearly show that the speedup effect still occurs for these particular motion paths. When both the collinear and the parallel sequence have the same physical speed, observers perceive the collinear sequence as faster in 70–90% of the trials. When the speed ratio is $2/3$ (speeds of $31^\circ/\text{s}$ and $47^\circ/\text{s}$), collinear sequences that are physically slower than parallel sequences are still judged as faster in 15–50% of the trials. This value can be compared to the results obtained with a speed ratio of $3/2$ (speeds of $47^\circ/\text{s}$ and $31^\circ/\text{s}$) where physically faster collinear sequences are seen as faster in 95–99% of the trials.

Similar results were obtained with different “wiggling” paths composed of moving Gabor patches (data not shown), suggesting that neither the circular trajec-

tory nor the use of Gaussian blobs can account for the above results. Additional experiments in which successive Gabor patches of an apparent motion sequence were in opposite phase yielded the same pattern of result (Georges, Seriès, & Lorenceau, 2000). Assuming that “collector” units are phase sensitive, this lack of effect of relative phase further argue against a contribution of these units in the speedup effect. Altogether, these results cannot be accounted for by a reduced ability to process the speed of these curvilinear configurations, and suggest that “collector” units do not account for the observed speedup illusion.

8. Discussion

We have presented the results of psychophysical experiments showing that oriented elements moving along their orientation axis appear faster to human observers than stimuli at an angle to the motion axis. This effect

peaks at 64°/s and decreases for higher and lower speeds. It is not observed at a speed of 4°/s. Control experiments indicate that this effect cannot be accounted for by an impaired ability to process high speed apparent motion, although on average, speed discrimination is worse than usually found for longer durations and intermediate speeds (McKee, 1981; Orban et al., 1984). Neither can our data be accounted for by decision strategies relying on the spatial parameters of the motion sequences (i.e. total length traveled, jump size between frames or separation between the boundaries of oriented elements).

This speedup effect is highly sensitive to orientation anisotropy, strongly depends on the relative angle between the orientation of the moving elements and the motion axis, and is still observed for curvilinear trajectories. This suggests that it involves units highly sensitive to orientation, a property mainly expressed by neurons in areas V1 and V2. This speed bias seems to result both from an overestimation of the speed of collinear sequences and from an underestimation of the speed of parallel sequences, suggesting that both facilitatory and suppressive mechanisms may be involved, although this conclusion relies on relative comparisons between oriented and non-oriented stimuli, that may not provide a “neutral” base line reference (see discussion below and our companion paper: Seriès et al., this issue). Finally, this effect contrasts with previous results indicating that line segments moving along their orientation appear slower than lines perpendicular to the motion path (Castet et al., 1993), but is not necessarily in contradiction with them, as the range of speed under which both effects are observed is quite different.

In the following, we consider and discuss several explanations that may potentially account for this speedup illusion and try to answer the following questions:

- At what processing stage may this effect occur?
- Why is the speed bias observed at high but not at low speeds?
- What neural mechanisms can account for its orientation tuning?

We first note that the effect is maximum at a speed of 64°/s for which the spatial separation between successive elements is 1° of visual angle, such that Gabor patches do not overlap during a motion sequence (Table 1). We also note that estimating the speed of collinear sequences requires the detection of motion along an element orientation, and thus presumably along cells’ preferred orientation axis. It is thus unlikely that “classical” direction selective cells in area V1 process directly the speed and direction of such apparent motion sequences, as most of them are selective to a direction perpendicular to their preferred orientation and respond only within the limits of their receptive field. Furthermore, V1 direction selective cells appear to be tuned to

speeds slower than the ones for which the observed speed bias was more prominent (Orban, Kennedy, & Maes, 1981). This suggests that the speed bias does not originate from the responses of classical direction selective cells that have been described in area V1 and modeled as motion energy detectors (Adelson & Bergen, 1985; Emerson, Bergen, & Adelson, 1992). Direction and speed selectivity to long range apparent motion presumably involve cells in area MT that receive direct inputs from V1 and that do exhibit the long range directional interactions necessary to process high speed apparent motion sequences with large jumps between frames (Newsome, Mikami, & Wurtz, 1986). Moreover, cells that are selective to a direction parallel to their preferred orientation have been described mostly in area MT, although this type of behavior has also been observed in V1 (Geisler, 1999; Wörgötter & Eysel, 1989). Unfortunately, little is known on the speed selectivity of these cells. To account for the speedup illusion reported herein, one could speculate on the existence of two different populations of cells with different speed tuning such that cells responding to collinear motion would be biased toward signaling higher speeds. Such an ad hoc hypothesis would face the problem of explaining the mechanism underlying the specific speed tuning of these cells (but see Geisler, 1999). However, whether speed discrimination results from the readout of the responses of MT cells at a higher decision stage (as it is the case for direction, see Newsome et al., 1989), does not imply that the origin of the effect necessarily lies in area MT, as any modification occurring in earlier areas could result in the same readout effect at the MT stage. One argument against MT being primarily involved is the fine orientation tuning of the effect (Experiment 2). MT cells do show some orientation selectivity but their orientation bandwidth is on average larger than that of V1 cells (Albright, 1984). MT neurons may thus not have the orientation-tuning required to account for the orientation dependence of the speed bias.³ For sake of simplicity, one should first wonder whether cells in area V1 have the potential to explain the effect (it is unlikely that the retina or the LGN are involved as they lack orientation selective cells).

Two characteristics of the speedup effect, closely related to V1 physiology and anatomy, are striking:

- (1) The sensitivity of the speedup effect to orientation resemble that of the recently uncovered “association field” (Field, Hayes, & Hess, 1993) presumably involved in contour integration. It has been proposed

³ Psychophysical experiments that estimate the orientation tuning of motion selective cells suggest both a broad and narrow tuning, depending on the type of stimulus and task (Anderson, Burr, & Morrone, 1991; Scott-Samuel & Hess, 2002; Snowden, 1992). However, whether these psychophysical data reflect the orientation selectivity of V1 or MT direction selective cells is not clear.

that this “association field” is the perceptual counterpart of long-range horizontal connections that link neighboring neurons with similar orientation preference (Gilbert & Wiesel, 1989; Kisvarday, Bonhoeffer, Kim, & Eysel, 1996; Ts’o et al., 1986) and whose receptive fields are aligned in the visual field (Schmidt, Goebel, Löwel, & Singer, 1997; Sincich & Blasdel, 2001). These connections were found to facilitate the processing of static collinear aligned configurations (Kapadia et al., 1995, 2000; Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995) and less so, or even inhibit the processing of parallel configurations (Knierim & Van Essen, 1992; Levitt & Lund, 1997; Li & Li, 1994; Polat et al., 1998).

(2) The speed at which the speedup effect is maximum is comparable to the speed at which neural activity propagates within long-range horizontal connections as indicated by studies using optical imaging (Grinvald, Lieke, Frostig, & Hildesheim, 1994) and intracellular recordings (Binguier et al., 1999). Independent estimates of the propagation speed through long range connections in area V1 are stable across species, and range between 0.05 and 0.5 m/s, much slower than feedforward or cortico-cortical feedback conduction speeds (3–20 m/s). The conversion of these values in degrees of visual angle per second in the visual field depends on the cortical magnification factor (see Seriès et al., this issue, for a discussion of this point). To a first approximation, these values range between 50°/s and 500°/s.

Why, then, would horizontal connections be involved in the speed effect reported here? One simple possibility is that horizontal facilitatory—and inhibitory—connections modulate the response latency of cells recruited by fast apparent motion sequences. If this was the case, the delay between the responses of cells activated in succession would differ from the physical delay between successive flashes of a motion sequence, such that the spatio-temporal correlation of V1 responses, (e.g. at the MT stage) would be biased toward signaling higher speeds. This hypothesis is thoroughly explored in our companion paper (Seriès et al., this issue) and will not be discussed in details here. Note that this model provides a number of testable predictions, some of which have already been confirmed in psychophysical experiments (Georges et al., 2000; Georges, Seriès, Frégnac & Lorenceau, in preparation). Moreover, intracellular recordings in area V1 of anaesthetized cat performed in our laboratory with the same apparent motion sequences as those used in the present study, although adapted to the specific cortical magnification factor of the cat, reveal latency shifts in the range predicted by the model (Baudot et al., 2000; Lorenceau et al., 2001).

For now, let us note that this quantitative model accounts for the high sensitivity to orientational anisotropy of the speed bias, as it involves V1 cells known

for their narrow orientation tuning. Since it takes into account the dynamics of activity propagating through horizontal connections, it is able to explain the effect of speed, namely the observation of a peak at a speed of 64°/s and the diminution of the speed bias at higher speeds. Such band pass behavior is expected if the hypothesized latency shifts depends on the temporal overlap and interactions between the synaptic responses evoked by horizontal and feed forward inputs (Seriès et al., this issue). It is also compatible with the maintenance of an effect for curvilinear trajectories, as horizontal connections link neighboring cells with slightly different orientation preferences, a property required for contour integration (Field et al., 1993). In addition, the observation of overestimation and underestimation of speed (Experiment 4) may indicate that horizontal connections have facilitatory and suppressive influences, maybe through excitatory and inhibitory connections (Chavane et al., 2000; Ts’o et al., 1986). However, the non-oriented stimuli used to probe these effects should elicit a response from cells tuned to all orientations, which in turn would propagate activity in the network of horizontal connections and modulate the responsiveness of neighboring cells. Although this effect should be isotropic and of a lesser amplitude than that elicited by oriented stimuli, the processing of a motion sequence along a particular axis should nevertheless be affected by this surround modulation, making it hard to claim that non-oriented stimuli are “neutral” and can be used to derive a valid baseline reference. Indeed, preliminary data collected in our lab by D. Alais indicate that static aligned circular Gaussian blobs induce an increase in contrast sensitivity similar to that reported by Polat and Sagi (1994).

Finally, although we propose that the origin of the speedup illusion mainly lies in the dynamics of horizontal connections in area V1, it remains possible that other areas that send feedback to V1 are also involved (e.g. area V2, but see Hupé, James, Girard, & Bullier, 2001).

The speedup illusion reported here is reminiscent of the line motion effect—the perception of a fast “sweeping” motion along a line flashed after a brief stimulation with a bright dot (Hikosaka, Miyauchi, & Shimojo, 1993). Although an attentional account of this phenomenon has been proposed (Hikosaka et al., 1993; Shimojo, Miyauchi, & Hikosaka, 1997), additional experiments (Faubert & Von Grünau, 1995) and modeling (Grossberg & Raizada, 2000) also suggest a contribution of low level mechanisms. Since the spatio-temporal structure of the reference and comparison apparent motion sequences used here is identical, it is unlikely that an attentional account can explain the present results. Although it seems possible that similar low level mechanisms underlie both the speedup and line motion effects, it should be noted that the temporal parameters

that maximize the line motion effect (a delay of 100–200 ms between the presentation of the inducing spot and the flashed line) are longer than the fast and brief (<100 ms) motion sequences used herein.

We evoked in the introduction the finding that a line segment moving along its orientation appears to move more slowly than a line segment perpendicular to the motion axis (Castet et al., 1993; Scott-Brown & Heeley, 2001). This may seem at odds with the present results. However, the observation that the speedup illusion disappears at slow speeds (4°/s), and preliminary data obtained with a Gabor patch moving at even slower speeds (Georges et al., 2000) suggest that both a speedup and a slowing down effect coexist, and are expressed for a different range of speed. We suggest that both effects may involve different mechanisms: a spatio-temporal vector averaging process for slow speed stimuli (Castet et al., 1993), and the recruitment of horizontal connectivity for high speed stimuli. In keeping with this dichotomy, the pattern of response to moving stimuli seen with optical imaging techniques suggests that the functional regime of oriented cells in primary visual cortex shifts with the speed of moving stimuli, with a break through around 20–30°/s, such that the orientation columns activated by slow stimuli switch by 90° when stimuli move at a speed above this limit (Crook et al., 1994; White, Basole, & Fitzpatrick, 2001).

To conclude, we have presented psychophysical experiments showing that the perception of speed is strongly influenced by the orientation of stimuli relative to their motion axis. Whether a speed bias at high motion speed plays a functional role in motion processing or is a side effect of the spatio-temporal dynamics of long range lateral interactions remains unclear. One intriguing possibility is that an anisotropic modulation of the time course of the response of V1 cells by preceding stimuli could provide a useful temporal tag to segregate figure and ground at higher processing stages.

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