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Segmentation by single and combined features involves different contextual influences

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Orientation discrimination of a texture line having orientation different from that of static background lines is facilitated when the lines are aligned along their orientation axis and when their separation is small (Experiment 1a). The facilitation by alignment remains when motion is added to the target (Experiment 1b). However, when the motion rather than the orientation has to be judged, alignment reduces sensitivity (d') regardless of whether the target has orientation the same as (iso-oriented) or different from background elements (Experiment 2). The inhibitory effect of alignment is confirmed when subjects have to discriminate the motion direction of an iso-oriented target (Experiment 3). Such inhibition by alignment is stronger when elements are close and may reflect a property of lateral interactions of motion detectors, since it is only present when observers have to judge the target motion direction. Overall, our results indicate an opposite role of the lateral interactions that facilitate grouping of iso-oriented and collinear elements, in segmentation by orientation contrast and motion contrast. In other words, global grouping (i) facilitates discrimination of orientation contrast, indicating a global process, and (ii) inhibits both detection and discrimination of motion contrast, suggesting the presence of a local process.

1. Introduction

Fragments of images are not processed in isolation, but instead are interpreted as part of a whole, global structure. The Gestalt psychologists were the first to describe the influence of global context on the perception of local features and to suggest that perceptual salience depends upon Gestalt laws of perceptual organization. According to the Gestalt laws of proximity, similarity, good continuation and common fate, some elements in an image segment from surrounding elements if they are remote from each other, dissimilar, misaligned or do not move in the same direction (Rock & Palmer, 1990). The initial outputs of low-level visual filters selective for basic features of a stimulus (e.g., spatial frequency, orientation, direction of motion and position) are insufficient to account for these visual context effects. To explain contextual influences, physiologists suggested and demonstrated that the response of cells in V1 to stimuli presented inside the classical receptive field (RF) can be modulated by stimuli laying in the surroundings of RF, while recent anatomical (Rockland & Lund, 1982, 1983) and physiological studies have investigated spatial (Gilbert, Das, Ito, Kapadia, & Westheimer, 1996; Kapadia, Ito, Gilbert, & Westheimer, 1995) and temporal mechanisms (Singer & Gray, 1995; Yen & Finkel, 1998) by which these context-dependent effects may arise in the striate cortex. It has been shown that these contextual influences can be both inhibitory and excitatory (for a review see Lamme, 2004). For example, single unit recording showed the existence of suppressive/inhibitory interactions between the classical and the surrounding RFs (Nelson & Frost, 1978; Sillito, Grieve, Jones, Cudeiro, & Davis, 1995). Although the presence of collinear flankers also acts to suppress the cell response with targets at suprathreshold contrast levels (Polat, Mizobe, Pettet, Kasamatsu, & Norcia, 1998), collinearity may produce facilitation when a near threshold stimulus inside the RF is flanked by high contrast collinear elements in the surround. However, a study of Kapadia et al. (1995) reports excitatory influences also using high contrast bar stimuli when these are co-aligned over both the classical and non-classical RF. Psychophysical studies often reported a suppressive effect of collinear flankers on contrast detection or discrimination (Snowden & Hammett, 1998; Solomon, Sperling, & Chubb, 1993). However, Polat and Sagi (1993, 1994) clearly showed increased contrast sensitivity for a target, a Gabor consisting of a cosinusoidal carrier multiplied by a Gaussian envelope, surrounded by two Gabor flankers when local and global orientations were aligned. The space constant of the Gaussian envelope (σ) was set equal to the wavelength of the carrier; this had the effect to scale the size of the Gabor as a function of the carrier's wavelength and permitted to set the target-flanker distance proportionally to the size of the Gabors. The centre-to-centre target-flanker distance was expressed in terms of multiples of the carrier's wavelength. In particular, Polat and Sagi (1993) using a low contrast Gabor vertically surrounded by two high contrast Gabors found a suppressive region

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of about two wavelengths (λ) in which the presence of the flankers increased the target contrast thresholds. Beyond this range they found a larger facilitatory region up to 10λ, in which there was a decrease of the target's contrast threshold. Polat and Sagi (1993) using a wavelength of 0.15°, a spatial frequency of 6.67 cpd (1/λ) and σ of 0.15°, found a facilitation at 3λ of target-flank distance (i.e., 3*0.15 = 0.45°) that corresponds to about 30 arcmin. Kapadia et al. (1995) also reported that observer's contrast detection for a bar was 40% improved by a second suprathreshold collinear bar at a distance of about 30 arcmin.

To summarize, there is both neurophysiological and psychophysical evidence of collinear facilitation in contrast detection of targets at both threshold and suprathreshold levels.

Contextual influences by collinear elements may also facilitate texture segmentation based on differences in orientation. Collinear facilitation by the flankers in a contrast detection task was also found when the target had to be segmented from randomly oriented background elements (Polat & Bonneh, 2000). In this case, although the background increased contrast thresholds, suppression became facilitation when two of the elements flanking the targets were made iso-oriented and collinear, even at relatively high target contrast levels (up to 40%). The distance capturing maximal facilitation was again at 3λ (corresponding to ~30 arcmin). The results outlined by Polat and Bonneh (2000) suggest that when employing appropriate distances, facilitation of texture segmentation by collinear flankers may occur when the target is defined by a relatively wide range of luminance contrast levels. The study of Polat and Bonneh (2000) is relevant because the facilitation by collinear flankers is found in a task involving both contrast detection and texture segmentation based on orientation contrast. Indeed, whereas improved detection of the isolated target indicates contrast enhancement, improved texture segmentation indicates reduced surround suppression from the randomly oriented background. In the conditions in which a facilitatory effect was found with a suprathreshold target, Polat and Bonneh (2000) measured improved target-background segmentation based on orientation contrast by the collinear iso-oriented flankers rather than contrast detection. In our recent study in which target and background elements had the same high contrast (Casco, Campana, Han, & Guzzon, 2009), we isolated the role of flankers collinearity in texture segmentation based on orientation contrast; that is, the observers' ability to discriminate the orientation of a central Gabor from a background of 45° oriented Gabors was found to increase when the target was flanked by two iso-oriented and collinear flankers compared with flankers iso-oriented and non-collinear or else ortho-oriented.

In addition to the facilitation of texture segmentation induced by flankers collinear with respect to the target, the facilitatory effect may be investigated by manipulating the collinearity of the background elements (i.e., the texture region). There is wide evidence that alignment of elements in the texture region also facilitates segmentation based on orientation contrast in several tasks: localization of differently oriented texture element (Meigen, Lagreze, & Bach, 1994), discrimination of a texture boundary (Giora & Casco, 2007) and of a texture figure (Casco, Campana, Grieco, & Fuggetta, 2004; Casco, Grieco, Campana, Corvino, & Caputo, 2005; Harrison & Keeble, 2008). Such facilitation from the region poses problems of establishing whether collinearity is a background or a target-to-background feature. Indeed, the facilitation by collinearity may occur both from elements near the target and from those in the texture region – where iso-oriented and collinear elements form perceptual structures that may facilitate segmentation based on orientation contrast. Studies by both Giora and Casco (2007) and Harrison and Keeble (2008) have shown a specific effect of the facilitation from the region, independent of that produced by target-to-flanker lateral interactions.

To summarize, previous studies show that flankers iso-oriented and collinear with the target facilitate its segmentation from the surrounding texture region. This may reflect the role of collinearity in increasing the saliency of the target as a consequence of the reduction of surround suppression by iso-oriented background elements. Moreover, segmentation based on orientation contrast may also be facilitated by the alignment of element in the far texture region.

In the present study we asked whether background collinearity could facilitate the target-to-background segmentation, both when the segmentation was based on motion contrast and on superimposed features-contrast, such as orientation and motion. To this purpose we compared contextual influences when background elements and target where aligned (collinear) and when they were misaligned (non-collinear), in three conditions of features-contrast: (i) when target saliency was due to orientation contrast alone; (ii) when target saliency was due to orientation and motion contrast; (iii) when target saliency was due to motion contrast alone. Thus, in our Experiments collinearity was both a background and a target-to-background feature.

Although contextual influences have been shown in neurons selective for both orientation and motion direction (Akasaki, Sato, Yoshimura, Ozeki, & Shimegi, 2002; Jones, Grieve, Wang, & Sillito, 2001; Kastner, Nothdurft, & Pigarev, 1997; Walker, Ohzawa, & Freeman, 1999), investigation to date has been limited to the inhibitory effect of a surround drifting in the preferred direction (Walker et al., 1999) and partially in the non-preferred direction (Jones et al., 2001). These results show that the presence or absence of figure-ground segregation due to either a difference of orientation or motion direction is critical for the strength of surround suppression (Akasaki et al., 2002). To our knowledge, the issue of whether discrimination of motion contrast can be modulated by features-alignment has never been studied. A modulation, however, is not unlikely since Kapadia et al. (1995) found that the detection enhancement at optimal coaxial separation was reduced considerably by applying a lateral offset of as little as 10 arcmin; this could suggest an inhibitory effect of alignment in motion detection since motion also produces a lateral offset.

We compared the effect of contextual influences by non-collinear and collinear background elements that form 45° oblique, collinear structures on various different tasks, considering not just texture segmentation based on orientation contrast (Experiment 1a) and motion contrast alone (Experiment 3), but also measuring orientation discrimination with a target defined by superposition of orientation and motion (Experiment 1b) and motion detection of a target similarly defined (Experiment 2). Moreover, we also asked whether the effect of alignment was different for small and large separations between elements. The seminal work of Gestalt psychology (Wertheimer, 1923) threw light on the role of elements separation on perceptual integration of texture elements into perceptual structures. The issue is still relevant because studies in recent decades have shown that inter-element spacing affects texture segmentation (Nothdurft, 1985) in addition to contrast detection. In addition, studies have shown that contrast enhancement by collinear flankers occurs only within a restricted inter-element separation of 20–30 arcmin (Polat & Bonneh, 2000, 1993, 1994; Polat et al., 1998).

2. General method

2.1. Apparatus and stimuli

Stimuli were generated by a Cambridge Research System VSG graphics card with 12-bit luminance resolution, and displayed on a gamma-corrected Sony monitor with a resolution of

1024 × 768 pixels, with square pixel (1 arcmin). Refresh rate was set at 100 Hz. Stimuli were free-viewed binocularly in a room with dim illumination and presented at the centre of a monitor placed at 114 cm from the observer's eye.

2.2. Frame definition

In all Experiments the term "frame" refers to a set of three identical displays for three monitor refreshes; thus, each frame has a duration of 30 ms. Each frame contained a background textured region made up of line-segments slanted 45° clockwise (Fig. 1). Line length was equal to 19 arcmin. Texture elements were arranged on 8 × 8 raster subtending 6 × 6°. The centre-to-centre separations between lines were 32 and 44 arcmin for the small and large separations, respectively. The target and background elements were either aligned or deviated from alignment by modifying both horizontal and vertical positions by a fixed distance of 8 arcmin around the centre of each raster cell, randomly in all directions. The target consisted in a line-segment segregating from the background on the basis of orientation contrast, motion contrast or both orientation and motion contrast. The target was one background line chosen randomly. When defined by orientation contrast, target line orientation (target tilt direction) differed with respect to background line orientation either clockwise (more-horizontal) or counter-clockwise (more-vertical). Target-background orientation contrast ($\Delta\Theta$) was 0, 3, 6, 9 or 12° away from the initial orientation of 45° when the target was moving and 0, 6, 12, 18 or 24° when it was static. The luminance of the stimuli was 34.21 cd/m^2. Background luminance was 2.06 cd/m^2.

2.3. Frames sequence

Each trial consisted of a sequence of two frames in which the background elements maintained the same position, whereas the target was either in the same position in the two frames (static condition) or displaced horizontally by a distance (Δd) in the second frame (moving condition). The two frames were separated by a blank interval (inter-frame-interval – IFI) with a duration corresponding to a single monitor refresh (i.e., 10 ms).

2.4. Subjects

Six subjects (including two of the present authors) with normal or corrected-to-normal vision, participated in each experiment. To guarantee a repeated-measures design across experiments, five observers (two authors and three naïve subjects) participated in all experiments.

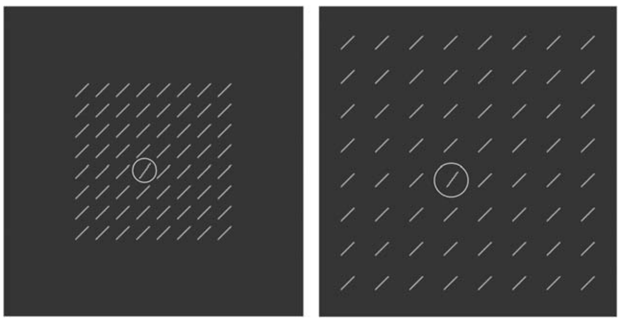

Fig. 1. Two 8 × 8 rasters with more-horizontal targets (ringed) than the other iso-oriented background elements. (a) Stimulus configuration with small inter-element separations. (b) Stimulus configuration with large inter-element separations.

2.5. Design

In all experiments, target tilt direction (more-horizontal and more-vertical) and the levels of $\Delta\Theta$ (Δd) were within-block factors. A block consisted of 10 randomly presented repetitions of each stimulus level. The levels of misalignment, and the inter-element separation were between-blocks factors. In each experiment observers performed two repetitions of each block of trials so that each data point was based on 20 observations. Each experiment took place in different daily session and each session comprised one block of each condition, performed in counter-balanced order with a resting interval between blocks. Before starting each experiment, subjects participated in a practice session consisting of 10 randomly chosen trials of the block they were going to perform first.

2.6. Data analysis

To assess the influence of spatial context on local judgments, we measured accuracy for identifying the direction of orientation (Experiment 1) or of horizontal motion (Experiment 3); data were fitted using a Probit (Finney, 1971) to determine the threshold. Each threshold estimate corresponded to the orientation contrast (or motion contrast) resulting in 75% correct responses. In Experiment 2 (in which we used a detection task), d' was calculated to assess sensitivity.

3. Experiment 1a: segmentation based on orientation contrast

Experiment 1a examined whether there is facilitation by elements' alignment in the segmentation of a target defined by orientation contrast.

3.1. Method

Stimulus, frame definition, frame sequence and experimental design were the same as described in the general method. We used five levels of orientation contrast (0, 6, 12, 18, and 24°), two levels of spatial separation (32 or 44 arcmin) and two levels of spatial jitter (0 or 8 arcmin). Examples of the stimuli are represented in the top row of Fig. 2 for the different alignment and spacing levels. Observers were asked to perform a binary-choice task, indicating whether the target was more-horizontal or more vertical than background elements.

3.2. Results and discussion

The psychometric functions for the six subjects are shown in Fig. 3. Those deriving from aligned elements (thick lines) are steeper, indicating that the orientation discrimination is improved by alignment. This result is confirmed by the ANOVA, which revealed a significant reduction of thresholds by alignment, from 17.1 to 12.2° ($F_{1,5} = 37.9$; $p = 0.002$). Moreover, thresholds are lower for the smaller inter-element separation of 32 arcmin ($F_{1,5} = 58.2$; $p = 0.001$). Thus, orientation discrimination was easier when background elements and target were aligned and close to each other. This result agrees with those obtained with contrast enhancement paradigm in both physiological (Das & Gilbert, 1999; Kapadia, Westheimer, & Gilbert, 2000) and psychophysical studies, which show collinear facilitation at similar separations to those we used (Polat & Sagi, 1993, 1994). The present results are in full agreement with our previous psychophysical findings that segmentation of one element by orientation contrast (Casco et al., 2009) is facilitated by spatially closed collinear and iso-oriented elements.

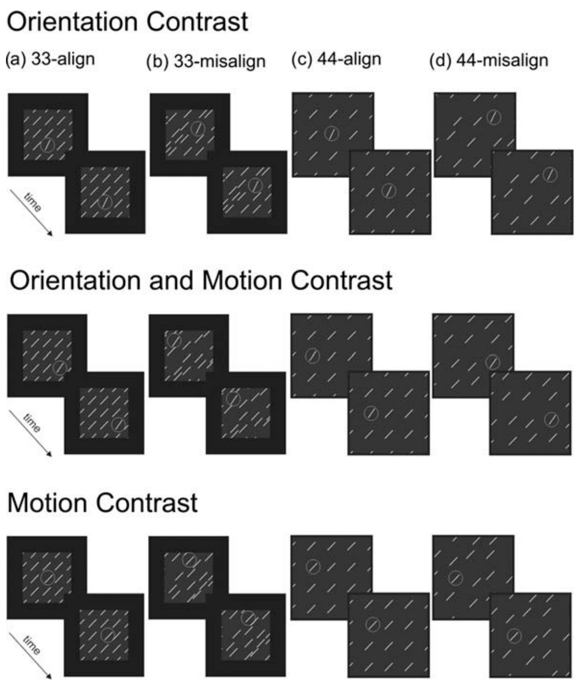

Fig. 2. Top row represents a view of the 8 × 8 matrix used as stimuli. Each stimulus is defined by a 2-frames sequence. Stimuli in the top row represent a target defined by orientation contrast (used in Experiment 1a) embedded in a background of aligned and close elements (inter-element spacing equal to 33 arcmin, top row-a), of misaligned and closed elements (top row-b), and aligned distant elements (inter-element spacing equal to 44 arcmin, top row-c) and misaligned and distant elements (top row-d). Middle row represents a target defined by orientation and motion contrast combined (used in Experiment 1b and Experiment 2) in the same four conditions: 33-aligned (middle row-a), 33-misaligned (middle row-b), 44-aligned (middle row-c), 44-misaligned (middle row-d). Bottom row represents a target defined by motion contrast (used in Experiment 2 and Experiment 3) in the same four conditions: 33-aligned (bottom row-a), 33-misaligned (bottom row-b), 44-aligned (bottom row-c), 44-misaligned (bottom row-d).

4. Experiment 1b: segmentation based on orientation and motion contrast

Experiment 1b examined whether the facilitation by elements' alignment also occurs with target defined by both orientation contrast and motion.

5.1. Method

Stimulus, frame definition, frame sequence and experimental design were the same as described in the general method. We used five levels of orientation contrast (0, 3, 6, 9, and 12°), two levels of spatial separations (32 or 44 arcmin), a Δd of 4 arcmin, and two levels of spatial jitter (0 or 8 arcmin). Examples of the stimuli are shown in the middle row of Fig. 2 for the various alignment and spacing levels. Observers were asked to indicate whether the target was more-horizontal or more vertical than background elements.

5.2. Results and discussion

The psychometric functions of the same six subjects who participated in Experiment 1b are shown in Fig. 4. Once again the psychometric functions are steeper in the aligned condition, indicating that when the target is defined by superimposed features, the facilitation by alignment is still present. Indeed, the effect of alignment is still significant ($F_{1,5} = 9.8$; $p = 0.026$), indicating that thresholds are reduced by alignment at both separations. Moreover, the effect of spacing is also significant ($F_{1,5} = 7.6$; $p = 0.04$) indicating lower thresholds for small spacing.

For a clearer interpretation of these data, thresholds obtained in Experiments 1a and 1b were compared with a general ANOVA; the results are summarized in Fig. 5.

Thresholds are always lower when target moves ($p = 0.001$), with aligned elements ($p < 0.001$), and with the smaller inter-element separation ($p = 0.002$). In other words, aligned elements facilitate segmentation based on orientation contrast both when the target is static and when the target moves.

Our suggestion is that facilitation of texture segmentation by alignment comes from a global process of lateral interactions that groups iso-oriented and aligned elements in the region into diagonal chains, i.e., discrimination of the target orientation when compared to the group seems easier than when compared to a single flanker.

The question we ask is why facilitation by alignment persists when the target is moving. Does the facilitation occur because of the task that forces the subject to judge the direction of orientation contrast? Or does it occur because there is a general facilitation by alignment in motion discrimination? In the first case, it would not necessarily be present if the subjects were asked to judge the lateral offset produced by motion: we formed this hypothesis on the basis of the evidence (Kapadia et al., 1995) that with static low-contrast targets and high-contrast flanker, lateral offset reduces the facilitation produced by the flanker; if the offset is large, it results in inhibition of target detection.

To distinguish between these two possible explanations we asked whether the segmentation of the moving target would be facilitated by alignment when subjects had either to detect or to discriminate their motion.

6. Experiment 2: motion vs. orientation and motion

In Experiment 2 we compared sensitivity with aligned and misaligned elements in two stimulus conditions: (i) with target defined by superimposed features in which the orientation contrast was highly discriminable; (ii) with target defined only by motion contrast. If the facilitation by alignment reflected specific contextual influences in discrimination of orientation contrast, regardless of whether the target was static or moved, we would not expect this facilitation in the condition in which orientation contrast was abolished. Since most studies investigating collinear facilitation used detection tasks, we also used a detection task in which observers have to detect the target, present in 50% of the trials.

6.1. Method

Stimulus, frame definition, frame sequence and experimental design were the same as described in the general method. In each block the target was defined by superposition of orientation either 0 or 10° away from the initial orientation of 45°, and motion contrast. We used two levels of spatial separations (32 or 44 arcmin) and a Δd of 3 arcmin for all subjects except AP (2 arcmin) and DG (5 arcmin) and two levels of jitter (0 or 8 arcmin). The stimulus condition with no orientation contrast is shown in Fig. 2 (bottom row) with a displacement 5 arcmin (that used by DG). The stimulus condition with orientation contrast present is shown in Fig. 2 (middle row) with an orientation contrast slightly larger (12 instead of 10 arcmin).

A yes–no task was used in which observers had to indicate the presence or absence of a moving target that segregated from the static background and was present in half of the trials.

A block consisted of 80 randomly presented trials resulting from 10 repetitions of target tilt direction levels (more-horizontal and more-vertical) and $\Delta\Theta$ levels (0 and 10°) for both present and absent trials. Target direction of tilt (more-horizontal vs. more-verti-

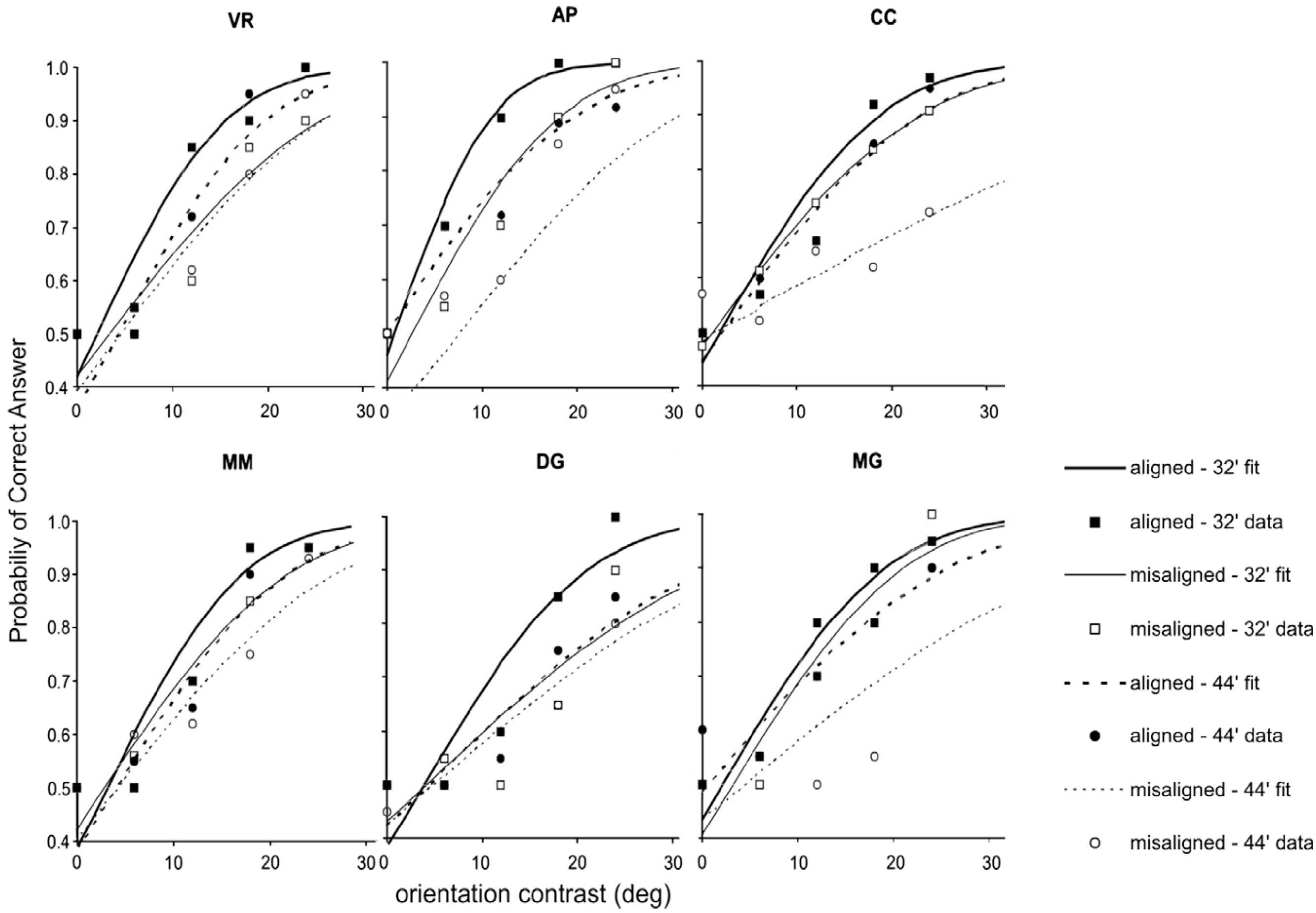

Fig. 3. Psychometric functions for the six subjects obtained in Experiment 1a, in which target was defined by orientation contrast. The probabilities of correct answer are shown as a function of the orientation contrast for small inter-element separations (continuous lines) and large inter-element separations (broken lines), with aligned (thick lines) and misaligned (thin lines) elements.

cal), and the two levels of target-background orientation contrast were within-block factors. Alignment and separation levels were between-blocks factors.

6.2. Results and discussion

The results, illustrated in Fig. 6, show that the effect of alignment is opposite to that found in Experiment 1, i.e., aligned elements did not facilitate detection but inhibited it. d' was lower in the aligned condition ($F_{1,5} = 11.3$; $p = 0.02$) and the effect was evident at both small and large spacing. Indeed, the interaction between alignment and spacing is not significant ($F_{1,5} = 2.29$; $p = 0.19$). Most importantly, although sensitivity increases when orientation contrast is added to motion contrast ($F_{1,5} = 16.6$; $p = 0.01$), the impairment by alignment is similar for targets having 0 and 10° orientation contrast. This clearly demonstrates that the inhibition by alignment is an effect specific for detecting motion. We suggest that alignment produces background grouping of elements into diagonal chains, and this impairs the local discrimination of the change of the target's relative position with respect to the background elements.

7. Experiment 3: effect of amount of displacement

Experiment 3 was designed to confirm the interpretation that discrimination of the lateral offset produced by motion is a local phenomenon, which relies on comparison of relative position between the target and one flank. To seek support for this interpretation, we measured motion-induced lateral offset thresholds for a target iso-oriented to background elements. We predicted that if based on local comparison of relative position, the motion discrimination task would be more difficult with aligned elements, since these might induce perception of diagonal chain that includes the target.

7.1. Method

Stimulus, frame definition, frame sequence and experimental design were the same as described in the general method. The target had no orientation contrast. Consistently with the previous experiments, we used two levels of spatial separation (32 or 44 arcmin), two levels of jitter (0 or 8 arcmin), and six levels of horizontal displacement (0, 1, 2, 3, 4 and 5 arcmin). Examples of the stimuli are given in the bottom row of Fig. 2 for the various different alignment and spacing levels. Observers performed a binary-choice task in which they had to discriminate the direction of motion: either leftwards or rightwards.

Thresholds for discriminating the direction of motion were obtained by measuring accuracy as a function of motion displacement, and were defined as the smallest motion displacement that allowed observers to judge correctly whether the target moved left or right in 75% of the trials.

7.2. Results and discussion

Fig. 7 shows that individual psychometric functions are steeper when elements are misaligned (thin lines), indicating lower

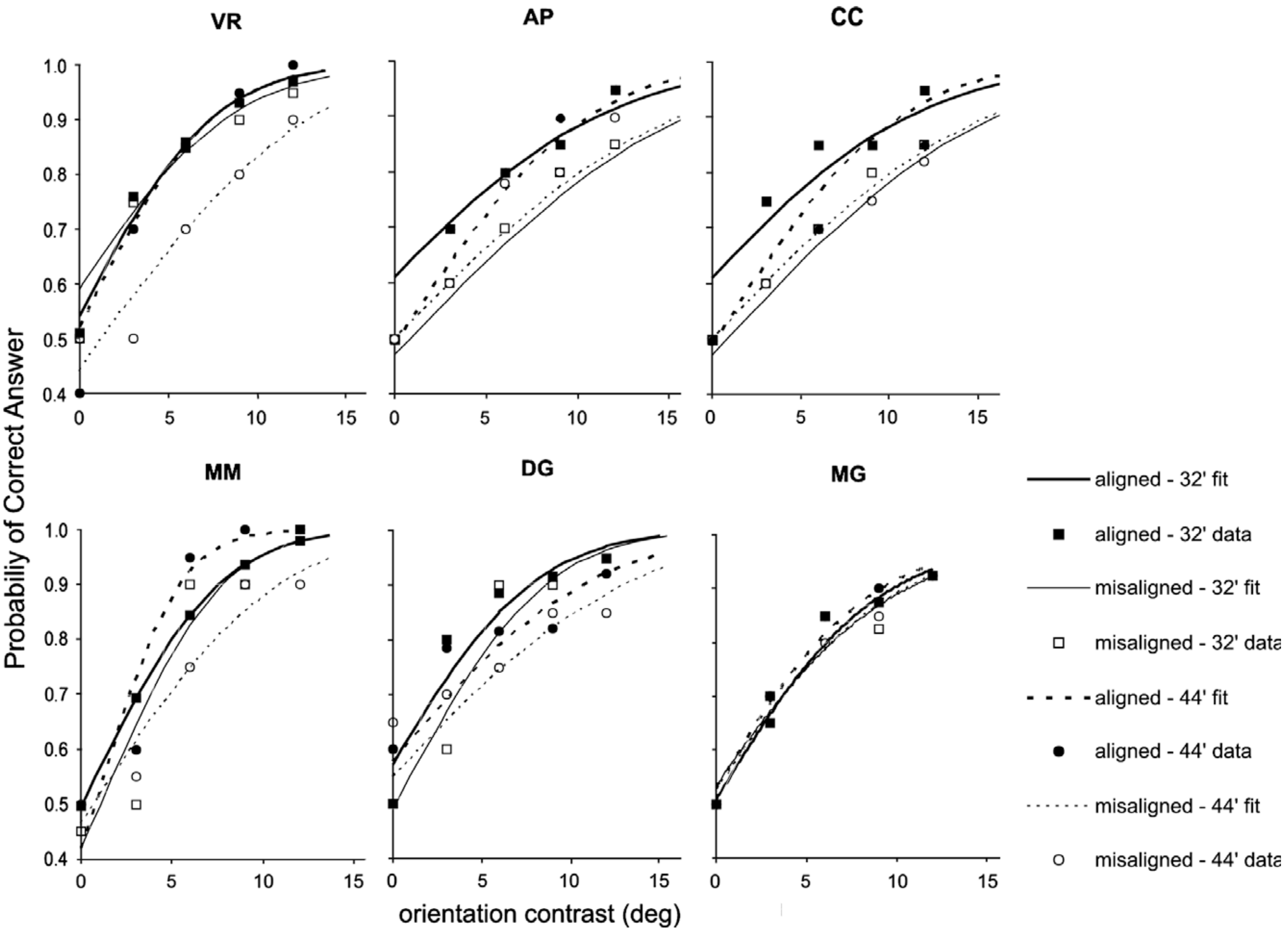

Fig. 4. Psychometric functions for the six subjects obtained in Experiment 1b, in which target was defined by the superimposition of orientation contrast and motion. The probabilities of correct answer are shown as a function of the orientation contrast for small inter-element separations (continuous lines) and large inter-element separations (broken lines), with aligned (thick lines) and misaligned (thin lines) elements.

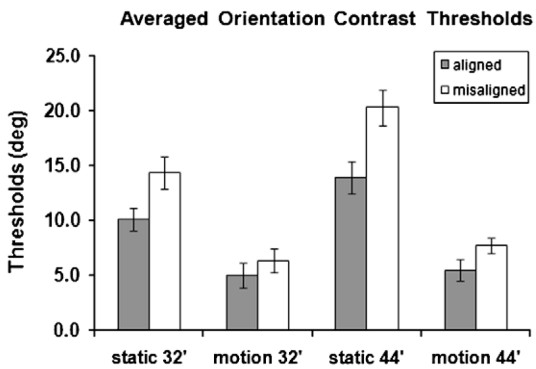

Fig. 5. Averaged orientation contrast thresholds obtained in Experiments 1a and 1b. For the aligned and misaligned conditions, thresholds are compared separately for static and moving targets at small and large separations (see text for more details).

thresholds in this condition. The facilitation by misalignment is confirmed by the ANOVA, showing a significant reduction in thresholds when elements are misaligned ($F_{1,5} = 7.17$; $p = 0.04$). Moreover, thresholds decrease at small separations ($F_{1,5} = 14.39$; $p = 0.013$), indicating that local comparisons between target and background elements, necessary to perform the motion discrimination task, relies on short-range interactions.

8. General discussion

The present study was designed to establish whether a background and a target-to-background structure resulting from elements' alignment affected segmentation by orientation and motion contrast in similar or different ways. To address this question we compared the effect that aligned and misaligned background elements had on different segmentation tasks, based on orientation contrast, orientation and motion superimposed, and motion alone. Discrimination of a target either static or moving and having different orientation from background elements is facilitated by alignment of the background elements at both small and large spacing (Experiment 1). Instead, when the task is to detect target's motion or discriminate the targets' motion direction, the alignment does not facilitate, but rather it inhibits, and this is confirmed by both higher sensitivity (d') (Experiment 2) and lower thresholds in the misaligned condition compared with the aligned condition (Experiment 3). Such inhibition by alignment in the motion discrimination task occurs regardless of whether the target is always iso-oriented to background elements (Experiment 3) or is iso-oriented in only half of the trials (Experiment 2). To investigate the effect of background and target-to-background collinearity we used the same stimulus configuration across all the Experiments, but we systematically varied the tasks. However, an anonymous reviewer argued that the differences we found between the results of Experiment 1b (orientation task) and 2 (motion detection) might depend on the fact that the choice of orientation and motion fea-

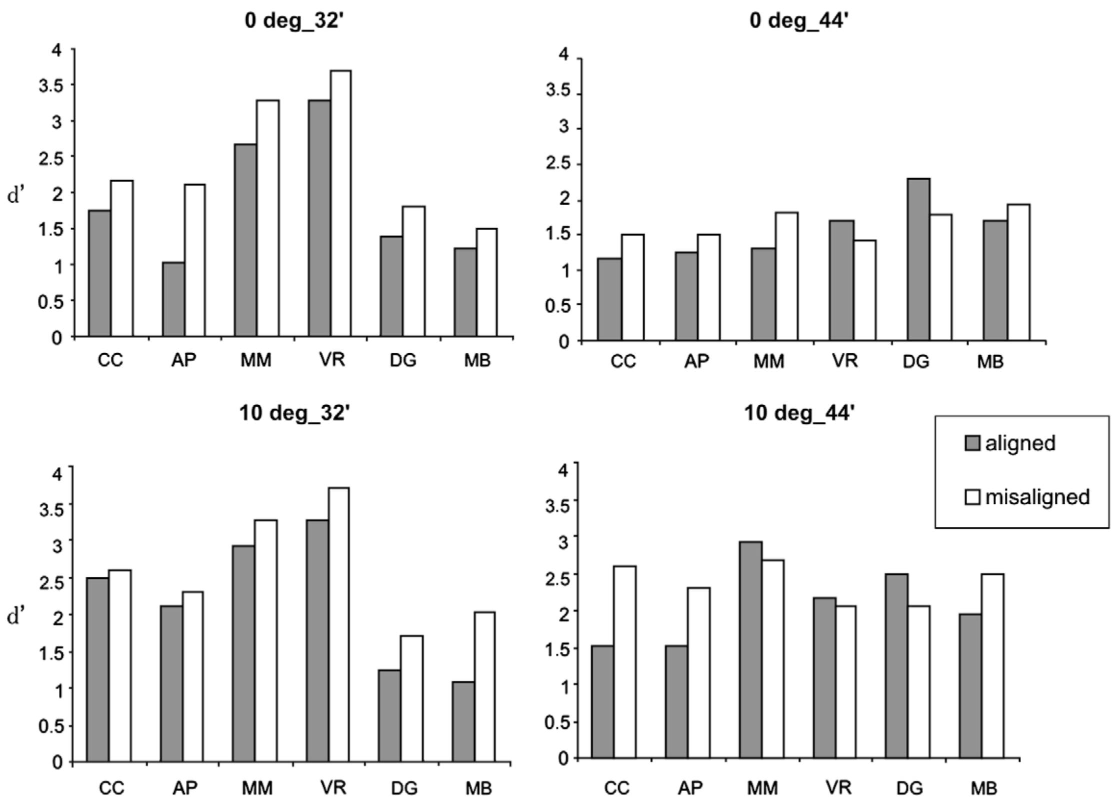

Fig. 6. d' for the six subjects with target defined by orientation and motion contrast for two levels of orientation contrast (0 or 10°) and two levels of inter-element separation.

tures were not symmetric. In particular, although the targets in both Experiments were defined by a superimposition of orientation and motion, the feature that permitted to discriminate the target from the background could be either orientation contrast in the Experiment 1b (i.e., more-horizontal or vertical than the background elements) or the presence vs. absence of the orientation feature in the case of the motion detection task (Experiment 2 – in which we used two orientation levels [0 and ±10°]). In order to make the two conditions symmetric some motion signals should be added to every background element in the motion task, for example employing different directions and/or speeds with respect to the target. Moreover, the orientation task could be made similar to the motion task by removing orientation signals from the background. However, it should be noted that introducing differences in speeds, motion direction or removing orientation signals from the background reduces the similarity between target and background elements, this could affect lateral interactions and consequently could not permit to establish the role of background and target-to-background collinearity. Thus, we measured the effect of collinearity by introducing voluntarily an asymmetry between tasks and maintaining the same stimulus configurations across all the Experiments. To some extent it is possible that in Experiment 1b when judging the spatial orientation of the target, the coexistent motion information could provide a signal that interacts with the orientation signal improving target segmentation. Such integration mechanism might operate maximally over a contour of collinear and aligned elements, revealing a global nature. On the other hand, when the relevant task feature become the motion-induced lateral offset, the operative range of such integration mechanism could be shifted towards local comparisons and therefore be impaired by global configurations. Thus, our results with moving target not only show the effect that motion offset increases the saliency of a target defined by orientation contrast but also reveal the new finding that the discrimination of its lateral offset, which relies on local comparison of relative position between target and flanks, is inhibited by global collinearity grouping.

It is worthwhile exploring the literature for any indication of dissociation between the effect of contextual influences with static and dynamic displays. Neurophysiological studies suggest an interpretation of facilitation by alignment relying on the well-known modulation of the response in V1 to stimuli presented inside the RF by stimuli lying outside the RF. In appropriate spatial conditions and task, these "contextual influences" by collinear and iso-oriented flanker/s outside the RF facilitate the response to a stimulus inside it (Kapadia et al., 1995; Polat et al., 1998), and this has been suggested to account for the facilitatory effect of collinearity on integration grouping (Casco et al., 2009; Field, Hayes, & Hess, 1993) and segmentation based on orientation contrast (Casco et al., 2009; Giora & Casco, 2007; Harrison & Keeble, 2008; Kapadia et al., 2000; Li, Piech, & Gilbert, 2006). Our results confirm the suggestion that features-contrast reduces inhibition by the surround (Knierim & van Essen, 1992), and support the suggestion (Akasaki et al., 2002; Chen, Dan, & Li, 2005; Jones et al., 2001; Kastner et al., 1997; Lamme, 1995; Walker et al., 1999) that the differential expression of the suppressive surround effect due to the presence of orientation/direction contrast between elements in the classical and non-classical RF might be the neuronal correlate of pop-out in the primary visual cortex.

Our facilitatory effect of alignment on static segmentation can be interpreted as reflecting a further disinhibitory mechanism (Walker, Ohzawa, & Freeman, 2002), which, together with features-contrast, contributes negatively to surround suppression in texture images by reducing it. Therefore, our results support the suggestion that target-to-flanker/s and target-to-background collinearity not only facilitate contrast enhancement of targets at threshold (Polat & Sagi, 1993, 1994) and suprathreshold levels (Polat & Bonneh, 2000), but also facilitate texture segmentation (Casco et al., 2004, 2005; Giora & Casco, 2007; Harrison & Keeble, 2008;

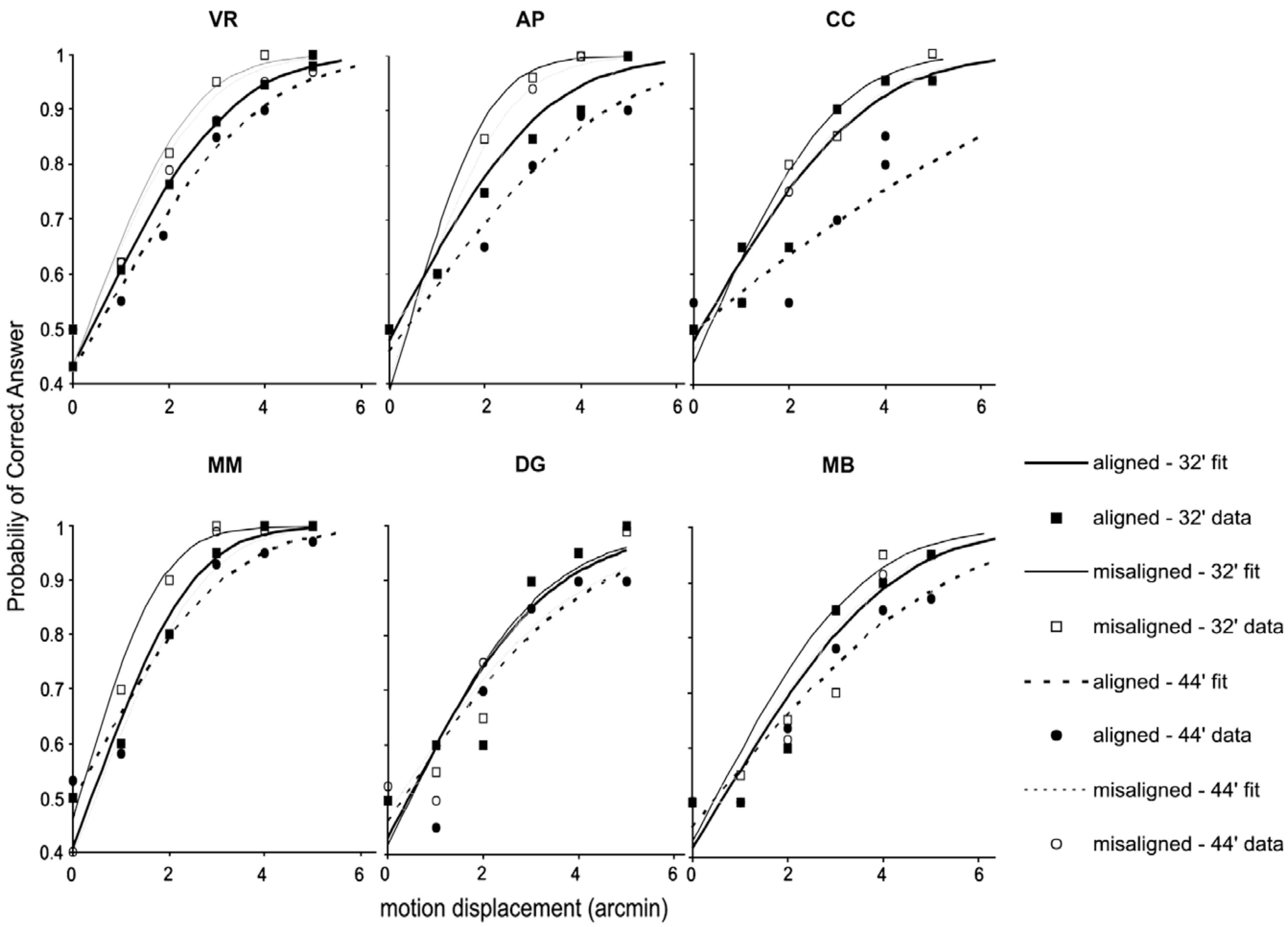

Fig. 7. Psychometric functions for the six subjects obtained in Experiment 3, in which target was defined only by motion. The probabilities of correct answer are shown as a function of the amount of displacement of the target for small inter-element separation (continuous lines) and large inter-element separation (broken lines), with aligned (thick lines) and misaligned (thin lines) elements.

Meigen et al., 1994). The same explanation can account for the facilitation we found in the orientation discrimination task when the target was defined by superimposed features although, as expected, this target is more salient than one defined solely by orientation contrast. The results obtained when motion was added to orientation contrast agree with previous finding that there are contextual influences in neurons selective for both orientation and motion direction (Akasaki et al., 2002; Jones et al., 2001; Kastner et al., 1997; Walker et al., 1999).

The new finding here is that there are opposite contextual influences that collinear elements in the texture produce on segmentation by orientation contrast and by motion contrast: these contextual influences were inhibitory when subjects had to either detect or discriminate motion contrast. It is possible that the motion is too fast to capture collinear facilitation, which is slower than inhibition (Polat & Sagi, 2006). Note however that our stimulus was not followed by the mask and therefore, considering the duration of visual persistence, lateral interactions had more than 200 ms to establish which, according to the results of Polat and Sagi (2006) is long enough to produce the full pattern of lateral interactions. On the other hand, our result of collinear inhibition in motion discrimination, together with the result of Kapadia et al. (1995), that the detection enhancement at optimal coaxial separation between target and flanker was reduced considerably by applying a lateral offset to the flanker of as little as 10 arcmin, suggests a general inhibitory effect of alignment on the response of mechanism encoding relative position between elements. While, the effects of alignment and spacing on discrimination by orientation contrast indicate that this task is facilitated when the target orientation can be compared to the orientation of the whole structure rather than to that of a single element, and impaired when these structures are perceptually weak. Instead, the discrimination by motion contrast is modulated by collinearity in the opposite way: segmentation by motion is worse when target and surrounding elements are aligned, suggesting that the integration of target and background iso-oriented lines into a diagonal perceptual structure impairs motion discrimination. Furthermore, motion discrimination is easier at short separations, a result supporting the involvement of short-range lateral interactions.

So why is motion discrimination hampered by alignment? We suggest that because of the aperture problem, unambiguous motion signals are located at line terminators (Pack, Gartland, & Born, 2004), which may be more difficult to extract when collinearity creates diagonal perceptual structures comprising both the target and aligned background elements. Extraction of this information may require local short-range comparison of the relative position of contiguous line terminators; this may explain the improvement at small separations. Georges, Series, Fregnac, and Lorenceau (2002) showed that a Gabor patch moving in apparent motion along a trajectory appears much faster when its orientation is aligned with the motion path than when it is at an angle to it and this speed bias decreased as the angle between the motion axis and the orientation of the Gabor patch increased. Such collinear motion-defined structure (i.e., motion streak; Geisler, 1999) might have many correspondences with respect to the static and aligned configuration we used. In particular, Georges et al. (2002) argued that this speed bias might rely on the existence of long-range interactions between V1 neurons that elicit differential latency modulations in response to apparent motion sequences. In our case, a similar mechanism could operate by integrating collinear elements in a diagonal structure. As a consequence, the motion-induced lateral offset of a single target should be more difficult to extract when collinearity creates such structures that include both target and aligned background elements. Thus, the extraction of local motion information may require more local short-range comparisons of the relative position of contiguous line terminators. One interesting speculation is therefore whether the effect of background and target-to-background collinearity might be different for movement in a direction orthogonal to the lines. This might improve motion detection in the collinear conditions since it might give rise to a better fit with the response of motion detectors tuned to motion perpendicular to orientation.

To conclude, despite the fact that stimulus features such as orientation and motion present similarities in relation to other local features such as luminance, color or stereo disparity (having a spatial property), they engage completely different mechanisms that use the information from the structured background in an opposite way.

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