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The Linkage of Visual Motion Signals

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Recovering a reliable 3D percept from the retinal sampling of dynamic images requires the linkage of motion signals across space and time. In this paper, we review recent experimental results that enhance our understanding of the perceptual processes of motion integration, segmentation, and selection that are necessary to solve this inverse optics problem. Simple paradigms involving the presentation of moving contours are used to assess our ability to link sparse motion information. Our results indicate that human motion perception strongly depends on both primitive stimulus characteristics, such as contrast, eccentricity, and duration, as well as higher level characteristics such as feature classification and spatial configurations. Further, the perceived direction of a moving object depends little upon its familiarity. Finally, pursuit eye movements of compositional stimuli are highly correlated with perceived motion coherence. This ensemble of results is analysed within the context of current theories of motion perception.

INTRODUCTION

Visual systems, whether natural or artificial, extract information from the external world through the discontinuous sampling of light intensities by the two-dimensional retinae. From this initial sketch, natural visual systems succeed in constructing a rich three-dimensional world in which objects are individualized, recognized and available for action and mental manipulations.

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How the visual system solves this inverse optics problem is a central issue in all studies of visual perception. The accurate interpretation of moving images requires the integration of information from the same object as well as the segregation of information from different objects. An additional requirement is that these complementary processes must be flexible enough to allow the grouping of objects into ensembles or the ungrouping of objects into parts.

In the following, we shall use the terms "binding" or "linking" to refer to the mechanisms by which neuronal activity within or across visual areas is combined to yield emerging perceptual qualities. We start with a brief description of current theories of visual binding, and related issues. We then explain why the analysis of visual motion requires specific linking mechanisms and present in more detail psychophysical studies that provide insights into the processes by which moving visual signals are transformed into distinct perceptual entities.

Binding by convergence

Over the past 50 years, our understanding of visual information processing has undergone tremendous change. For example, in the 1970s, the extrastriate visual cortex was thought to consist of six areas organized in a relatively simple, feedforward hierarchy (Van Essen, 1979; Zeki, 1978). Subsequent research has created a much more complex picture of an elaborately interconnected network of over 30 visual areas with highly specialized functional roles (Van Essen & DeYoe, 1995). Yet, although the number of identified visual areas has changed radically, their organization is still thought of as a roughly hierarchical structure in which neural computations become increasingly complex. According to this view, neurons at the lower levels of the hierarchy are thought to process elementary characteristics from relatively small regions of visual space. The results of these analyses are then passed onto and processed by higher level units that integrate information across larger spatial and, possibly, temporal extents. Anatomical and physiological evidence support this convergence scheme. For instance, the responses of rods and cones to distribution of light intensities are combined both spatially and temporally through convergent projections that yield neural units tuned to new image characteristics. In this manner, neurons that are able to detect contrast at different spatial scales are constructed. Further processing of orientation, colour, and movement is achieved through the combination of the outputs from lower level detectors (eg. Chapman, Zahs, & Stryker, 1991; Hubel & Wiesel, 1968). According to this view, at each cortical level, detectors respond to those features to which they are preferentially tuned, within a fixed location in retinal space. Moreover, neurons tuned to different dimensions such as motion, colour, or form are distributed in distinct areas distributed along parallel pathways.

The finding that some neurons in remote visual areas respond to complex stimuli also supports the idea of a hierarchical organization of the visual system. For example, detectors selective for faces, hands, and body postures, have been described in the monkey infero temporal (IT) cortex (Perrett, Harries, Mistlin, & Chitty, 1990; Perrett et al. 1985). Neurons tuned to higher order components of the optic flow– translation, rotation, or expansion– induced by internal or external movements have also been identified in area MST of the motion pathway (Maunsell & Newsome, 1987; Orban et al. 1992). Moreover, visual displays of human or animal movement selectively activate individual STP neurons (Oram & Perret, 1994). It should be noted here that most of these "cardinal" neurons, found in area IT, MST, or STP, have direct relations to internal representations of motor commands, suggesting that some neurons could be designed for the selective analyses of biologically relevant events, thus allowing fast, automatic and highly selective processing (Singer, 1995).

Dynamic binding within cell assemblies

A conceptualization of the visual system as strictly hierarchical structure also raises a number of questions. For example, is there a limit to the complexity that individual neurons can process or is there a detector for each of the complex arrangements of elementary characteristics that humans are able to perceive? If so, how does the visual system perceive new objects or novel views of known objects? How are detectors conducting complex analyses constructed from the outputs of detectors of lower complexity? Finally how are different characteristics, such as colour and motion, analysed in different areas, bounded together? To solve these problems, a strictly hierarchical system requires an infinite number of detectors– the problem of combinatorial explosion– as well as a dynamic mechanism to create new detectors. An additional difficulty with this "binding by convergence" scheme (Singer, 1995), which implicitly assumes a one to one correspondence between single neurons and object representations, is its sensitivity to neuronal death. The selectivity for complex feature constellations found in IT, MST, STP suggests one possible solution to the problem of combinatorial explosion inherent to hierarchical structures. That is, an infinite number of detectors may not be required because humans or animals interact with a finite number of objects and trajectories in the physical world.

However, we are not blind to novelty: A previously unseen object is processed by the visual system within 150 ms. In order for the visual system to isolate this object from its background or surrounding objects, the requirement of a hierarchical structure is that a population of low-level detectors tuned to the elementary characteristics of this object somehow converge to elicit a response from a target detector. This further implies the existence of a reservoir of cells with latent connections, waiting for their specific inputs. The finding that neurons recorded in area IT show emergent selectivity after training to sets of fractal images (Miyashita, 1933) suggests that indeed some neurons can dynamically select and stabilize a pattern of connectivity. However, these training dependent changes occur on a rather slow time scale. They are not compatible with the instantaneous perception of new objects, and may rather be involved in recognition processes and long term memory. Thus, the theoretical problems raised by a hierarchical structure makes it unlikely the visual system uses exclusively such a coding strategy.

One promising theoretical alternative to the classical hierarchical view is that visual representations consist in the coactivation of a population of cells distributed among different cortical areas rather than being instantiated in individual cells, (Abeles, 1982; Hebb, 1949; Von der Marlburg, 1981). In line with these theoretical conceptions, neuroanatomical studies (review in Gilbert, 1992) have revealed both long-range horizontal cortico-cortical connections and feedback cortico-geniculate projections. Although the functional role of these diffuse lateral pathways is still a matter of debate, they may provide information about the visual context of a stimulus and subserve the formation of cell assemblies. Remote influences of stimulation outside the classical receptive field of single neurons demonstrated both in psychophysics (Polat & Sagi, 1993, 1994) and physiology (Frégnac & Bringuier, 1996; Knierim & Van Essen, 1992; Stemmler, Usher, & Niebur, 1995) are probably mediated by such connectivity. The additional finding that synchronized bursts of neural activity occur during visual stimulation with colinear oriented bars in anaesthetized and paralysed cats supports the idea that these connections are useful to signal a global perceptual coherence. These synchronizations were found to centre around a 40 Hz frequency and could be observed between units separated by several millimetres across or within different cortical areas (Eckorn, et al. 1988; Gray, König, Engel, & Singer, 1989). It has subsequently been proposed that the synchronization between neural units may instantiate the rules put forward early in the century by the Gestalt psychologists to account for perceptual organization, such as good continuity, similarity, common fate, etc. (Singer, 1995 for a review), but such theory needs further testing to determine precisely the origin and the spatio-temporal characteristics of synchronized activity.

Binding and attention

The binding problem has long been a centre of interest in the domain of attention (Schneider, 1995; Treisman, 1996; Treisman & Gelade, 1980). The finding that search for conjunctions of object properties (e.g. orientation and colour) embedded within arrays of distractors is difficult and induces illusory conjunctions– spurious associations between features– led to the proposal of a feature integration theory of attention (Treisman, 1996; Treisman & Gelade, 1980). Although a matter of much debate (e.g. Green, 1991; Van der Heijden, 1995), this theory suggests that features analysed in parallel within different visual areas (location, orientation, colour, etc.) are bounded together by an attentional mechanism. Despite the fact that we have not tested this theory directly, we present evidence that this may not be the general case, since in our situations, binding motion signals seems to depend primarily on low-level characteristics and little on voluntary attention.

Binding motion signals

The perception of motion, in addition to its essential role in vision, is particularly well suited to the study of binding processes for two main reasons. First, early motion signals, made within small receptive fields, are inherently ambiguous (see later). As a result, the unambiguous interpretation of object motion requires the selection, integration, and segmentation of motion signals in the external world. Second, the anatomy and physiology of the motion pathway (V1, V2, MT, MST) may be better understood than any other cortical pathway. Armed with a solid understanding of velocity tuned neurons within and across visual areas, vision scientists are better able to hypothesize associations between the behaviour and structure of the visual motion pathway.

The field of motion perception in general, and motion integration in particular, has produced an impressive array of research paradigms and displays of dynamic lines, gratings, plaids, and random dot kinematograms. To provide a unified understanding of motion integration processes, we have adopted a progressive approach in which increasingly complex stimuli are used to investigate sequentially more sophisticated processes of visual analysis. Each stimulus is designed to address specifically a particular stage of motion information processing. Elementary stimuli, such as translating line segments, are used to tackle relatively low-level stages of motion integration. Compound stimuli, constructed from the elementary stimuli, are used to address higher stages of motion integration within a unitary experimental approach. For the purpose of coherence, we shall restrict ourselves to those studies that fall directly within this cascade of motion processing stages. We first introduce some fundamental issues of motion perception, summarize previous results, and then turn to a more complete description of some recent findings.

THE APERTURE PROBLEM

Why does the accurate interpretation of moving images require the linkage of motion measurements? In early stages of image processing, image motion is analysed by simple and complex cells commonly found in the primary visual cortex (Hubel & Wiesel, 1968). These units have relatively small receptive fields and are conjointly selective to the orientation and the direction of translating bars or gratings (Henry, Bishop, Tupper, & Dreher, 1974). This conjoint selectivity creates several problems for the interpretation of motion because these neurons will respond identically to differing velocities. For example, whenever the motion of a relatively long edge is measured through a small receptive field, the resulting motion signal is ambiguous because the component of motion parallel to the edges orientation can not be obtained. Thus, simple and complex neurons can "see" the component motion perpendicular to contour orientation but are "blind" to the component of motion parallel to the contour, as shown in Figure 1 (Henry et al. 1974; Marr & Ullman 1981). As a result all moving edges sharing the same perpendicular component of motion but differing parallel components will yield the same neuronal response. This ambiguity, known as the aperture problem, has received extensive study because both biological and computational visual systems have receptive fields limited in size.

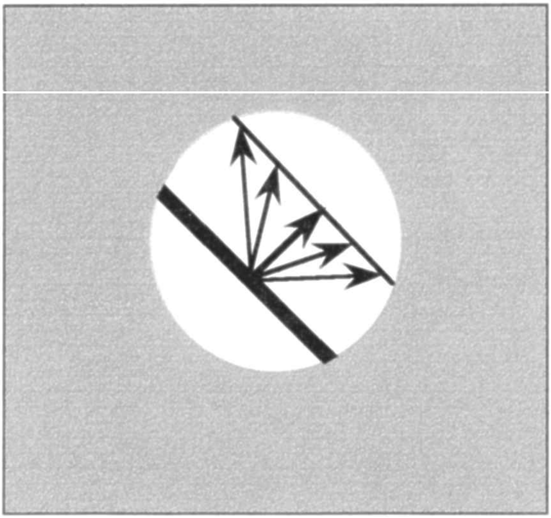
The visual system is thought to overcome this local uncertainty by binding individual ambiguous motion signals across differently oriented edges (Fennema & Thompson, 1979). In addition to motion integration, segmentation and selection processes must also be considered, to avoid spurious combinations of contours across different objects. In this paper, we present evidence that moving spatial discontinuities such as line ends, corners, or regions of high curvature provide strong constraints to perform these sophisticated computations, presumably because reliable 2D estimates of velocity are available for these specific features.

In the following, we first bring evidence that the perceived velocity of simple moving bars or lines already implies the combination of detectors' responses across space and time. We then turn to the problem of integration across different features and argue that the perceived direction of complex patterns depends on a weighted combination scheme that involves the computation of various kinds of two-dimensional features. Finally, we present results obtained with the "masked diamond" paradigm, showing that transitions between segmentation and integration of motion signals distributed over space depend on both low-level characteristics, presumably influencing the processing of two-dimensional features, and on higher order factors, shedding light on the architecture and dynamics of neural processes underlying motion linking.

BIASES IN THE PERCEIVED DIRECTION AND SPEED OF TRANSLATING LINES

When a line or a bar translates over the retina, it activates a number of units selective for the direction of motion. Some of these units, stimulated by the inner part of the contour, face the aperture problem and only provide information about the 1D component motion normal to the line orientation. Other units may respond the motion of line ends and provide local estimates of the 2D velocity field. When both responses are different, for instance when an oblique line translates horizontally, recovering the actual direction of the line requires

(a)



(b)

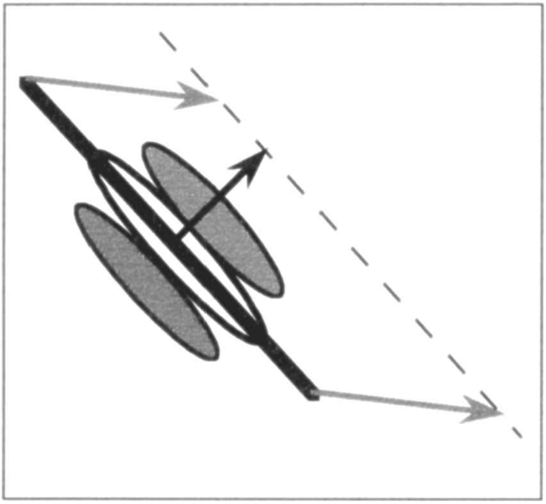


FIG. 1. Illustration of the aperture problem, both at the macroscopic level of perception (a) and at the microscopic level of neuronal response (b). Since the parallel component motion cannot be estimated, only the component normal to orientation is "seen".

the combination of these discrepant responses. A number of psychophysical studies provided insights into this combination process. Early in the century, Wallach (1935, 1976) designed an impressive set of demonstrations concerned with the perceived direction of bars or gratings moving behind apertures, similar to "barber poles" (Figure 1a). Manipulating the aspect ratio or the shapes of a variety of such apertures, he first observed that the perceived direction of motion was mainly determined by the direction of the line endings at aperture borders. Shimojo, Silverman, and Nakayama (1989) refined this interpretation by differentiating extrinsic line ends, resulting from an occlusion, and intrinsic line ends, that belong to the contour itself. Changing the status of line ends through the manipulation of the disparity (positive or negative) between a grating and an aperture, these authors found that the perceived direction is mainly constrained by intrinsic but little by extrinsic line ends. These observations led Lorenceau, Shiffrar, Wells, and Castet (1993) and Castet, Lorenceau, Shiffrar, and Bonnet (1993) to systematically study the factors that influence the perceived velocity of simple moving lines (see also Kooi, 1993). Indeed, such a simple stimulus presumably involves the combination of signals arising from the centre of the lines, where only ambiguous 1D information is available, and signals from intrinsic line ends that locally provide the 2D information necessary to recover the physical velocity, or at least to restrict possible 3D interpretations. If the lines are tilted relative to the axis of motion, these signals are different. Such stimuli were used to assess the relative contribution of 1D and 2D signals through measures of their perceived direction and speed.

The main outcome from these studies is that the perceived direction and speed of tilted lines is biased towards the component motion orthogonal to line orientation at short durations or at low contrast (Figure 2). In addition, these biases increase with line length and tilt relative to the axis of motion. The bias progressively disappears as duration and contrast increase, and is reduced above medium speeds (> 4°/sec). One important conclusion to draw from these studies is that the integration of motion signals along contours is a dynamic, time-consuming process involving the parallel processing of 1D and 2D motion along contours.

Models proposed to account for these data involve either the propagation of motion signals along contours to minimize a motion energy function through iterative calculations (e.g. Hildreth, 1904; Lamouret, Lorenceau, & Droulez, 1996) or a vector averaged combination between poorly sensitive units with long integration time constant, tuned the motion of line ends, and motion units that respond to contour motion (Castet et al., 1993; Lorenceau et al., 1993; see also Mingolla, Todd, & Norman 1992; Rubin & Hochstein, 1993). The former stresses the dynamics of cooperative interactions within the neural network, whereas the later emphasizes the need for mechanisms selective to line ends' motion. Note, however, that both approaches are not exclusive and might simultaneously be implemented within the cortical network.

At this point, we have presented experimental data concerned with integration along moving contours. Remote 2D features also modulate the perception of moving contours. For instance, a translating curved line appears non-rigid as long as the display lacks 2D features (Nakayama & Silverman, 1988). The addition of 2D terminators, either on or off the line, yields a coherent percept

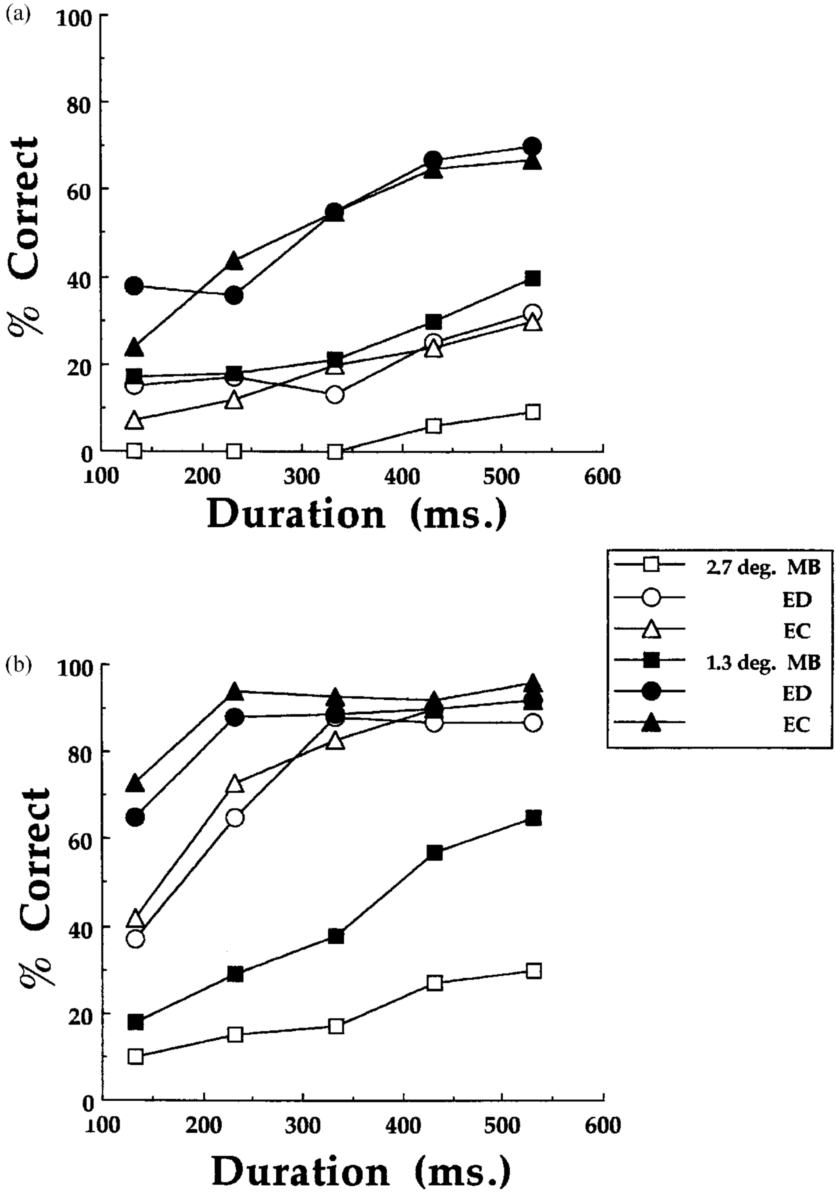


FIG. 2. Performance of correct direction discrimination of translating oblique lines four observers as a function of duration, (a) contrast 39%, (b) contrast 70%. Note that performance increases with increasing duration. Perceptually, low contrast moving lines appears to change their direction over time. Initial perceived direction is orthogonal to line orientation and progressively switch toward the veridical direction of motion.

whose perceived rigidity decreases with increasing distance between the terminators and the line. In the same vein, Shiffrar, Li, and Lorenceau (1995) estimated the influence of moving dots on the perceived direction of gratings moving behind apertures with varying aspect ratios– a spotted version of Wallach's barber pole. They observed that the perceived direction changes smoothly from orthogonal to grating orientation toward the direction of the dots as these later were made more numerous. However, the dots failed to "capture" the grating when extrinsic line ends at aperture borders, moving in the same direction as the dots, were removed (e.g. by using apertures in the shape of parallelograms). Furthermore, the perceived direction of gratings was unaffected by the dots when a disparity between the dots and the grating was introduced. In this case, transparent motion of two planes at different depths is seen. These different results reveal the existence of cooperative/competitive interactions between motion signals of varying degrees of ambiguity, though they are distributed over unconnected regions of space. Integration is observed when the distance between motion signals– in a 3D space– is not too large and provided that the contours possess some motion energy in the resultant direction. In addition, the perceived direction of motion seems to result from a complex combination process that assess different weights to motion signals depending on their degree of ambiguity.

INTEGRATION ACROSS DIFFERENT CONTOUR ORIENTATIONS

Computational models of motion integration stress the fact that a combination from multiple orientations permits a solution to the aperture problem (Fennema & Thompson, 1979). Theoretically, two orientations are sufficient to specify a 2D velocity by extracting the only velocity vector compatible with all possible motions. Two superimposed gratings at different orientations (i.e. plaid patterns) were subsequently used to test whether human observers also implement such a combination scheme, known as the intersection of constraints (IOC) rule (Adelson & Movshon, 1982). When the component gratings of the plaid stimulus are drifting, observers perceive a coherent motion, provided that the spatial frequency, speed, contrast, or colour of the component motions are not too dissimilar (Adelson & Movshon, 1982; Krauskopf & Farell, 1990; Stone, Watson, & Mulligan, 1990). Subsequent tests (Ferrera & Wilson, 1990, 1991; Yo Wilson, 1992) indicated that under specific conditions, the perceived direction and speed of motion is biased relative to the predictions of the IOC rule, which led Wilson and Kim (1994) to propose a vector averaging scheme which combines the outputs of first and second order motion signals (e.g. texture boundaries). Further studies emphasized the role of local contrasts at grating intersection (nodes), that do move in the direction predicted by an IOC, and efforts made to isolate their contribution (eg. Alais, Burke, & Wenderoth, 1996; Derrington &

Badcock, 1992; Gorea & Lorenceau, 1991) convincingly demonstrate that nodes contribute to perceived direction and speed, as well as perceived transparency of plaid patterns (Stoner, Albright, & Ramachandran, 1990; Vallortigara & Bressan, 1991). Again, local moving discontinuities, the nodes, appear to determine what signals are or not bounded together, although their analysis calls for specific, non-linear mechanisms that complement the more classical linear analysis performed by first order mechanisms. Evidence that the nodes are processed at a monocular level (Alais, et al., 1996) suggest that an early non-linearity, occurring prior to binocular convergence, may be involved (see also Noest & Van den Berg, 1993).

THE MASKED DIAMOND

Although plaids have proven to be a powerful tool for the study of motion coherence and transparency, they are not particularly well suited to address the issue of integration across space, which corresponds to the more general case encountered in a natural, noisy environment. The analogy of a leopard running through a forest is often used to describe the competing problems of motion integration and segmentation across space (Ramachandran, 1990). What are the specific rules used by the visual system to isolate the motion signals related to the various regions of a single object while segmenting these signals from those belonging to different objects?

Early in the century, the Gestaltists proposed a motion binding principle, known as the law of common fate, in which components moving in the same direction with the same speed are bounded together and interpreted as belonging to the same object (Koffka, 1935). However, this simple rule is insufficient to constrain a unique interpretation of visual motion, because motion in a three-dimensional (3D) space projects on a two-dimensional (2D) retinal space. Furthermore, the common fate principle implicitly assumes that visual neurons analyse 2D motion whereas most cortical neurons signal only one-dimensional 1D motion (see earlier). Thus, identical retinal motion may correspond to different trajectories or conversely movements in different directions with different speeds may correspond to a unique motion of a single object. To restrain the space of the possible solutions to a unique interpretation, and to determine what signal correspondences should be established between different signals over time (Ullman, 1979), computational models often use a number of a priori assumptions or constraint− rigidity or smoothness− (Hildreth, 1984; Horn & Schunck, 1981; Ullman, 1979). Does natural vision employs these different constraints? To address this important question, we constructed a new class of compositional stimuli consisting in contours presented behind windows or apertures distributed in space. We then used these stimuli to assess the spatio-temporal characteristics of motion integration.

In a first series of experiments (Lorenceau & Shiffrar, 1992), a simple outlined translating diamond was presented behind four apertures. The relative position of the apertures was manipulated so that the diamonds corners were always either hidden or visible, as shown in Figure 3.

In these experiments, a new paradigm well suited to estimate observers' ability to link component motion into a global percept was used: The diamond translated along a circular path, clockwise or counter-clockwise. A two alternative forced choice discrimination task, rather than a subjective estimate of perceived coherence, was used to minimize procedural biases.

Such a circular translation (i.e. a revolution) presents several advantages: Each segment maintains its orientation and moves back and forth along a straight axis within each aperture; thus, one segment in isolation does not

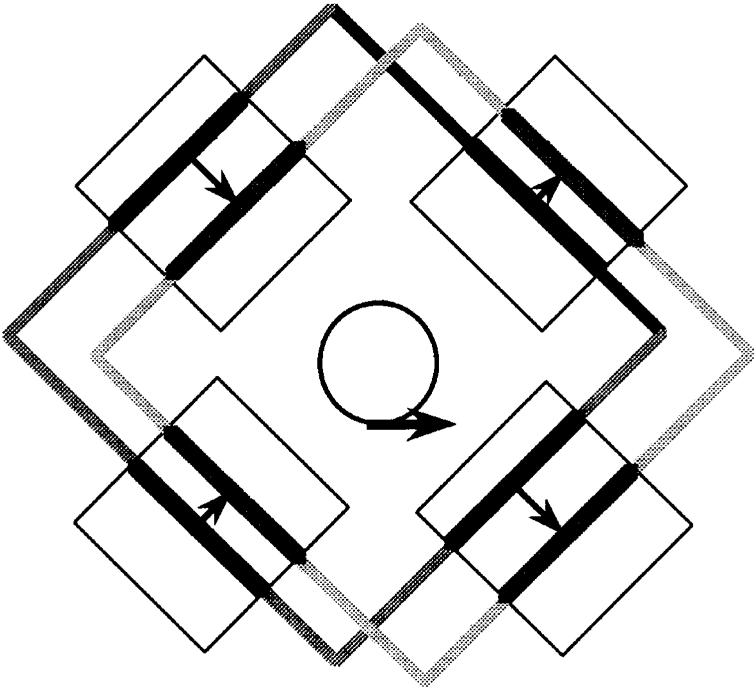


FIG. 3. Masked diamond paradigm: Because of the aperture problem, a moving line viewed through a relatively small aperture is ambiguous. We examined the visual system's ability to link individually ambiguous motion signals when a translating diamond figure is viewed through four stationary apertures. The apertures were positioned so that the diamond's corners were never visible (i.e. thin lines on the figure were invisible). As a result, the diamond's translation can only be determined by linking motion signals across two or more visible edges. In our experiments, the diamond translated along a circular path in a clockwise or counter-clockwise direction. The diamond's orientation did not change. Since the motion of each visible segment is constrained by the aperture shape, it translates back and forth and does not provide sufficient information to perform a clockwise/counter-clockwise discrimination. Integration across segments is required for that task.

provide sufficient information to perform the task; such motion maintains eccentricity, even at long durations; finally, recovering the global direction of motion implies that the direction, but also the continuously changing speeds of each segment, are integrated across space and time[1]. We used this paradigm in a number of different conditions, including variations of aperture shapes, orientation, size, contrast, contour luminance distribution, and viewing eccentricities. Our goal was to determine precisely the factors that govern the perceptual transitions between integrated and segmented percepts.

A striking observation is that whenever the apertures are visible, either because they have a different luminance from the background or because they are outlined, the diamond appears rigid and its direction can easily be determined. Decreasing the contrast between the aperture and the background decreases coherence and observers fail to discriminate the diamond's direction. When the apertures and the background have the same hue and luminance, observers report seeing a jumbled mess of four moving segments. Clear perceptual transitions between a moving whole and its moving parts are induced by this contrast manipulation. To get more insights into this phenomenon and test different potential explanations, we further manipulated the salience of line ends, either by using jagged apertures that produce a symmetrical and rapid change in contour length during the motion, or by manipulating the distribution of the luminance along the contour (i.e. high luminance at the centre and low luminance at the line ends or the reverse). As a general rule, we found that motion coherence and discrimination performance improve as terminator salience decreases. Similar improvement in performance is observed when the overall contrast of the segments decreases, suggesting the existence of a threshold above which the diamond is segmented into parts.

Eccentric viewing conditions produce dramatically different results. Whatever the aperture visibility, the diamond is always seen as a rigid object whose direction is effortlessly detected. This effect is not easily explained by a change in the size of the receptive fields with eccentricity, as a large reduction of the size of the stimulus does not facilitate motion integration in central vision. Rather, the effect of eccentric viewing conditions could reflect the relative inability of peripheral vision to resolve local discontinuities. A summary of these different results is presented in Figure 4. In this figure performance in our direction discrimination task is plotted as a function of the different conditions tested.

At this point several hypotheses that could be invoked to account for these phenomena can be discarded. For example, the idea that motion integration is

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[1] Note that the direction– clockwise vs. counter-clockwise– would be easily performed by any model that can determine the sign of the phase lag (± 90°) that exists between the motion of orthogonal segments. However, our experiments demonstrate that human observers cannot make use of this cue.

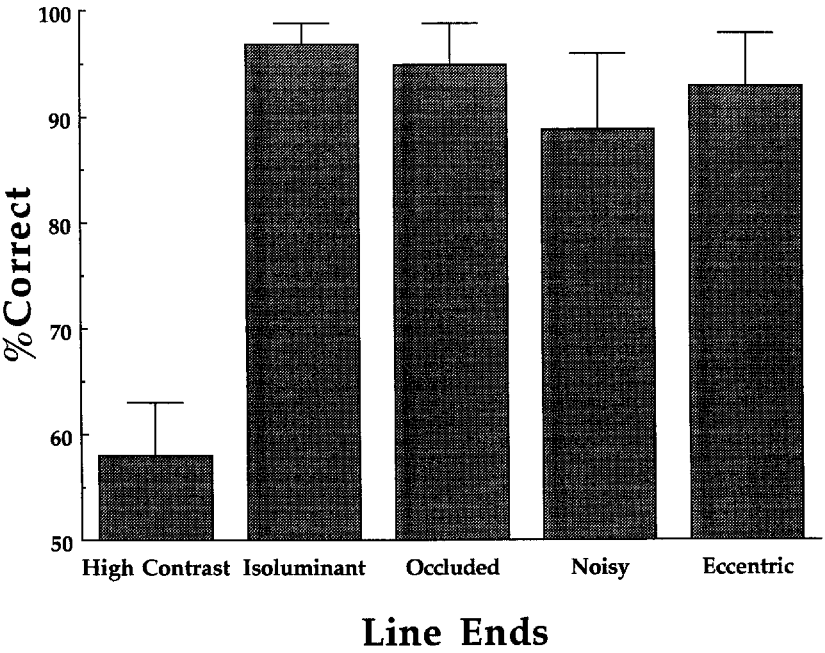

FIG. 4. Performance in the masked diamond paradigm for a variety of experimental conditions. Note that foveal viewing conditions with invisible apertures yields poor performance.

facilitated with visible as compared to invisible apertures because the former, but not the later, provide a static frame of reference cannot explain why low-contrast stimuli are perceptually coherent in central vision. Also, neither the idea that human observers use a constraint of rigidity to recover object motion nor the role of attention in binding is supported by our results: Prior knowledge that a rigid diamond is moving does not help to determine its direction and attentional efforts to glue the otherwise incoherent segments into a whole, coherent percept were useless.

A complementary demonstration with a stereoscopic diamond stimulus strengthens the view that early parsing of the image relies on 2D discontinuities: if a high contrast diamond has a positive disparity relative to the apertures, and thus appears in front, its motion appears incoherent, whereas negative disparities, inducing a percept of a diamond moving behind the apertures, produce a highly coherent percept (Figure 5).

Thus, despite the fact that the monocular image is identical in both conditions, the perceptual outcome is dramatically different (Lorenceau & Shiffrar, unpublished observations). This effect brings additional support to the hypothesis of Shimojo et al. (1989) that a change in terminator classification, from extrinsic to intrinsic, explains the transitions from motion integration to motion

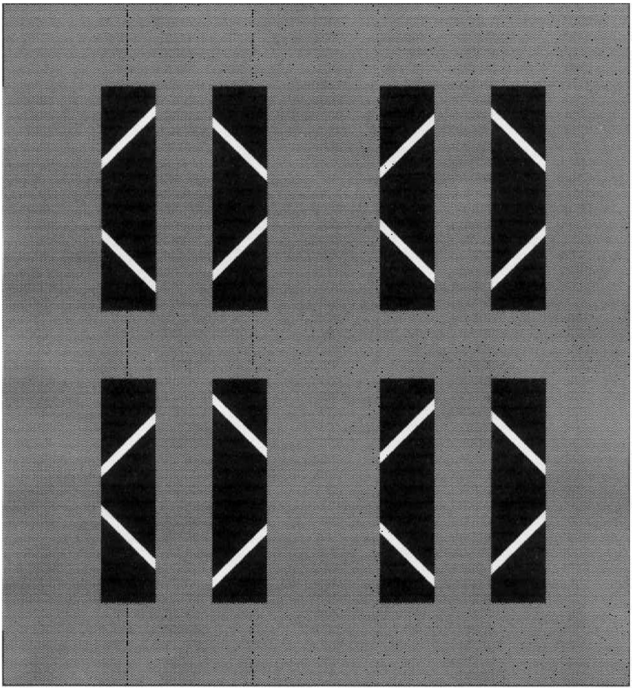

FIG. 5. Stereograms of a diamond presented behind or in front of apertures. (upper) When the diamond is perceived behind the apertures, motion integration is easy. (lower) Motion integration fails when the diamond's segments are perceived in front. The motion available monocularly is the same in both cases.

segmentation. The present results further clarify the role and characteristics of intrinsic line ends processing.

Another issue concerns the combination rules, Intersection Of Constraints (IOC) or vector averaging (VA) of component motions used in motion linking. Previous studies with aperture stimuli (Mingolla, Todd, & Newman, 1992; Rubin & Hochstein, 1993) or plaid patterns (Yo & Wilson, 1992) have shown that global perceived direction is biased toward the VA of component motions although the IOC rule accurately predicts the veridical motion. We re-examined this issue using occluded diamonds for which the IOC and VA predictions are very different (Lorenceau, 1998). Observers were asked to adjust an elliptic diamond's trajectory until it appears as a circular motion. If a VA combination rule was used in this task, the adjusted trajectory should not be circular but markedly elliptic, which in our experimental conditions should have an aspect ratio of 1:7. Such aspect ratios were never observed. Rather, adjusted aspect ratios (0.86) were close to, but significantly lower than 1, as expected if observers used an IOC-like combination rule. The observed aspect ratios are very different from VA predictions, suggesting that observers did not use this combination rule to bind component motions into a global trajectory. Comparisons between the experimental conditions employed in Rubin and Hochstein's or Mingolla et al.'s experiments and Lorenceau's suggest that the different results obtained in these experiments are likely to be explained by the spatial characteristics of the stimuli, rather than by differences in the methods. We shall come back to this point in a later section when discussing the influence of spatial organization on motion linking.

So far, these experiments indicate that a translating diamond appears non-rigid when its corners are occluded. This raises the question of whether the effect reported above is specific to translating motion or also exists with rotational motion[2]. To determine whether the visual system integrates motion information across rotating objects, Shiffrar and Pavel (1991) examined the perception of a rotating polygon behind stationary apertures. Interestingly, they found that such a rotating figure appears to shrink and expand when the diamond's corners were hidden but not when they were visible. In addition the figure appears perfectly rigid in the latter but not in the former conditions. The experimental results reported in this paper indicate that when a simple, rotating polygon is viewed through a set of disconnected apertures, observers are unable to link motion measurements accurately across the disconnected edges. Thus, although theories of motion perception are based on the assumption that the visual system overcomes the ambiguity of individual motion measurements by linking measurements across different oriented edges of the same object, observers are not always able to perform this crucial task. Moreover, while researchers have proposed that the visual system is biased by selecting image interpretations that are consistent with rigid objects, observers non-rigidly interpreted these rigidly rotating displays. The fact that subjects interpreted the polygon's motion correctly whenever the polygon's corners were visible suggests that contour discontinuities may play a fundamental role in motion linkage.

NEURAL PATHWAYS AND MOTION LINKING

Is it possible to determine more precisely the neural substrate underlying these effects? Recently, Livingstone and Hubel (1987) proposed that the magnocellular pathway of the geniculostriate system may be responsible for the application of Gestalt-like linking rules. More specifically, these researchers proposed that “magno functions may include deciding which visual

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[2] A rotational motion (Shiffrar & Pavel, 1991) creates a situation in which the orientation of every polygon contour changes over time. Since motion processing units in the early visual system are selective for particular orientations, it is likely that different units are continuously recruited through out the rotation. For that reason, comparisons between these results and physiological studies of the motion integration properties of area MT are limited.

elements, such as edges and discontinuities, belong to and define individual objects in the scene" (Livingstone & Hubel, 1988, p. 748). We conducted a set of experiments to test this magno-linking hypothesis (Shiffrar & Lorenceau, 1996). Because of the physiological properties of cells in the magnocellular pathway, including their responsiveness to transient stimulation (Merigan & Maunsell, 1993), researchers have suggested that the magnocellular system analyses motion-related information (Livingstone & Hubel, 1987). The following studies were based on the assumption that if the magno system is responsible for linking motion signals when they define an object, then linking should decrease with decreases in magno system activity.

We took advantage of the poor sensitivity of magno cells to chromatic contrast (e.g. Shapley, 1990) to modulate their contribution to motion interpretation. In these experiments, a red diamond viewed through a set of four apertures was presented against a green background. The apertures had identical hue and luminance as the background and were thus invisible. Under these conditions, only four red segments were visible against a green background.

The isoluminance point was first estimated for each observer with a flicker photometry procedure, in order to minimize the luminance contrast to which the magno system could respond. We then measured direction discrimination performance for varying line widths as a function of luminance contrasts added to each segment. In this manner, the contribution of the magno system was modulated. We found that for short durations of movement (166 ms), performance is close to perfect for all conditions tested. At a longer duration (1.3 sec), performance is not homogeneous across the different conditions: Direction discrimination is close to perfect for thin lines when the diamond is defined only by chromatic contrast. As line width and luminance contrast increase performance decreases (Shiffrar & Lorenceau, 1996), presumably because the visibility– and localization– of line ends increase with contrast and width.

Important conclusions to draw from these experiments are the following: (1) motion integration is best at isoluminance which does not support the idea that the magno system, less responsive than the parvo system for chromatic contrast, is primarily responsible for motion linking. (2) Performance is better at short duration, as compared to long duration. This indicates that motion integration precedes motion segmentation. This effect can be understood in light of the effect of duration on the perceived direction of single moving lines described earlier. According to our view, units that respond to line ends would have long integration time constant, as compared to contour units, and thus may be unable to influence motion interpretation. Initially, the fast combination of early responses to contours across space and time would yield the percept of a coherent global motion. The late involvement of line ends tuned units would induce motion segmentation, as observed at long duration. Note that if motion linking involved a time-consuming propagation process (Hildreth, 1984), one would expect that motion coherence would follow motion segmentation and not the reverse. Altogether, these experiments suggest that motion integration does not solely involves the magno system. Instead motion integration results from complex dynamic interactions, that presumably involve both the magno and the parvo pathways.

ALIGNMENTS, JUNCTIONS, CLOSURE, AND MOTION LINKING

As mentioned previously, the accurate interpretation of object motion requires the segmentation of velocity estimates from different objects. Fourier models of motion analysis satisfy this requirement by segmenting velocity estimates from contours differing significantly in contrast, spatial frequency, speed, and direction (Adelson & Movshon, 1982). How might feature-based models satisfy this segmentation requirement? To address this question, we examined how form information might influence the motion integration and segmentation processes with a variety of displays in which elementary structural characteristics were manipulated.

Many computational models of the segmentation of static objects make use of some non-accidental properties of objects, such as proximity, colinearity, or junctions (Hummel & Biederman, 1992). A number of psychophysical studies have also demonstrated that these characteristics are critical to identify objects a visual scene (Biederman, 1987; Boucart & Humphreys, 1992; Donelly, Humphreys, & Riddoch, 1991). The effects of these factors on perceptual organization. are also evident in masking experiments, suggesting that binding depends upon lateral interactions between oriented components. For instance, the detection of a target– a small Gabor patch– is modulated by the presence of similar flanking masks, resulting either in an enhancement of sensitivity for masks collinear to the target or in a decreased sensitivity for masks at angles with it (Polat & Sagi, 1993, 1994). The additional finding that the detection of virtual curves or Gabor patches hidden in a texture of similar patches depends on their degree of colinearity also support the existence of an association field involving lateral interactions between neurons (Field, Hayes, & Hess, 1993). Finally, the closure of these virtual curves modulates contrast sensitivity over space, resulting in sensitivity maps with peaks and troughs at specific locations (Kovacs & Julesz, 1993). Although these different results stress the role of lateral connections in the perceptual organization of static displays, few studies tested the potential influence of these properties on motion linking. Rather, efforts were made to remove these cues, as is clear from the extensive studies of motion perception through the use of random dot kinematograms that lack any form cues. Studies of “motion cooperativity” that employ these random dot stimuli he suggested spatial extents of 50 min (Nawrot & Sekuler, 1990) and 15 min (Chang & Julesz, 1983) within which velocity estimates are integrated. These variations in the spatial estimates of velocity integration suggest that distance alone may not determine motion integration. Some models use a since distance parameter to define what velocity estimates should be integrated (Grzywacz & Yuille, 1991). However, if figural or colinearity cues suggest that velocity estimates define same object, then the distance over which those velocities are integrated may shift (Braddick, 1993).

Potential interactions between form and motion could involve low-level structural characteristics such as alignments or colinearity between neighbouring components, more global properties of objects such as closure or surface interpretation, or top-down influences of stored representations of known objects. We undertook series of experiments to test whether these different properties influence the linking of motion signals across space.

To get insights into this question, we first design experiments to contrast a well-structured and a random distribution of dot stimuli (Lorenceau, 1996). One display consisted of a regular distribution of dots along the border of a virtual square, whereas the second was made of the same dots distributed at random within the area of a square pattern. Thus, the former contained dot alignments and defined a closed shape while the later lacked any of these properties. Our paradigm for testing motion integration abilities was then applied to these stimuli in the following way: Half the dots moved sinusoidally along a horizontal axis, whereas the remaining dots moved sinusoidally, ± 90° out of phase, along a vertical axis. Integrating dots' velocity under these conditions is formally equivalent to adding a sine and a cosine motion, which results in a circular motion translation, either clockwise or counter-clockwise, depending on the sign of the phase lag. With such stimuli, each dot defines a local 2D velocity which, when reliable, drives the segmentation into component motions (Lorenceau & Shiffrar, 1992). In order to favour perceptual coherence, local motion uncertainty was introduced by adding variable amounts of "motion noise" to each dot trajectory. Direction discrimination performance measured under these conditions reveals that motion integration is facilitated for dot stimuli that contain some form of structural information as compared to random dot configurations, although this difference tends to decrease as duration of motion increased (300 ms to 600 ms). This difference is large in central vision and diminishes with increasing eccentricity, as shown in Figure 6.

In addition, performance increases with the amount of noise added to each dot which agrees with our previous observation that motion integration is more likely when each 2D signals is less salient and reliable (Lorenceau & Shiffrar, 1992). An additional finding is worth mentioning: Extensive training with these dot stimuli produces an improvement of performance over time. However, improved performance is observed mainly for structured dot patterns but not with random patterns, suggesting that observers may learn to use structural information to bind motion signals.

Although these experiments suggest that some form of structural information plays a role in motion processing, they are insufficient to determine

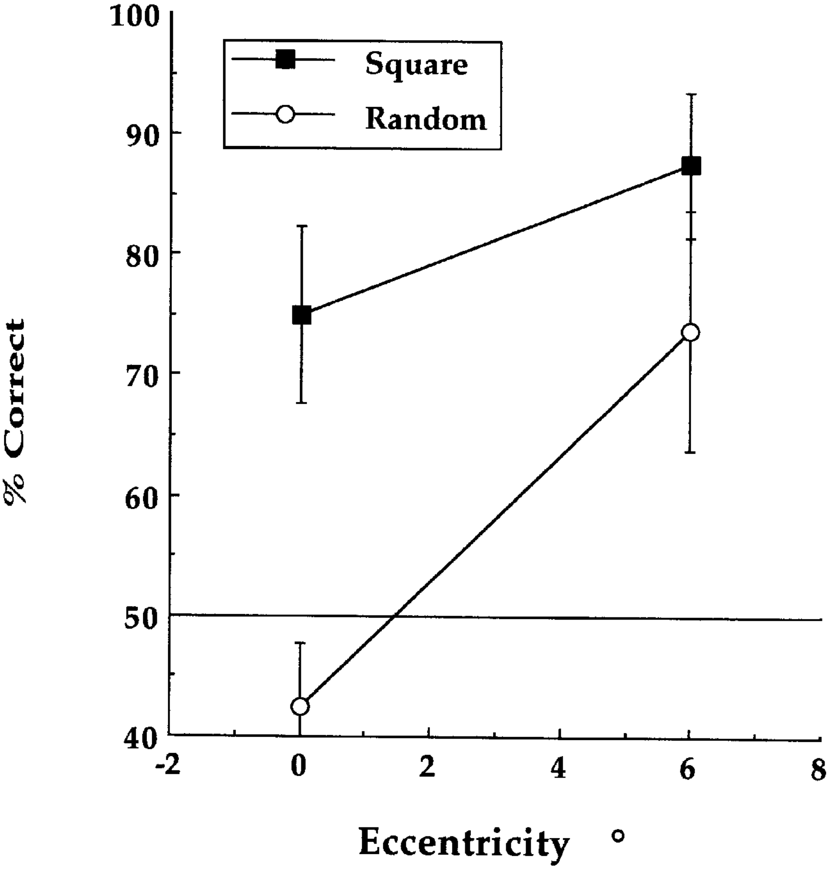

FIG. 6. Performance in a clockwise vs. counter-clockwise direction discrimination for a Square dot pattern and a random dot pattern, as a function or stimulus eccentricity (see also Lorenceau, 1996).

whether performance is enhanced for the square pattern because the dots are aligned, because these alignments define specific junctions (i.e. corners), or because they define a closed geometrical figure. We therefore decided to test these different alternatives more specifically in additional experiments. In particular, do virtual junctions defined by dot alignments or by contours at different orientations facilitate motion linking?

To test this possibility, the display was simplified. Two line segments were arranged so as to define either L junctions (i.e. a corner) or T junctions (resulting from accidental occlusion). In these experiments (Shiffrar, Pavel, & Lorenceau, 1995), the vertices formed by two lines could be visible or not. In this later condition, the lines were presented behind two different apertures whose spatial separation was varied. These lines then translated leftward at various angles slightly above or below a stationary target located a few degrees away and disappeared well before reaching target location. Observers had to decide whether the lines trajectory was above or below the stationary target. The results are straightforward: Performance is close to perfect for visible vertices whether they are Ls or Ts. However, performance decreases for virtual vertices in proportion to the spatial separation between line ends. Interestingly, although performance falls off quickly with Ts, it remains high for Ls. Additional experiments with textures of patches of drifting gratings, arranged so as to form virtual L or T junctions, confirm and extent these findings. Motion linking is easy at low contrast whatever the spatial configuration of the gratings. As contrast increases performance decreases steeply for T configurations, but is little affected for L configurations. In addition, we found that these effects are more important for low as compared to high spatial frequencies, for a constant spatial separation between grating patches. Altogether, these results support the idea that the relative position and spatial organization of corner edges modulate the perception of object motion. One possible explanation of these effects relies on the existence of anisotropic lateral interactions, either facilitatory or inhibitory, between oriented neurons that respond to neighbouring contours or grating patches. If, as we think, direction discrimination performance reflects the influence of lateral spatial interactions, then our results are evidence that the strength and extent of these interactions increase with increasing contrast, and scale with the spatial frequency of drifting gratings (Lorenceau, Zago, & Shiffrar, 1996; Polat & Sagi, 1994).

HIGHER ORDER FACTORS AND MOTION LINKING

The previous series of studies suggests that low-level form information plays an important role in motion linking. Will form influence motion processing at higher levels in the visual system? Numerous researchers have proposed that visual information is conveyed along two major, generally independent pathways in the extrastriate cortex (Desimone & Ungerleider, 1989; Maunsell & Newsome, 1987; Ungerleider & Mishkin, 1982). One pathway, known as the "dorsal stream" feeds into the posterior parietal cortex and is thought to be involved in spatial analyses and motion perception. The other pathway, known as the "ventral stream", feeds into the inferior temporal cortex and appears to play a key role in object recognition. Since a moving object evokes responses in widely separated areas, questions arise as to how these different signals are bounded into a single percept. One popular approach to this question considers that binding occurs through an attentional mechanism (Treisman, 1996).

This organization of the visual cortex led us to ask whether the identity of an object influence the interpretation of its motion? To address this question, the translating diamond paradigm described earlier was adapted to stimuli consisting in familiar as well as unfamiliar complex objects (Lorenceau & Boucart, 1995). Familiar objects (animals or vehicles) and unfamiliar polygons (derived from a spatial rearrangement of the familiar objects' outlines) were presented behind apertures such that only straight fragments were visible, as shown in Figure 7.

The same direction discrimination task described previously was used as a measure of motion binding across contours. If prior knowledge of a moving object's identity facilitates the linkage of its parts into a coherent whole, then performance in this task should be better with familiar as compared to unfamiliar figures. On the other hand, if object identity is processed independent of motion analyses, then object familiarity may not enhance motion linking. Indeed, object identity might even act as a distractor that perturbs subject performance on the motion task. Our results favour the later hypothesis: Observers were not as accurate and response times were 30 ms slower for familiar as compared to unfamiliar objects. Thus, the effect of familiarity appears detrimental to motion linking and may reflect an automatic identification process that interferes with the motion task (see also Boucart, Humphreys, & Lorenceau, 1995 for a discussion of this point). This finding suggests the existence of some form of competition, rather than cooperation, between the parallel processing of form and movement.

One possible exception to this general rule is suggested by recent studies showing that while form and motion analyses may proceed independently in the ventral and dorsal pathways, respectively, the two pathways converge in anterior superior temporal sulcus or STS (Baizer, Ungerleider, & Desimone, 1991). Physiological studies of anterior STS indicate that cells in this area respond maximally to the presentation of precise combinations of biological forms and movements (Oram & Perrett, 1994; Perrett et al., 1985; 1990). That is, Perrett and his colleagues have identified numerous cells that respond selectively to moving human and primate bodies and yet remain unresponsive to moving inanimate control objects. Thus, form and motion analyses may converge for the analysis of moving biological forms in the STS.

To understand how the visual system links biological motion signals across space, we conducted a study in which subjects viewed dynamic, stick figure renditions of a walker, car, or scissors through apertures (Shiffrar, Lichtey, & Heptulla-Chatterjee, 1997). In a free identification procedure, subjects readily identified the human figure but were unable to identify the car or scissors through invisible apertures. Recognition of the walker was orientation specific and robust across the range of normal human walking speeds. These results support the theory that human observers analyse biological motion displays more globally than non-biological displays (Bertenthal & Pinto, 1994; Shiffrar, 199; Vaina, Lemay, Bienfang, Choi, & Nakayama, 1990).

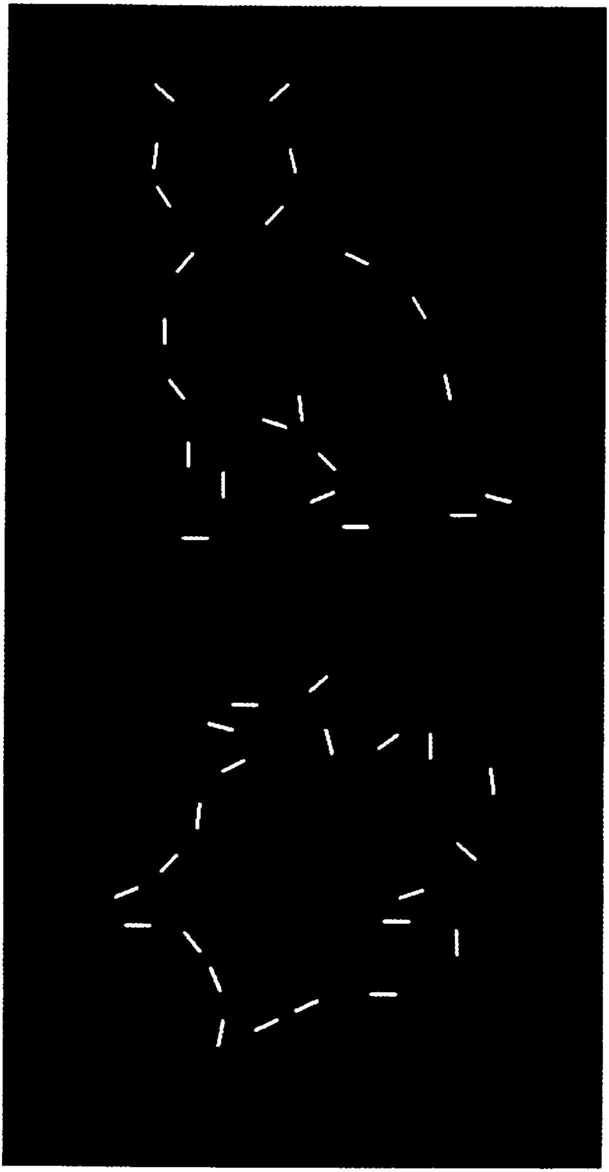

FIG. 7. Example of the stimuli used to estimate the influence of familiarity on motion integration performance. Outlines of familiar and unfamiliar figures are presented behind multiple apertures that mask the corners. Segment motion must be integrated across space to perform a clockwise/counter-clockwise direction discrimination task.

EYE MOVEMENTS AND MOTION LINKING

In previous experiments, a fixation point at the centre of the displays was provided to minimize eye movements. Although motion duration was often short, which reduces the possibility to initiate eye movements, we did not directly control eye movements.

The transitions between coherent and incoherent perceived motion described earlier are well suited to better understand the relationships between perceived motion and active movement of the eyes. In particular the role of the retinal slip in driving pursuit eye movements can be assessed since simple manipulations of contrast that do not affect retinal motion nevertheless produce large perceptual changes. Most models of pursuit assume that the retinal slip is the driving force used to accurately pursue moving objects. According to these models observers should be able to track high- and low-contrast diamond with similar accuracy.

To test this hypothesis, we used the masked diamond paradigm and recorded pursuit eye movements while observers attempted to actively pursue the centre of the configuration (Beutter, Lorenceau, & Stone, 1996; Stone, Lorenceau, & Beutter, 1996). In our experiments, pursuit eye movements were recorded for 3 seconds while observers were viewing the masked diamond in circular translation (see earlier), either at low or high contrast or with visible– black on a grey background– apertures. These manipulations deeply affect perceived coherence, but the motion available for tracking is the same. Since the centre that must be tracked is never displayed on the screen, observers must pursue within a homogeneous region of the visual field. Control experiments with a moving dot or a full diamond served as base line performance. During off-line analysis the saccades were detected and removed from the recordings. A circle was then fitted to the raw data and the gain and phase relative to the real centre trajectory were estimated. This analysis indicates that the gain and phase of pursuit are tightly related to perceptual coherence. Efforts to pursue the diamonds centre fail in the incoherent high contrast condition. Under these conditions observers are more likely to track individual segments. In contrast, the phase and gain are close to those of the control conditions when coherence is high (i.e. at low contrast or with visible apertures). This pattern of result suggest that voluntary tracking eye movements depend little on top-down influence and is primarily driven by bottom-up interactions, or re-entrant cortical loops (Stone, Beutter & Lorenceau, submitted).

SUMMARY AND CONCLUSION

In this paper, we have presented a number of experimental results concern with the linkage of motion signals across space and time, using simple lines or more complex configurations of moving contours seen through apertures. Motion linking processes appeared through a variety of visual illusions that provide insights into the nature and dynamics of the mechanisms involved. Biases in the perceived direction and speed of simple moving lines permit one to isolate the contribution of local responses to moving contours and line ends together with the dynamics of their interactions. Motion capture of translating lines by moving 2D features further suggests that motion linking results from a weighted combination of motion signals depending upon their degree of ambiguity. In addition, linking moving contours across space strongly depends upon the salience of 2D features, which provides support for feature-based models of integration in which competing signals govern the segmentation of object parts or their integration into a coherent entity (e.g. Nowlan & Sejnowski, 1994). That performance is almost perfect at low contrast but decreases at higher contrasts suggests that the segmentation process involve mechanisms with poor contrast sensitivity. This finding is compatible with a progressive recruitment of inhibitory interactions. The idea that inhibition is involved in the segmentation process is strengthened by the observation that benzodiazepines, which act as GABA agonists, reinforce the segmentation of component motion (Giersch & Lorenceau, 1996). The observation that motion linking is a fast process that precedes motion segmentation, although it appears counter-intuitive, may help to understand the architecture and dynamics of the cortical network. At least it suggests the existence of a feedforward unconstrained pooling of motion signals across space, maybe through a direct input from V1 neurons onto MT, followed by a more sophisticated time-consuming segmentation process that relies on the processing of 2D features. Although the motion of veridical features, either dots or line ends proved crucial for motion binding, we also bring evidence that virtual features, produced by the spatial arrangements of contours also modulate the linking of motion signals. This later results suggests that lateral, long-range horizontal connections intervene in motion integration, and constrain motion linking. This finding is evidence that form and motion information are not processed independently by the visual system, but may interact at an early stage of visual processing. Our results do not seem to support the view that top-down influences are involved in motion linking since neither the prior knowledge that rigid objects are moving, nor the familiarity with these objects, permit to overcome the perception of non-rigidity reported in our experiments. In addition, the inability to make accurate pursuit eye movements under incoherent conditions argues against the idea that directed attention can be used as a glue to stick motion signals into a single object. Rather, motion linking appears to depend primarily upon low-level stimulus characteristics. Accurate attentional tracking may be possible only when these characteristics favour the formation of a coherent percept.

The studies summarized in this paper have implications for the neural substrate that implement motion linking. For instance, our results with isoluminant red/green stimuli are at odds with the view that the projections of magno cells in

V1 onto area MT are exclusively involved in motion linking. That transitions between a coherent and an incoherent percept primarily depend upon the salience of 2D features support a scheme in which motion linking is governed by the response of specific feature detectors. It is tempting to establish a link between our findings and the existence of hypercomplex cells described in area V1 and V2 of the macaque monkey. A variety of such cells, described by in a large number electrophysiological studies (Orban, Kato, & Bishop, 1979; Peterhans & Von der Heydt, 1989; Saito, Tanaka, Fukada, & Oyamada, 1988; Versavel, Orban, & Lagae, 1990) are plausible candidates to process 2D features. However, further electrophysiological studies are needed to test this possibility.

Recently, it was suggested that the synchronization of neuronal responses elicited by a visual stimulation mediates the binding of visual information. It is impossible to determine from our psychophysical observations whether such synchronization is involved under our conditions. Nevertheless, we think that, if such a mechanisms is related to binding, our experimental conditions constitute a critical test of this theory.

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