Cooperative and competitive spatial interactions in motion integration

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Abstract

Recovering the velocity of objects moving in the visual field requires both the integration and segmentation of local neuronal responses elicited by moving stimuli in primary visual cortex. Herein, we investigate the effects of the contrast, density, spatial proximity, spatial frequency, and spatial configuration of component motions on these complementary processes. Measuring the ability of human observers to discriminate the global direction of motion displays composed of spatially distributed patches of drifting gratings whose motion is locally ambiguous, we provide psychophysical evidence that linking component motion across space is facilitated at low contrast and high patch density. Furthermore, direction discrimination depends on the spatial frequency of component gratings and is more accurate for spatial configurations that contain "virtual" L junctions as compared to configurations composed of "virtual" T junctions. We suggest that the conditions yielding global motion coherence can be accounted for by the existence of anisotropic cooperative/competitive, contrast-dependent, long-range interactions among oriented direction-selective units. In addition, we bring evidence that motion segmentation processes rely upon the processing of moving local spatial discontinuities. The results are discussed in the light of recent psychophysical and physiological evidence that long-range excitatory and inhibitory interactions within primary visual cortex modulate perceptual linking.

Keywords: Collinearity, Spatial discontinuities, Motion integration, Segmentation, Long-range lateral interactions

Introduction

Over the past decades, a number of psychophysical, physiological, and computational studies have improved our understanding of the mechanisms by which the visual system determines the motion of objects from the local estimates of velocity sampled by early motion sensors. Theoretical considerations and experimental evidence, summarized below, indicate that early motion signals from the same object must be integrated while signals from different objects must be segmented to form independent perceptual entities. In turn, these conflicting demands call for specific mechanisms to select those motion signals that must be bound together from those which must not. Outcomes of such processes are the perception of coherency, noncoherence or transparency of distribution of motion signals, or the ability to accurately determine the velocity (direction and speed) of component or global motion. In the laboratory, plaids, Random Dot Kinematograms (RDKs), or multiaperture stimuli have been widely used to stress the existence of such processes and characterize the different factors that modulate the perception of motion. Briefly, coherence in plaid patterns (i.e. two super-imposed drifting gratings) was found to strongly depend upon the

similarity—in spatial frequency, speed, color, contrast—between component gratings.

For instance, when two similar drifting gratings are super-imposed, a single coherent plaid pattern emerges, whose perceived direction does not necessarily coincide with either component motion. If plaid components are dissimilar—in spatial frequencies, speed, contrast, or color—the perception of transparent motion is favored, suggesting that in this case sensors tuned to the gratings' characteristics do not merge their responses into a single coherent percept (Adelson & Movshon, 1982; Krauskopf & Farell, 1990; Smith, 1992). Manipulating the luminance contrast between local intersections and component gratings also strongly affects motion coherence (Stoner et al., 1990). Extensive studies of these effects in humans and monkeys (Stoner et al., 1990; Vallortigara & Bressan, 1991; Stoner & Albright, 1993, 1998) indicates that depth ordering and perceptual coherence are tightly related, and may involve the same cortical structures.

RDKs lack form information and are, for that reason, well suited to tackle "pure" motion mechanisms. Using this class of stimuli, competitive, as well as cooperative interactions between overlapping random distributions of moving dots were reported (Williams & Sekuler, 1984). The degree of cooperativity was found to depend on the amount of noise added to each dot trajectory (Lorenceau, 1996), on the overlap between velocity distributions (Williams & Sekuler, 1984; Watamaniuk & Duchon, 1992), on the duration and size of the displays, or on dot density (Watamaniuk et al., 1989). Models proposed to account for these effects rely on

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the existence of inhibitory interactions between units selective to different directions and facilitatory interactions between units selective to similar directions of motion (Marshak & Sekuler, 1979; Williams & Phillips, 1987; Hiris & Blake, 1996)

Multiaperture stimuli, consisting of spatially distributed moving components presented behind apertures, have proved useful to study the experimental conditions that yield motion integration across space. Studies using this class of stimulus probed the role of low-level variables such as contrast, duration, eccentricity, or the salience of local features in motion integration (Shimojo et al., 1989; Lorenceau & Shiffrar, 1992, 1998; Shiffrar & Lorenceau, 1996; Takeuchi, 1998). As a general trend, motion integration over space, resulting in the perception of a globally coherent motion, occurs whenever the salience of line or grating terminators at aperture borders is decreased (Lorenceau & Shiffrar, 1992). Moreover, these experiments suggest a straightforward distinction between extrinsic terminators—resulting from occlusion at aperture borders—and intrinsic terminators—belonging to component lines or gratings: the former were found to have no net effect on motion integration while motion integration or segmentation were strongly constrained by the later, depending on whether their direction of motion was congruent or not with the global direction of motion (Shimojo et al., 1989).

From these complementary approaches emerged a general agreement that the analysis of motion involves at least two stages, and a number of computational models developed to account for both psychophysical and physiological results adopted this scheme (e.g. Jasinschi et al., 1992; Wilson & Kim, 1994; Simoncelli & Heeger, 1998). According to these models, local motion detection would be performed at a first stage by direction-selective sensors, presumably in area V1, whose responses are well approximated by a set of motion energy filters (Adelson & Bergen, 1985; Emerson et al., 1992). The outputs of these filters would then be pooled at a second stage, presumably in area MT (Movshon et al., 1986; Rodman & Albright, 1989), to allow an accurate and noise-resistant estimate of the global velocity. In addition to experimental evidence, there are at least two theoretical reasons that justify this two-stage scheme. First, the velocity of an oriented contour moving behind an aperture, or by analogy, analyzed by direction-selective neurons with spatially limited receptive fields, is underconstrained. This is the well-known aperture problem whereby only the component of motion perpendicular to an oriented edge is available for further computation. Due to their receptive-field size, neurons in area V1 may encounter this aperture problem. Second, a single local estimate of velocity may be unreliable or noisy and input data may be sparse. Pooling numerous motion estimates permits in principle a solution to the aperture problem and helps to overcome the inherent variability of each local velocity estimate (Grzywacz & Yuille, 1991; Braddick, 1993; Stoner & Albright, 1993).

One important issue raised by this two-stage scheme concerns the spatial extent over which local estimates at the first stage should be pooled together at the second stage. Pooling over large regions of the visual field permits obtaining reliable estimates of velocity, even with sparse data, but it may also override the various objects' motion, and thus provide an inaccurate description of the optic flow field. On the other hand, pooling motion estimates over too small an area may be inadequate to solve the aperture problem and to determine the veridical velocity of moving objects. Thus, the visual system is confronted with two apparently conflicting constraints: combine motion estimates over large regions of the visual field on the one hand but also avoid the pooling of motion estimates that belong to different objects on the other. Numerous

psychophysical experiments provide evidence that the human visual system satisfies these conflicting demands, as differentiation of nearby motion signals as well as integration over large areas can be observed. For instance, using narrow adjacent stripes containing either dots moving coherently in one direction or dots moving in random directions, Nawrot and Sekuler (1990) observed that a single stream of moving dots is seen, a phenomenon called motion assimilation. If, on the other hand, the stripes are made larger, those filled with random motion appear to move in a direction opposite to the coherent motion within the remaining stripes, thus yielding motion contrast (see also, Chang & Julesz, 1983; Mukarami & Shimojo, 1993; Zhang et al., 1993; Qian et al., 1994; Bravo & Watamaniuk, 1995).

As a practical solution to this problem, many models of motion processing use a smoothness constraint to determine the optic flow field[1] (Horn & Schunk, 1981; Hildreth, 1984; Grzywacz & Yuille, 1991). Problems that arise with these models concern the spatial extent of the smoothing operator and its dependency upon various factors such as the contrast, the spatial and temporal frequency content of the image, and the presence of occlusion cues. One way to avoid the problem of choosing and fixing a spatial integration constant is to use an adaptive smoothing of motion signals to break the smoothing connections and in this manner select the velocity estimates that must or not be included in the pool (Braddick, 1993). However, it not yet clear how such selection process is implemented within the visual system and what could be the relevant criteria used for such selection.

To get insights into the spatial constraints involved in motion integration and segmentation processes, we used multiaperture stimuli to investigate the effects of varying spatial distributions of local drifting gratings on direction discrimination performance. Specifically, we estimated the effects of the sparseness of motion signals, the spatial-frequency content of the image, and the saliency of contour discontinuities. Last but not least, we tested the possibility that spatial constraints, such as local collinearity or closure, play a role in selecting the various local velocities that must combine to yield a coherent motion percept. We considered the possibility that long-range lateral interactions between neurons responding to gratings that form either L- or T-like junctions are involved in motion selection which a motion discrimination task could reveal. As a matter of fact, a number of psychophysical experiments with static stimuli already demonstrated that such lateral interactions, either facilitatory or inhibitory, modulate perceptual grouping (Field et al., 1993; Polat & Sagi, 1993, 1994; Kovacs & Julesz, 1993; Pettet et al., 1998), giving additional support to the early assumptions of the Gestalt theory that collinearity and closure are useful cues to group sparse signals into a single perceptual entity.

This notion of association fields is supported by anatomical studies that demonstrate the existence of a dense horizontal connectivity between columns of similar orientation which extends over several millimeters within the primary visual cortex (e.g. Rockland & Lund, 1982; Gilbert & Wiesel, 1982, 1989; Gilbert, 1992). The functional role of horizontal connectivity was probed through electrophysiological recordings of cortical neurons. Remote stimulations in the periphery of the classical receptive field of visual neurons were found to modulate cortical activity, either

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[1]The smoothness constraints assumes that nearby estimates of velocity are similar. However, because nearby velocity estimates may result from the aperture problem, they may well be very different, although they could "belong" to a single object.

by suppressing or facilitating neuronal response, depending on the relative orientation, direction of motion, or contrast between the center and surround of the receptive field (Nelson & Frost, 1985; Allman et al., 1985; Knierim & Van Essen, 1992; Hirsch & Gilbert, 1991; Kapadia et al., 1995; Frégnac et al., 1996). These interactions often appeared to be direction- or orientation-selective and are thought to reveal a context-dependent sensitivity of cortical neurons that may underlie a "shaping" of the visual information at early stages and possibly account for the different psychophysical findings summarized above.

Up to now, these effects of spatial configurations of Gabor patches were observed with static stimuli. Our experiments aim at generalizing these findings to moving gratings and at determining the potential influence of lateral interactions on integrating spatially distributed motion signals. Part of this work has been presented in abstract form elsewhere (Lorenceau et al., 1996).

Experiment I

Psychophysical (Cannon & Fullenkamp, 1991) and electrophysiological studies (Levitt & Lund, 1997) have shown that the strength and the nature—inhibitory or facilitatory—of lateral interactions depend on the relative contrast between a center stimulus and its surround. In addition, previous studies on motion integration with multiaperture stimuli have shown that contrast strongly affects motion coherence (Lorenceau & Shiffrar, 1992; Takeuchi, 1998). Low-contrast (<10%) stimuli favor motion integration which breaks down at high contrasts (>10%). We hypothesized that if lateral interactions play a role in motion integration their contribution should also depend on the contrast of the inducing elements. To investigate further the dependence of these lateral interactions on

contrast, we measured the ability of observers to discriminate the global direction of spatially distributed component motions as a function of contrast and for a variety of spatial configurations.

General methods

Stimulus characteristics

All stimuli were generated using an Adage 90/10 graphics card (1280 × 1024 × 8) based in a PC 486, and displayed on a Sony monitor (19-inch GDM 1950) refreshed at 60 Hz.

The displays consisted of arrays of patches of sine-wave grating presented behind apertures. The gratings, oriented 90 deg apart, were positioned so as to form either "virtual" T-junctions or "virtual" L-junctions (Fig. 1). What is meant by virtual junctions is that, if the gratings were extended beyond the apertures until they meet, the junctions that would occur are of the T or L type, as shown in the inset of Fig. 1. The spatial frequency of the gratings, either 1 or 6 cycles/deg (cpd thereafter), was the same for all patches within a single trial. Their Michelson contrast could take one out of four different values (6, 10, 30, and 70%). The mean luminance of the gratings was the same as the background luminance and kept at 10 cd/m². The number of patches (4, 16, or 64) and their size covaried such that the overall stimulus always covered the same area of the visual field. Since the eccentricity of the outer patches was maintained, the center-to-center distance between patches decreased as their number increased. In Experiment I, circular patches of either 12, 3, or 0.75 deg² were used, yielding a total area of 48 deg². The center-to-center separation for these three patch sizes were 6, 3, and 1.5 deg of visual angle, respectively. In Experiments II and III, the smallest patch size was
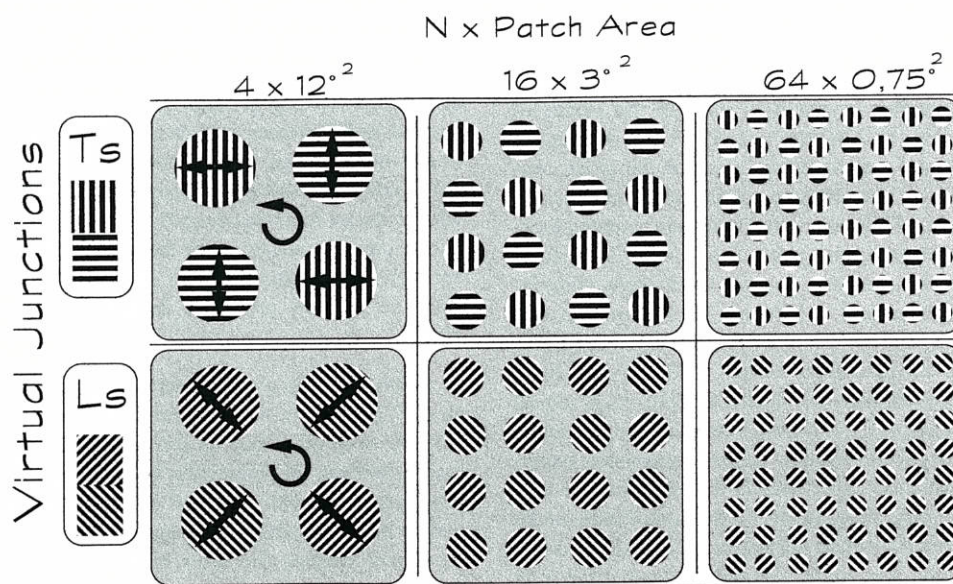
Fig. 1. Stimuli used in Experiment I. Patches of drifting gratings are distributed across space and arranged so as to form either "virtual" L (lower panel) or T junctions (upper panel). The relative angle between gratings is maintained at 90 deg. Three different displays (right, middle, and left panels), with varying number of patches, are used. The size and position of each patch is chosen in order to stimulate the same area of the visual field (48 deg²). In the experiments, each grating (either 1 or 6 cpd) oscillates sinusoidally in a direction orthogonal to its orientation. A phase lag of ±90 deg is introduced between the sinusoidal motion of gratings at different orientations, such that binding together all component motions yields the percept of a coherent motion along a circular trajectory $[A \sin(wt) + A \sin(wt \pm 90 \deg)]$ as illustrated in the left panels. The task of the observers is to determine whether the global motion is clockwise or counterclockwise.

used but the spatial distribution of component gratings within each aperture was varied. In Experiment IV, we used square apertures at two orientations (vertical/oblique), each covering either 16, 4, or 1 deg^2 for a total area of 64 deg^2.

Motion characteristics

We used look-up table animation to produce a sinusoidal drift (i.e. to and fro) of each component grating in a direction orthogonal to their orientation. Therefore, the two directions of motion in our displays were always 90 deg apart. A cosine and a sine drift was assigned to gratings at different orientations, such that their combination $[A \cos(w) \pm A \sin(w)]$ would result in a global circular translation, clockwise, or counterclockwise. Hence, binding the different component velocities would produce a global percept with constant velocity along a circular path (Fig. 1), although none of the individual gratings possesses such motion. Therefore, integrating component velocities is necessary to recover the global, clockwise, or counterclockwise direction of motion. To minimize the possibility that observers associate a particular conjunction of directions, for instance up and right, with a global direction, the starting point on the trajectory was chosen at random on each trial, by steps of 45 deg. The amplitude of the sinusoidal motion, 0.48 deg of visual angle, was the same for all gratings and conditions. Depending on the gratings' spatial frequency, the temporal frequency was either 1 or 6.3 Hz, yielding a maximum speed of about 1 deg/s for all conditions (0.83 rev/s).

Task

Observers viewed the stimuli binocularly from 92 cm, with their head maintained in a chinrest. They were asked to indicate whether the global direction of the stimulus was clockwise or counterclockwise in a 2-alternative forced choice (2AFC) design. Observers were instructed to fixate the center of the display, although no fixation point was provided. A trial began with the static presentation of the stimulus for 800 ms, followed by 300 ms of clockwise or counterclockwise motion; the stimulus then stopped and remained static until the observer pressed the left or right arrow key of the computer keyboard to indicate the perceived direction of motion. After the observer's response, a new stimulus, chosen at random among the conditions used for the block, was presented. Within a block two different spatial frequencies (1 and 6 cpd), two directions of motion (clockwise and counterclockwise), two spatial configurations (referred to L and T "virtual" junctions in the following), and four contrast levels were intermingled, yielding 32 experimental conditions. Each condition was presented 10 times such that a block of trials represented 320 trials. The different spatial configurations (large, medium, and small patches) were presented in different blocks. Overall, each subject performed three blocks of 320 trials. Four observers participated in these experiments. They were familiar with psychophysical experiments but had no particular experience in the experimental situation used here, nor were they aware of the hypotheses under investigation. Three observers had normal or corrected-to-normal vision. A fourth observer was strabismic and used either the right or left eye to perform the different experimental blocks.

Results

Before analyzing the results, let us briefly describe the phenomenological appearance of our experimental displays. At low contrast, all stimuli appear as globally coherent, although coherence is less with large grating patches. At high contrast, the stimuli appear as incoherent moving gratings, organized in two motion flows. Informal observations at high contrast indicate that high coherence is perceived in periphery (>10 deg; see also Lorenceau & Shiffrar, 1992). In central vision, high coherence is perceived provided the luminance of the background is different from the mean luminance of the gratings (i.e. with a dark background). According to previous studies (Shimojo et al., 1989), terminators at aperture borders are classified as extrinsic under these conditions, and do not interfere with motion integration. All these observations agree well with previous results obtained with aperture stimuli (Lorenceau & Shiffrar, 1992). Note, however, that subjective coherence with these displays is less than with coherent plaids, except at very low contrast. Finally, if the patches of drifting gratings are rectangular, contiguous, and arranged so as to form a tiled floor (see inset of Fig. 1), the global motion is rigid and coherent when composed of L junctions, but is perceived as two independent flows when only T junctions are present. Repulsion between the two directions of motion similar to that reported in earlier studies (Marshak & Sekuler, 1979; Hiris & Blake, 1996) is often reported under these later conditions

To analyze the data, direction discrimination performance was pooled across directions. The percentage of correct discrimination, averaged across observers, is plotted as a function of contrast in Fig. 2 for two spatial frequencies and three patch sizes. The upper panels represent performance for the lowest spatial frequency (1 cpd); the lower panels represent performance for the highest spatial frequency (6 cdp). The left, middle, and right panel correspond to performance for large, medium, and small patch sizes, respectively. In each panel, the open symbols correspond to L configurations and the filled symbols to T configurations.

In the following, we describe the main effects of the different factors under investigation on performance, as revealed by a one-way analysis of variance (ANOVA).

Contrast. Contrast level has a profound, albeit complex, effect on performance. As a general trend, performance decreases as contrast increases ($F(3,9) = 12.4$, $P < 0.002$). However, this effect of contrast is quite different for low and high spatial frequencies. For 1-cdp gratings, performance is always better at 6% contrast and decreases at higher contrasts, whatever the patch size or the junction type. With 6-cpd gratings, performance is largely independent of contrast, although performance slightly increases when contrast increases from 6 to 10%, which probably reflects a poorer contrast sensitivity at the lowest 6% contrast. Interactions between contrast and the other experimental factors are all significant, so we now provide a detailed analysis of these different effects.

Patch size. On average, performance is independent of patch size ($F(2,6) = 2.6$, ns). However, this lack of effect of patch size is likely to be explained by the large effect of contrast on performance. Indeed, the interaction between patch size and contrast is significant ($F(6,18) = 5.56$, $P = 0.002$). At low contrasts, performance increases with decreasing patch size, whereas at high contrasts performance decreases with decreasing patch size, a trend which is more pronounced for a low than a high spatial frequency. From the present results, one cannot determine whether performance depends on the number of patches, on the patch density, or on the proximity of grating patches at different orientation. This issue is addressed in more detail in Experiment II.

Spatial frequency. Although the pattern of results for low and high spatial frequency appears quite different, the global effect of spatial frequency does not reach statistical significance ($F(1,3) =$
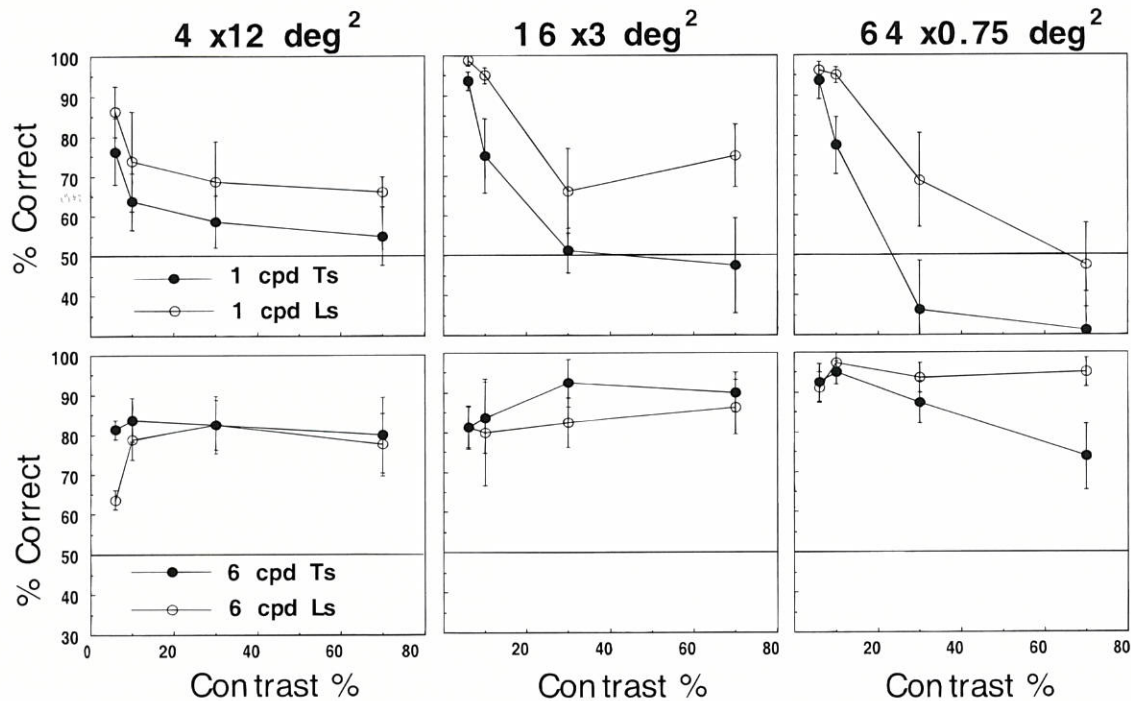
Fig. 2. Percentage of correct responses averaged across direction of motion (clockwise and counterclockwise) and observers ($n = 4$). Left, medium, and right panels correspond to large, medium, and small grating patches, respectively. Upper and lower panels correspond to 1 and 6 cpd gratings, respectively. Open circle: L configurations; filled circle: T configurations. Errors bars represent ± one standard deviation.

6.68, $P < 0.08$.[2] Again, this lack of effect is likely to be explained by the profound influence of contrast on performance, as suggested by the significant interaction between contrast and spatial frequency ($F(3,9 = 15.57, P < 0.001$). Performance drops close to or below chance level with increasing contrast at a low spatial frequency ($F(3,9) = 18.2$; $P < 0.001$) but is independent of contrast at a high spatial frequency ($F(3,9) = 1$; ns).

Junction type. Overall, performance is better for configurations that form virtual L junctions as compared to virtual T junctions ($F(1,3) = 10.8$, $P = 0.04$). This effect is particularly clear at a low spatial frequency ($F(1,3) = 30.1$; $P < 0.02$) but is not significant at a high spatial frequency ($F(1,3) = 0.2$; ns). It is worth noting that the effect of the junction type is absent at low contrasts and increases with increasing contrast as indicated by a significant interaction between contrast and junction type ($F(3,9 = 5.77$; $P = 0.01$). Also note that with high-contrast low spatial-frequency T configurations, performance drops below chance level (50%). Under these conditions, the observers often report seeing a global motion in a direction opposite to the predicted one.

This effect is quite compelling and was also found in other studies with dot patterns and a similar circular translation (Lorenceau, 1996).

The present results indicate that the discrimination of the global direction of spatially distributed component motions strongly depends on their contrast, their spatial frequency, and their spatial distribution. The statistically significant interactions between these factors suggest that there exist complex nonlinear interactions between units locally processing the component velocity. We shall analyze these effects in more detail in the general discussion.

Direction discrimination also depends, but to a lesser extent, on the size of the grating patches. It is worth noting that the effects of contrast and of the type of configuration (L *vs.* T) are attenuated as patch size increases. For large patches, performance averaged across conditions hardly exceeds 80% and is independent of contrast for 6-cpd gratings, and varies only from 80% to 65% as a function of contrast with 1-cpd gratings. This trend suggests that large, distant grating patches recruit distinct neuronal populations that do not easily interact to yield either strong perceptual coherence or perceptual segregation, in contrast with the results obtained with small patches.

Experiment II

The interaction between contrast and patch size found in Experiment I may reflect either the effect of the number of patches, the varying distances between patches, or the higher density of orientation (or motion) contrasts that occurs when the number of patches increases. To disentangle these possibilities, the following control experiment was designed: we used a high patch density identical to that of Experiment I (64 circular patches with a radius of 0.5 deg of visual angle separated by 1.5 deg of visual angle), but modified

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[2]Direct comparisons between performance for grating patches of 1 and 6 cpd may be misleading, however, since the number of visible cycles, and thus the orientation and direction bandwidths, is quite different. However, it is unlikely that the number of visible cycles can account for the difference between high and low spatial frequencies, since the pattern of results for a high spatial frequency within small patches is quite different from the pattern of results for a low spatial frequency within large patches, despite the fact that the number of cycles—and thus the orientation and direction bandwidths—is similar in both cases. Also note that the large bandwidths associated with small patches should favor motion integration, as they are more likely to overlap, thus facilitating the determination of a common direction (see Williams & Sekuler, 1984).
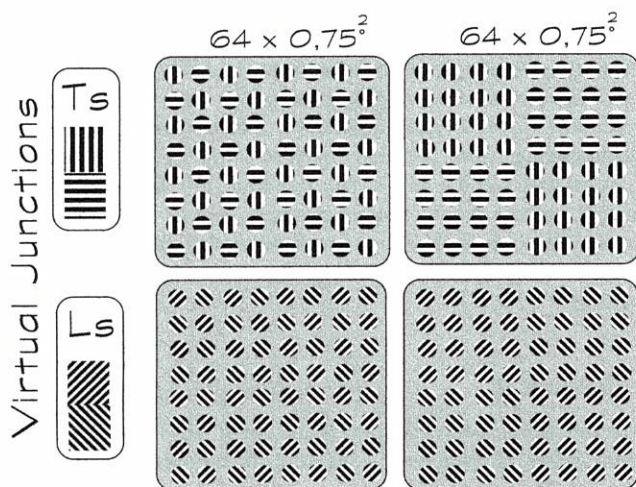
the distribution of grating orientations within each patch such that each quadrant of the display (16 patches) contained the same orientation (Fig. 3). We then compared direction discrimination for this new stimulus with the small-patch condition used in the previous experiment (a new set of data was collected for this condition). Recall that under this condition, neighboring patches have different orientations. For both conditions, the overall area of stimulation, the distance between patches (1.5 deg), the number of different orientations (2), and the relative angle between orientation or direction (90 deg) were the same. Therefore, if the effect of patch size described above is mainly due to increasing distances between patches, performance should be similar under these new conditions. If, on the other hand, the variable density of orientation or motion contrasts is the relevant factor, performance should be worse for the condition that contains fewer orientation contrasts and similar to that obtained with large patches in Experiment I, as compared to the condition where the density of orientation contrasts is high.

Method and stimuli

The ability to integrate component motion over space was measured with the same method as in Experiment I. Observers ($n = 3$) were asked to discriminate the global direction of circular motion (clockwise *vs.* counterclockwise). The temporal and motion parameters were identical to those of Experiment I, although only low, 1-cpd gratings were used. Within a block (160 trials), a single configuration (T or L) was presented. However, the virtual junctions were either local and present between any two neighboring patches, as in Experiment I, or global. In this case, virtual junctions are present only between the four quadrants of the array of patches, thus defining large L or T virtual junctions. Note that within each quadrant, the gratings are collinearly arranged.
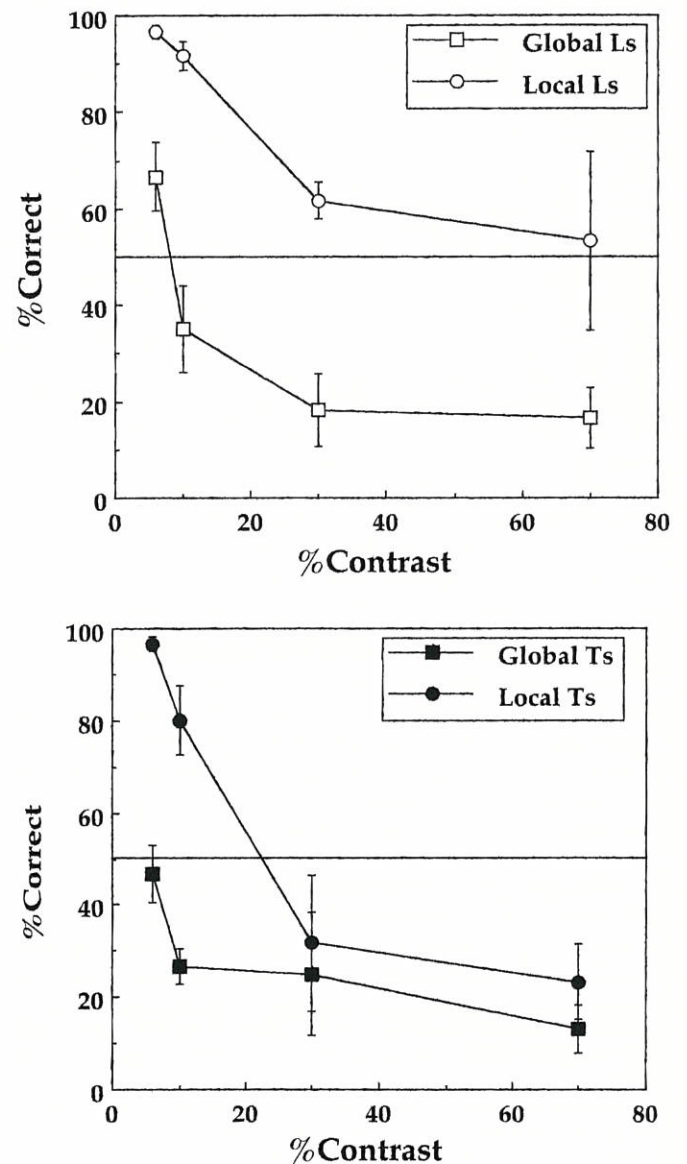
Results

The data for the two directions of motion were pooled before the percentages of correct responses were calculated. The results, averaged across observers, are displayed in Fig. 4 as a function of contrast for the L and T configurations. As shown in this figure, performance decreases with increasing contrast ($F(3,6) = 22.3$; $P < 0.01$) and is better for L configurations as compared to T configurations ($F(1,2) = 46,1$; $P < 0.01$), which replicates the results of Experiment I. Interestingly, performance is worse with a low as compared to a high density of orientation or motion contrasts ($F(1,2) = 304.9$; $P < 0.01$). As in Experiment I, performance drops below chance level at medium to high contrast, suggesting a strong tendency to perceive a global motion in a direction opposite to the veridical. Also note that performance is poorer with a low density of orientation or motion contrasts, as compared to the results of Experiment I with large patches. The

Fig. 3. Stimuli used in Experiment II. Gratings with the same orientation are either grouped into quadrants or evenly distributed across space. Although the overall number, separation, and size of the grating patches are the same in both displays, the density of orientation, or motion, contrasts is different.

Fig. 4. Results of Experiment II: the percentage of correct direction discrimination is plotted as a function of contrast for L like (upper panel) and T like (lower panel) configurations. Circles (Local Ls and Ts) and squares (Global Ls and Ts) refer to a high and a low density of orientation or motion, contrasts, respectively. Chance level (50%) is indicated by a line. Errors bars represent ± one standard deviation.

present findings suggest that the density of local orientation—or motion—contrasts, rather than patch size or patch density *per se*, is likely to account for the different performance observed with different patch sizes in Experiment I.

Another aspect of the results is worth mentioning. With the high-density L configurations used in Experiment I, gratings with the same orientation are aligned, thus forming elongated contours, whereas T configurations do not possess such characteristics (see Fig. 1). One could argue that the facilitated integration for the former as compared to the latter configuration is explained by the presence of such collinear arrangements. However, the new stimulus configuration used in Experiment II also contains collinear gratings within each quadrant for both the T and L configurations. Despite the existence of collinear gratings in both L and T displays, performance is not similar for these two conditions, suggesting that the presence of collinear arrangements is unlikely to account for the differences between T and L configurations found in Experiment I. Complementary evidence that collinearity between neighboring gratings may not account for the different performance for T and L configurations comes from the results of Experiment I with the largest patch size: performance is better for L as compared to T configuration although both configurations are lacking collinear arrangements. This suggests that the differences in performance found between L and T stimuli are due to the local organization of neighboring gratings rather than their global characteristics. Since the difference between L and T is only a matter of relative positions between gratings—the amplitude spectrum is identical for both L and T configurations—the present results are evidence

that this factor plays an important role in integrating component motions and support the hypothesis according to which long-range lateral interactions between orientation-selective neurons are involved.

Experiment III

In Experiment I, the differences in performance between T and L configurations are large with 1-cpd gratings but small with 6-cpd gratings, except at very high contrast and with small inter-patch distances (Fig. 2, right panel). One possible explanation of this difference is that high spatial-frequency gratings activate neurons with small receptive fields and that the range over which lateral interactions are active scales with receptive-field size, as previously suggested by Polat and Sagi (1993), rather than depending on absolute distance. If this hypothesis is correct, the effects of T and L configurations on motion integration should appear for 6-cpd gratings provided that the inter-patch distance is sufficiently small. We tested this hypothesis, using arrays of 6-cpd grating patches with varying inter-patch distances.

Method and stimuli

The stimuli, the task, and the temporal parameters were identical to those of Experiment I except for the following changes: all gratings were oblique and could form either an L or a T configuration, distributed within a hexagonal array of 12 patches (Fig. 5). This global arrangement was used to minimize the potential contribu-
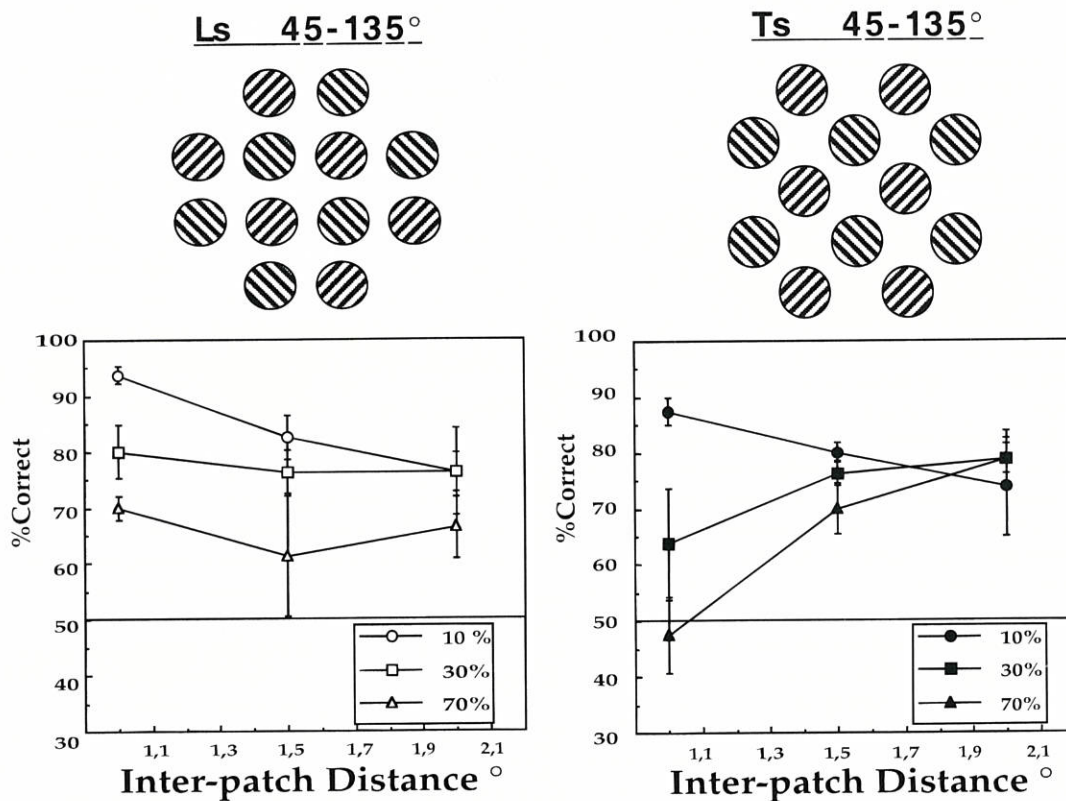
Fig. 5. Results of Experiment III: percentage of correct discrimination for L and T like configurations composed of 6 cpd gratings as a function of inter-patch distance, with grating contrast as a parameter. Left panel: L configurations; Right panel: T configurations. Error bars represent ± one standard deviation.

tion of the global orientation of the stimulus array. The grating contrast could take one out of three different values (10, 30, and 70%). Each patch was circular with a radius of 0.5 deg of visual angle. The center-to-center inter-patch distance was either 1, 1.5, or 2 deg of visual angle. Thus, for the shortest distance, neighboring patches were in contact, while a distance of 1.5 deg was equal to the shortest distance used in Experiment I. Four observers performed 20 trials for each of the 18 conditions (3 contrasts × 3 distances × 2 configurations).

Results

The percentages of correct responses, calculated after pooling the responses for clockwise and counterclockwise directions and averaged across observers, are presented in Fig. 5 as a function of inter-patch distance, with contrast as a parameter. The main results of this experiment are the following: the main effects of contrast, distance of junction type, are not significant. This lack of effect is likely to be due to the existence of a significant interaction between contrast and distance ($F(4,12) = 4,75$; $P < 0.02$), as performance strongly depends on contrast at short but not large inter-patch separation. A significant interaction is also observed between the junction type (L or T) and inter-patch separation ($F(2,6) = 5,13$; $P = 0.05$). With L configurations, performance depends little on inter-patch distance, whereas performance strongly depends on inter-patch distance with T configurations although in a contrast dependent way: at low contrast, performance decreases with increasing distance, whereas the reverse is observed at medium and high grating contrast.

These results indicate that the effects of the spatial configuration of drifting gratings on motion integration are not specific to low spatial frequencies, but also exist at high spatial frequencies, provided that the inter-patch distance is sufficiently small. The results of the present experiment support the hypothesis according to which lateral interactions are involved in our direction discrimination task and suggest that the range over which lateral interactions may modulate motion integration performance scales with the spatial frequency, and presumably with the receptive-field size of underlying neurons.

Experiment IV

In Experiment I, direction discrimination was measured as a function of contrast for displays consisting of circular patches of gratings distributed over space. Performance was found to decrease with increasing contrast for low spatial frequencies. At high contrast, direction discrimination was close to or even dropped below chance level, suggesting that motion segmentation dominated under these conditions. One possible explanation of this effect is that increasing contrast increases the saliency of aperture borders which favors a segmentation of the input image into multiple independent static patches and in turn disrupts motion integration across apertures. Indirect evidence supportive of this view comes from a study by Zhang et al. (1993) who found that the perceived direction of an aperture that contains a drifting grating markedly depends upon the softness of the aperture border (i.e. its spatial-frequency spectrum). As stated by the authors: "Increasing aperture softness favors a motion integration mechanism while decreasing softness favors a motion contrast mechanism" (Zhang et al., 1993, p. 2726). If only the spatial-frequency spectrum at the aperture border was the relevant variable, the effect of contrast should not depend upon the aperture shape, provided that its border is clearly visible.

On the other hand, it is possible that the important variable is the motion of line-ends whose contribution to the integration/segmentation processes would also increase with increasing contrast. According to this latter hypothesis, the shape of each aperture would influence motion integration because the aperture shape constrains the direction of line-ends' motion (Wallach, 1935), thus defining motion boundaries. To test this possibility, we used apertures in the shape of a square or a diamond. When the gratings and the aperture had the same orientation,—that is when the gratings were parallel to aperture's borders—the grating terminators all moved in the same direction and grating length did not change over time. When the orientation of the apertures and the gratings differed (by 45 deg) the terminators moved along apertures' borders in two different directions and the length of a grating cycle varied over time, introducing accretion and deletion of portion of the gratings. The relative motion between terminators together with the length changes are strong cues (i.e. kinetic occlusion) that the gratings are presented behind occluders. The goal of this experiment was to test whether motion discrimination performance is influenced by the relative orientation between apertures and gratings, in order to probe the role of moving spatial discontinuities in motion segmentation.

Method and stimuli

The method and experimental procedure are the same as in Experiment I, except that the shape of the apertures was different. The apertures consisted of either vertical squares or oblique diamonds. The relative orientation between gratings and apertures was either 0 deg or 45 deg. When the apertures and the gratings had the same orientation, all terminators moved in the same direction and the length of the gratings remained the same, whereas when the apertures and the gratings had different orientations, the terminators moved in different directions and the length of the gratings varied over time (Fig. 6). We shall refer to these conditions as "Common Fate" (CF) and "Relative Motion" (RM) conditions in the following. The size (1, 4, or 16 deg^2) and the number (64, 16, or 4) of apertures covaried such that the total area of stimulation (64 deg^2) was the same in all conditions. The spatial frequency of the gratings was either 1 or 6 cpd and the two types of configurations (L or T) were used. The same four observers as in Experiment I performed six blocks of 320 trials each.

Results

The results averaged across directions and observers are displayed in Fig. 7. The results for 1-cpd gratings and 6-cpd gratings are presented as a function of contrast for large, medium, and small patch size. The left and middle panels represent performance for the CF and RM conditions, respectively. As the observers who performed in this experiment were the same as in Experiment I, performance for circular patches is shown for comparison (right panels). Open symbols refer to L configurations, and filled symbols to T configurations.

Overall, the results are similar to those of Experiment I: performance decreases as contrast increases ($F(3,9) = 28.4$; $P < 0.001$) and is better for L as compared to T configurations ($F(1,3) = 21.5$; $P < 0.01$). In contrast with Experiment I, however, the effect of patch size is also significant ($F(2,6) = 10.8$; $P < 0.01$): small patches yield better performance than large patches. This effect of patch size is significant for low, 1-cpd gratings ($F(2,6) = 14.8$; $P < 0.01$) but does not reach significance for high,
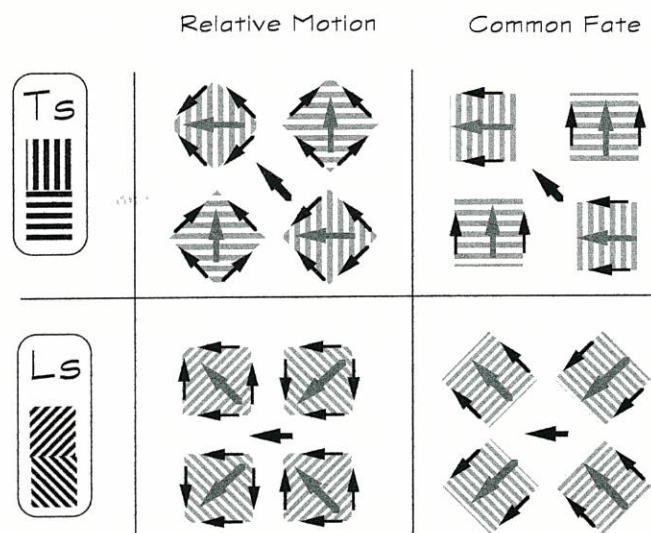
Fig. 6. Illustration of the stimuli used in Experiment IV: gratings are presented behind apertures at different orientations. The distribution and number of patches is as in Experiment I except that the patches are vertical or oblique squares. Note that when the relative angle between the gratings and the apertures equals 0 deg (referred as Common Fate conditions, CF), the grating terminators (black arrows) all move in the same direction within an aperture and grating length does not changes over time; when the relative angle between the apertures and the gratings is 45 deg (referred as Relative Motion conditions, RM) grating terminators at aperture borders move in different directions and grating length changes over time, thus introducing kinetic motion boundaries. A translation is illustrated for clarity in this figure: gray arrows represent the direction of each grating; thick arrows represent the global motion. In the experiment, a circular translation was used (see Method section for details).

6-cpd gratings ($F(2,6) = 4.84$; $P = 0.056$). Performance strongly depends on contrast for a low as compared to a high spatial frequency as indicated by a significant interaction between contrast and spatial frequency ($F(3,9) = 75.4$; $P < 0.001$). For the former spatial frequency, performance sometimes drops below chance level, consistent with observers' report of perceived global direction under these conditions.

In addition, the comparison between CF and RM conditions suggests that the relative orientation between the apertures and the gratings also modulates performance. In particular, direction discrimination performance of 1-cdp gratings is better for RM conditions than for CF conditions ($F(1,3) = 28.2$; $P = 0.012$), with the direction of L configurations being more easily discriminated for RM conditions, even at the highest contrasts. This effect does not reach significance for 6-cpd gratings ($F(1,3) = 8.3$; $P = 0.069$). With high, 6-cpd gratings, performance is independent of contrast for L configurations ($F(3,9) = 2.77$; ns) but decreases with increasing contrast for T configurations ($F(3,9) = 24.7$; $P < 0.001$). For the latter, performance decreases with increasing contrast for RM conditions ($F(1,3) = 17.8$; $P < 0.03$). It is worth noting, however, that inter-individual differences are very large under these conditions, as two out of the four observers performed poorly under these particular conditions.

This experiment was designed to test whether apertures in multi-aperture stimuli act as static cues that induce motion segmentation or whether the motion boundaries at aperture borders also contribute to motion segmentation. To that end, direction discrimination

with apertures at different orientations were compared. Although one cannot reject the hypothesis that the aperture borders as such are involved in the segmentation of the displays into local motion components, the effect of aperture orientation suggests, however, that the movement of line-ends motion also plays a role. The existence of relative motion between line-ends in the RM conditions produces motion boundaries which tend to facilitate motion integration, at least for low spatial-frequency gratings, whereas CF conditions favor motion segmentation. It is worth noting that the orientation of the aperture as such does not seem to be the relevant variable: comparing performance between vertical and oblique apertures rather than between CF and RM conditions does not yield a coherent pattern of results: differences in performance between L and T configurations are huge when apertures are vertical but small when apertures are oblique (compare the empty and filled symbols from the left and middle panels of Fig. 7). Comparing performance between CF, RM, and our previous results with circular apertures, which also introduces kinetic occlusion cues, brings additional evidence that relative motion between line-ends rather than aperture shape or orientation is the relevant factor: indeed, direction discrimination performance for circular gratings is intermediate between the CF and RM conditions. This conclusion does not seem to apply to high spatial frequencies, since performance is worse for RM conditions than for CF conditions, at least for T configurations. We do not yet have an explanation of this effect, but we have already mentioned the large inter-individual differences observed for these particular conditions.

Experiment V

In Experiments I, II, and IV, performance drops below chance level at high contrast, especially with T configurations. This indicates that observers reliably perceive a motion in a direction opposite to the expected one, suggesting that some form of motion combination is at work. This effect raises two questions. First, what is the relationship between reversed perceived direction and perceptual coherence? Second, is this effect related to differences in grating orientations, since in Experiment I the T configurations were made of vertical and horizontal gratings? To answer these questions, we estimated motion coherence under conditions similar to those of Experiment I with displays made of gratings at 45 and 135 deg.

Method and stimuli

Eighteen circular patches (radius 0.5 deg) of sine-wave gratings (2 cpd) oriented at 45 or 135 deg were distributed in a hexagonal array similar to that used in Experiment III (see Fig. 5) and arranged to form either T or L configurations. The center-to-center separation between patches was 1.5 deg. The gratings could take one of five contrast levels (4, 12, 20, 40, or 80%). The motion of component gratings was as in Experiment I, such that binding component motions would yield a global motion percept along a clockwise or counterclockwise circular translation. A trial started with 600 ms of the static stimulus, followed by 500 ms of clockwise or counterclockwise motion. At the end of a trial, observers ($n = 5$) used one of two keys to indicate whether the motion appeared coherent or incoherent. Thus, a block consisted of 10 conditions, each presented 20 times. As a control, a second group of five observers performed a clockwise *versus* counterclockwise discrimination task with the same stimuli.
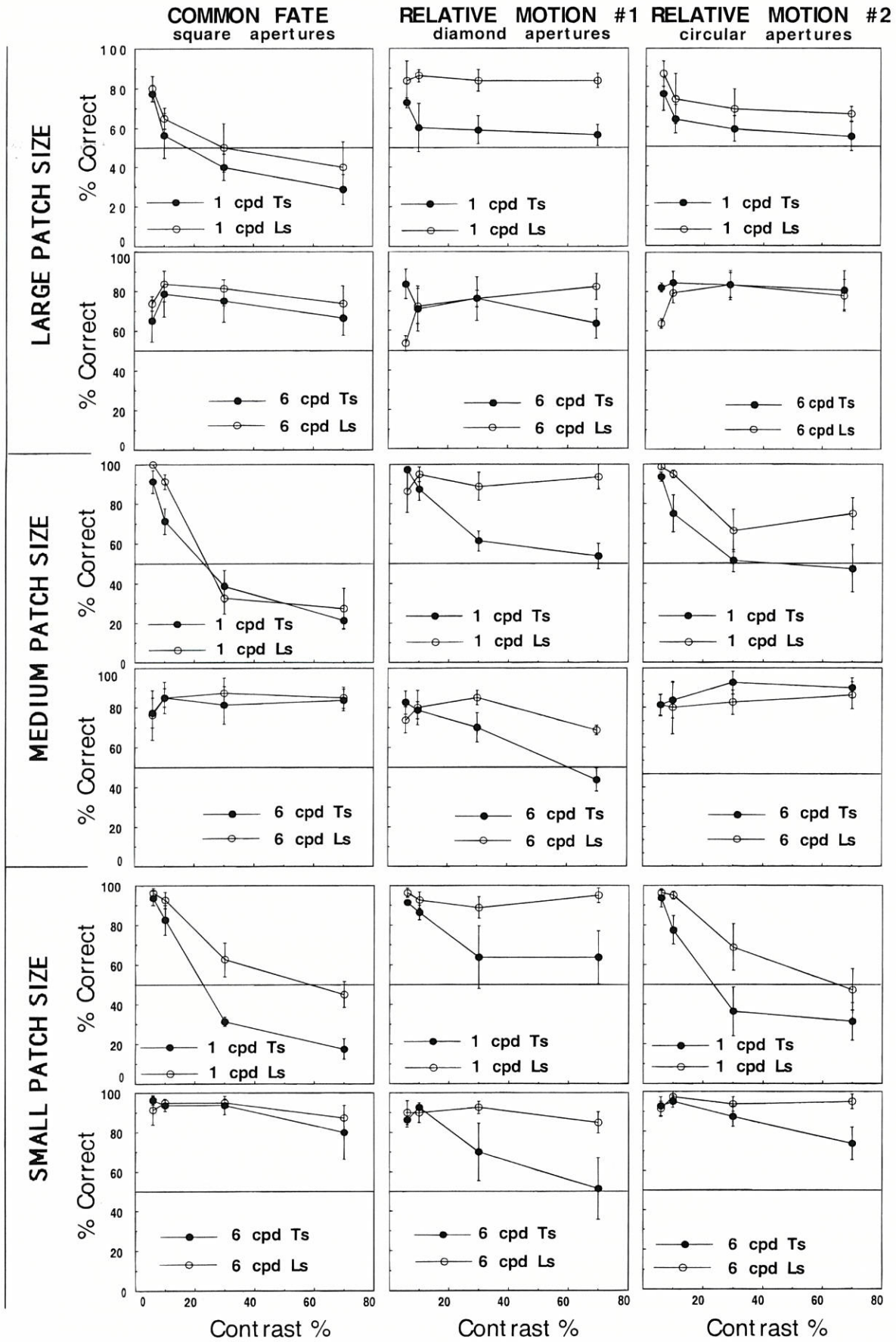
FIGURE 7

Results

The results in the coherence task, averaged across observers and directions, are plotted as a function of contrast for T and L configurations (Fig. 8A). As can be seen, perceived coherence remains at a high level for L configurations whatever the contrast level, but decreases steeply as contrast increases with T configurations. An analysis of variance indicates that the difference between T and L configurations is significant ($F(1,4) = 11.1$; $P < 0.03$).

Direction discrimination performance in the control group (Fig. 8B) closely follows the pattern of results found in Experiment I. Again, the difference between L and T configurations is significant ($F(1,4) = 8.17$; $P < 0.05$). Also note that T configurations yield below chance level performance. Although the pattern of results for the coherence and the discrimination tasks are slightly different and involved different observers, there are striking similarities between perceived coherence and direction discrimination performance, suggesting that the latter is a reliable, although strictest, estimation of perceptual coherence. The present results further indicate that the conditions yielding reversed perceived direction of motion are not perceived as coherently moving stimuli. Below chance level performance at high contrast suggests, however, that interactions between motion components occur under our conditions.

In addition, the results of the present experiment suggests that the differences between T and L configurations found in the previous experiments are unlikely to be explained by differences in grating orientation, since similar differences occur with gratings at 45 and 135 deg (also note that in Experiment III with high spatial-frequency gratings T and L configurations yield different discrimination performance, despite the fact that similar orientations were used).

General Discussion

The present study brings evidence that a number of variables control the perceptual transitions between integration and segmentation of component motions. We now discuss in more detail the mechanisms that could underlie these effects.

Effect of contrast on motion integration

The results of the present experiments indicate that motion integration, as measured by our direction discrimination task, is easier at low as compared to high grating contrast. It is well established that lowering contrast decreases the visibility of high spatial frequencies. Although the sine-wave gratings used in the present experiments were of low and intermediate spatial frequencies (1 and 6 cpd), high spatial frequencies also exist at aperture borders. As grating contrast increases, the energy of these high spatial frequencies also increases. It is thus possible that the effect of contrast on motion integration results from a change in the visibility of high spatial frequencies. This would
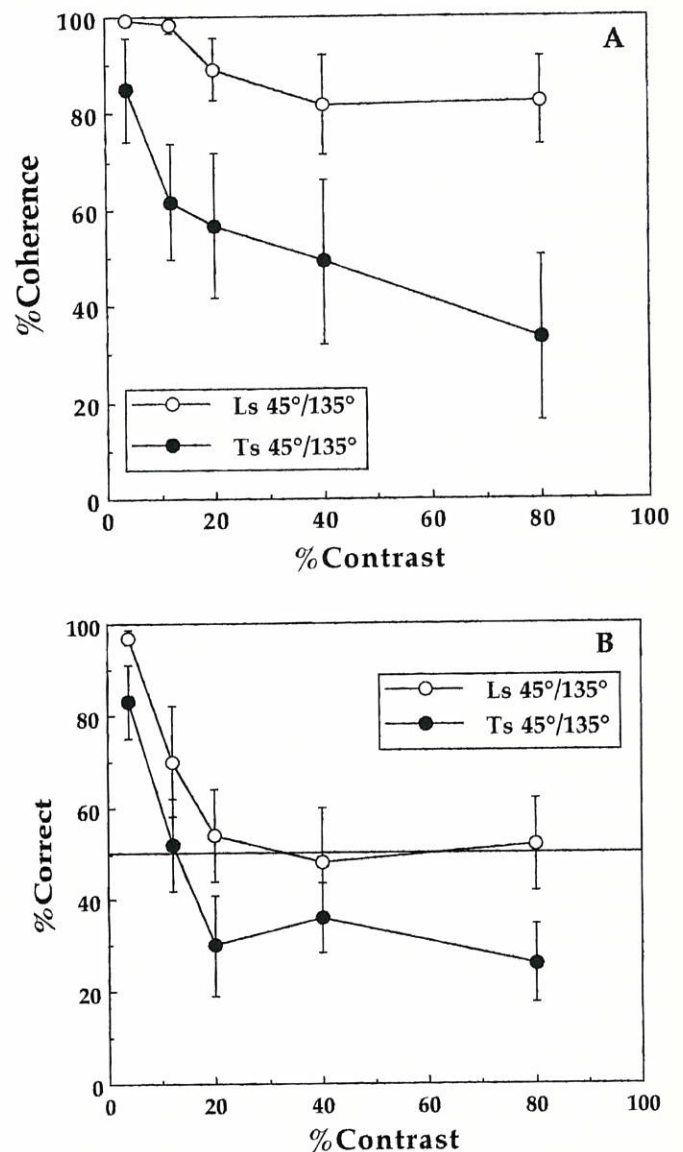
Fig. 8. Results of Experiment V: (A) Percentage of trials perceived as coherent as a function of contrast for L (open circles) and T (filled circles) configurations made of 2-cdp gratings oriented at 45 and 135 deg. (B) Percentage of correct direction judgments for a control group ($n = 5$) using the same stimuli as in A. Errors bars represent $\pm$ one standard deviation.

suggest that the perceptual segmentation of our displays into distinct component motions found at high grating contrasts heavily relies upon high spatial frequencies. However, it is not clear why high spatial frequencies *per se* would drive motion segmentation. In effect, displays composed of gratings with high

Fig. 7. Results of Experiment IV for large, medium, and small patches: percentage of correct direction discrimination for the Common Fate (CF) and Relative motion (RM) conditions (left and medium panels) as a function of contrast for 1-cpd gratings (upper panels) and 6-cpd gratings (lower panels). L and T configurations correspond to open and filled circles, respectively. The results from Experiment I with circular apertures are also shown for comparison (right panels). Errors bars represent $\pm$ one standard deviation.

spatial frequencies (6 cpd in our case) are more easily perceived as coherent than are displays made of low spatial frequencies, as direction discrimination remains at a high level for these high spatial frequencies whatever the contrast level (Fig. 2, bottom panels). In addition, the observation of strong motion coherence when the background luminance (either black or white) differs from the mean luminance of the gratings argues against a prominent role of high spatial frequencies in motion segmentation: indeed, under these conditions, the sharp transition in luminance between the aperture borders and the gratings introduces high spatial frequencies with high energy in the Fourier spectrum but motion coherence is enhanced rather than decreased. It seems thus unlikely that the easy motion integration observed at low contrast is solely due to the reduced visibility of high spatial frequencies.

Another account of the effect of contrast on motion integration, suggested by Takeuchi (1998), takes into consideration the fact that, when optimally stimulated, MT neurons have a better contrast sensitivity than V1 neurons, presumably because MT neurons pool the responses of a large number of V1 neurons across direction and space (Sclar et al., 1990; although indirect pathways that bypass V1 may also be involved). According to this view, V1 neurons would not reliably respond to local component motion at very low contrast, whereas MT neurons would be able to signal the global direction of motion. As contrast increases, the responses of V1 neurons would become more reliable, overcome the response of MT units, and drive the segmentation into local component motions.[3] Although compelling, this view does not explain why coherent motion is seen when the background luminance differs from the mean grating luminance, even at high grating contrast. In addition, the contrast levels that yield a coherent global motion percept in the present experiment (6–10%) are well above contrast threshold, suggesting that the different contrast sensitivity of V1 and MT neurons may not by itself account for the transition between motion integration and segmentation. One possibility is that moving spatial discontinuities, such as line-ends, are processed by units with low contrast sensitivity whose response depends on the nature, intrinsic or extrinsic, of these features and in turn control the perceptual transitions between global coherence and motion segmentation. The strong relationships found between occlusion cues and perceptual transparency and coherence (e.g. Anderson & Sinah, 1997; Stoner & Albright, 1998) together with the observation that the disparity between moving components and apertures strongly influence motion integration (Shimojo et al., 1989; Lorenceau & Shiffrar, 1998), support this hypothesis, although the exact nature and location of these hypothetical units remains to be determined. It is worth noting that recent electrophysiological studies in awake monkey indicate that the responses of direction-selective MT neurons stimulated by drifting gratings depends on the disparity between the grating boundaries and its moving surround (Stoner et al., 1997). If one assumes that the processing of occlusion cues and disparity share a common mechanism, this would suggest that such units are already present within or before area MT.

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[3]The underlying assumption is that coherent or incoherent motion is controlled by the relative firing rates between V1 and MT neurons. In Takeuchi's approach, the firing rate of MT neurons as measured by Sclar et al. (1990) needs to be reduced by a factor of 2 in order to favor V1 neurons relative to MT neurons, so as to predict component motion perception at high contrast.

Effect of the spatial distribution of component motion on motion integration

One intriguing effect observed herein concerns the role of the spatial relationships between neighboring patches on motion integration, namely the enhanced direction discrimination of the global motion found for L as compared to T configurations. The differences in performance observed between L and T configuration suggest that the spatial relationships between neighboring units responding to component motions play an important role in motion integration. Studies using plaids of RDKs were unable to reveal this, given the spatial structure (or lack of it) of these stimuli.

We propose below a qualitative account of these effects. Our interpretation relies on the proposal, based on psychophysical and physiological evidence, that cortico-cortical connectivity is involved in contour integration (Gilbert, 1992; Field et al., 1993; Polat & Sagi, 1993, 1994; Kapadia et al., 1995; Polat & Norcia, 1996; Frégnac, 1996 for a review; Adini et al., 1997). We further suggest that the perceptual effects evidenced with static stimuli extend to motion perception.

In a series of experiments with static Gabor patches, Polat and Sagi (1993, 1994) report that the sensitivity to a test Gabor patch is either enhanced or suppressed by the presence of flanking Gabor masks, depending on the collinearity and distance between the test and flanking patches. From their data for different spatial frequencies and spatial separations between the test and the flanking masks, these authors further suggest that the absolute distance between the test and the masks is not the critical factor, but rather that the range of lateral interactions scales with the spatial frequency of the Gabor patches, with higher spatial frequencies processed by units with smaller receptive fields. In line with these experiments, and to account for the capability of human observers to identify a path of Gabor patches within a field of randomly oriented elements, Field and colleagues (1993) developed the notion of an "association field" which integrates information across neighboring filters tuned to similar orientations.

We think this framework may account for many of the present findings. We suggest that the different performance for T and L configurations found in the present experiments, and the fact that these differences depend on the contrast, the patch density, and the spatial frequency of drifting gratings can be accounted for by the existence of lateral nonlinear interactions between units recruited by our aperture stimuli.

We propose that our results provide support for the following biologically plausible assumptions:

1. Inhibitory long-range lateral interactions are strong for T configurations but much weaker, or even facilitatory, for L configurations. This assumption is illustrated in Fig. 9, where units selective for gratings at a particular orientation and spatial frequency together with their "association fields" are represented. According to this view, two neighboring units activated by the grating patches would strongly inhibit each other when stimulated with T configurations. Such inhibitory interactions have already been reported both in the orientation domain (Blakemore & Tobin, 1972) and in the motion domain (Marshak & Sekuler, 1979), leading to biases in perceived orientation and direction. Such inhibitory interactions could account for disrupted motion integration. Whether these interactions may also account for the obser-
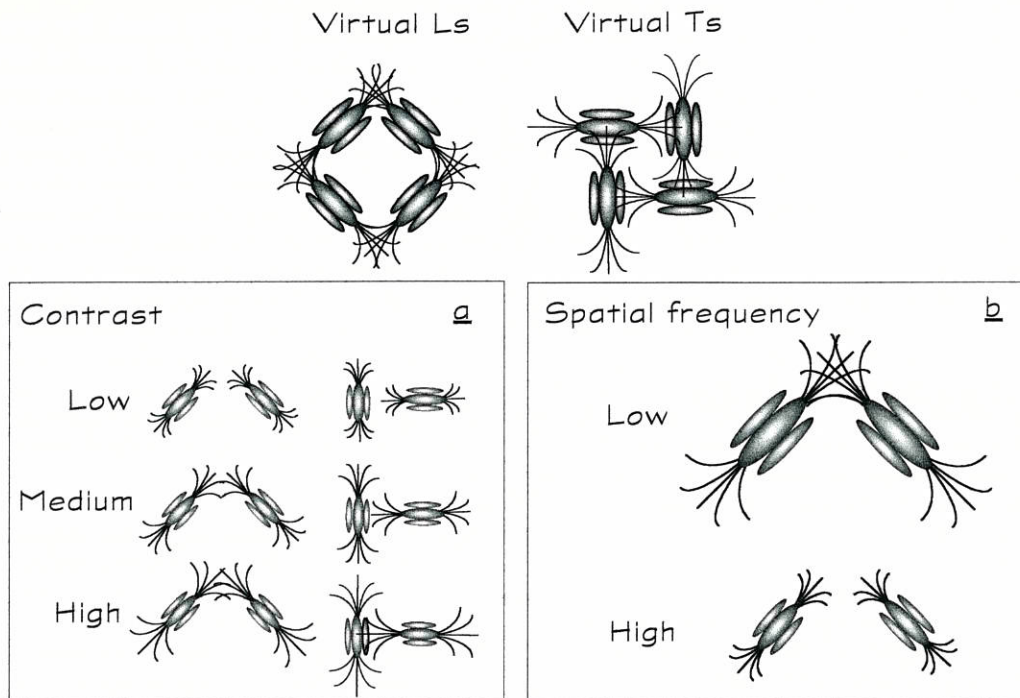
Fig. 9. Association field hypothesis illustrated for L and T like configurations. We suggest that long-range lateral interactions are facilitatory, or weakly inhibitory, for L configurations but strongly inhibitory for T configurations. (A) Hypothetical effect of contrast on the strength of long-range lateral interactions. The spread of activity through long-range lateral connections is small at low contrast and increases with contrast. (B) Hypothetical effect of spatial frequency on the range of lateral interactions. Low spatial frequencies are processed by units with large receptive fields, high spatial frequencies are processed by units with small spatial receptive fields. In both cases, the range of long-range lateral interactions scales with receptive-field size. A fixed inter-patch distance, similar to that used in Experiment I, IV, and V is shown.

vation that direction discrimination performance drops below chance level at high contrast is less clear.[4]

The topological organization of the "association fields" for L configurations may favor motion integration through facilitatory interactions. However, the observation that direction discrimination is worse at high as compared to low contrasts with L configurations is at odds with this view, suggesting that inhibitory lateral interactions may also come into play. It is worth noting that the exact nature, facilitatory or inhibitory, of these lateral interactions may be obscured by the competitive influence of a segmentation process which relies upon the processing of local spatial discontinuities existing at aperture borders (see Experiment IV). The finding that performance is independent of contrast with L configurations when the apertures and the gratings have different orientations (RM conditions in Experiment IV, Fig. 7) favor this later interpretation.

2. The observation that motion integration is independent of the spatial configuration (either T or L) at low contrast but is

worse at high contrast for T as compared to L configurations suggests that the effectiveness and nature of the long-range lateral interactions depend on contrast: The higher the contrast the larger the spatial extent over which lateral interactions are active. This assumption is illustrated in Fig. 9a. At low contrast, the weakness of lateral interactions together with the weak saliency of segmentation cues at aperture borders would favor motion integration, independent of the spatial organization of the component gratings. From the results of VEP studies with static Gabor patches, Polat and Norcia (1996) suggest that facilitatory long-range lateral interactions are maximally activated at low contrast (4–8%) and that inhibitory interactions are progressively recruited at higher contrasts. If true, this progressive increase of inhibitory interactions could explain why performance decreases with increasing contrast for L configurations. Although our own data may not permit drawing any firm conclusion on that point, since segmentation into component motions based on the processing of spatial discontinuities may counteract facilitatory interactions, the lack of effect of the spatial configuration at low (6%) contrast found here is at odds with their conclusion. However, one can wonder whether the weak response evoked with low-contrast stimuli in Polat and Norcia's study is reliable enough to assess the relative strength of facilitatory interactions. Additional studies would be necessary to clarify this point.

3. Finally, one simple account of the effect of spatial frequency on motion integration, in agreement with the conclusions of

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[4]It is worth noting that similar reversed motion was observed with dot patterns lacking oriented components (Lorenceau, 1996). One possible explanation of this phenomenon relies on the observation that tracking one of the two motion components produces a reversed retinal motion, on which observers could base their decision. This interpretation would not, however, explain why reversed motion is often seen with T configurations but rarely with L configurations, unless one assumes that tracking strategies are governed by the perceptual appearance of moving stimuli, a view which has some experimental support (Beutter et al., 1996).

Polat and Sagi (1993, 1994), is that the range over which lateral interactions are influential scales with the size of the receptive field recruited by our stimuli. Which size of receptive field is activated scales with the spatial frequency of the gratings used (Polat & Sagi, 1993). The finding that motion integration is weakly dependent on the spatial configuration for distant high spatial-frequency patches, whereas it strongly depends on this variable for short distances high contrast displays (see Experiment III), is compatible with the hypothesis that the range over which lateral interactions are efficient depends upon the size of the underlying receptive fields. This dependency between receptive field size and the range of lateral interactions is depicted in Fig. 9b.

According to the above assumptions, motion integration in our direction task would be modulated by nonlinear contrast dependent long-range interactions. Poor performance with T configurations would result from inhibitory interactions through association fields, an effect which would increase with contrast. Facilitatory or weakly inhibitory interactions through association fields, elicited by L configurations, would account for the better direction discrimination observed with these stimuli. Finally, the differences between high and low spatial frequencies, as the effect of patch density, would result from the scaling of the range of lateral interactions with receptive sizes which themselves depend upon the spatial-frequency content of the stimuli.

Although we discussed the present motion integration experiments in the light of psychophysical evidence obtained with static stimuli, there exist noticeable differences between the experimental procedures and displays used in these and the present study that deserve comments. One obvious difference concerns the spatial organization of the stimuli and specifically the presence of collinear arrangements. Most studies with static Gabor patches used truly collinear (Polat & Sagi, 1993, 1994; Polat & Norcia, 1997) or curved paths (Field et al., 1993). Field et al. (1993) suggest that enhanced contour extraction within fields of randomly oriented elements occurs for small-to-medium relative angles not exceeding 60 deg. In the present experiments with drifting gratings, relative angles between gratings were always 90 deg, and only the relative position between grating patches was manipulated to build either T- or L-like junctions. One can therefore wonder whether interactions through association fields can be observed at all for L configurations, given the 90 deg relative angle between component gratings used in the present study. However, Field et al. used a background of randomly oriented elements to mask the curved target path of Gabor patches. It is therefore possible that, for large relative angles, spurious associations between elements of the target path and elements of the background has impaired performance and yielded an underestimation of the maximum relative angle (or curvature) through which associations between Gabor patches can operate. It thus remains possible that lateral interactions also exist for L-like junctions. In addition, it is worth noting that the relevant parameter for estimating the orientation selectivity of lateral interactions may not be the relative angle *per se* but rather the degree of curvature between oriented elements, which depends on both relative orientation and spatial separation. The tradeoff that exists between these two variables may render the estimation of the strength of lateral interactions difficult.

Our interpretation relies on the hypothesis that lateral interactions between oriented units, similar to those proposed to account for the results obtained with static stimuli, account for the present findings; however, our task involves the discrimination of

the global direction of moving stimuli. One cannot exclude the possibility that the effects of the variety of spatial parameters examined here reflect lateral interactions between direction-selective units, rather than between orientation-selective units. Recent studies and models of motion perception (Watamaniuk et al., 1994; Grzywacz et al., 1995) suggest that lateral interactions between low-level motion sensors are necessary to account for the detection of a trajectory embedded in random motion noise (but see McKee & Vergheese, 1998). Koechlin et al. (1996), among others, also developed a model of motion processing which involves both inhibitory and facilitatory lateral interactions between MT-like direction-selective units, to account for the results of a variety of psychophysical experiments. Since many V1 neurons are selective for both direction and orientation and given that their preferred direction of motion is orthogonal to the preferred orientation, it seems difficult to disentangle these two possibilities from the present results. This raises the question of where these interactions might occur in the brain, since direction-selective units are found in both V1 and the MT/MST complex. We are not aware, however, of physiological studies demonstrating the existence of long-range lateral interactions within area MT, although there is evidence for a center-surround antagonism in MT receptive fields (Maunsell & Newsome, 1987). Experiments with RDKs using spatial distributions of component directions similar to those used herein, but lacking orientation, may help to clarify this point.

A number of physiological studies described cortico-cortical horizontal connections between neurons selective to similar orientations that extend over several millimeters in primary visual cortex (Rockland & Lund, 1982; Ts'o et al., 1986; Gilbert & Wiesel, 1989; Hirsch & Gilbert, 1991; Gilbert, 1992). Electrophysiological recordings in cat and monkey further indicate that neuronal responses are facilitated or inhibited by the addition of stimuli in the periphery of their receptive field (Maffei & Fiorentini, 1979; Knierim & Van Essen, 1992; Kapadia et al., 1995; Frégnac et al., 1996). In addition, coupled oscillations or synchronization of activity between co-oriented collinear neurons with nonoverlapping receptive fields has been reported (Eckorn et al., 1988; Eckorn, 1994; Gray et al., 1989; Singer & Gray, 1995). Accumulating evidence suggests that the network of horizontal connectivity may account for the modulation of neuronal responses observed in these experiments (Frégnac et al., 1996; Frégnac & Bringuier, 1996; Levitt & Lund, 1997; Polat et al., 1998), although feedback projections from higher areas or divergent inputs from the thalamus could also be involved.

Comparisons between these physiological findings and the present psychophysical data are highly speculative, however, and one should only take as a hypothesis that needs additional work the possibility that cortico-cortical interactions in primary visual cortex constrain the initial shaping of an input image which would then feed motion areas and be used in motion integration and selection.

Conclusion

Using aperture stimuli composed of patches of drifting gratings, we found that the integration of component motions into a global coherent motion strongly depends upon the spatial relationships between neighboring gratings and the motion of spatial moving dicontinuities. We suggest that the present findings can be accounted for by two mechanisms: long-range nonlinear interactions within primary visual cortex may constitute a physiological basis that accounts for the differences between T and L configurations.

In parallel, the processing of spatial discontinuities would drive the integration/segmentation balance. It has often been suggested that form/motion interactions may involve reciprocal projections between areas from the parietal, motion-specific pathway and areas from the ventral, form-specific pathway. We suggest an alternative view, according to which long-range lateral interactions at an early stage may already provide constraints to shape the responses of neurons in primary visual cortex that feed higher motion-processing stages.

Acknowledgments

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