Perception & Psychophysics
2001, 63 (5), 847-861

Differential activation solution to the motion correspondence problem

LEE A. GILROY and HOWARD S. HOCK
Florida Atlantic University, Boca Raton, Florida

and

ANNEMIE PLOEGER
University of Amsterdam, Amsterdam, The Netherlands

The correspondence problem arises in motion perception when more than one motion path is possible for discontinuously presented visual elements. Ullman's (1979) "minimal mapping" solution to the correspondence problem, for which costs are assigned to competing motion paths on the basis of element affinities (e.g., greater affinity for elements that are closer together), is distinguished from a solution based on the differential activation of directionally selective motion detectors. The differential activation account was supported by evidence that path length affects detector activation in a paradigm for which motion correspondence is not a factor. Effects on detector activation in this paradigm also were the basis for the successful prediction of path luminance effects on solutions to the motion correspondence problem. Finally, the differential activation account was distinguished from minimal mapping theory by an experiment showing that the perception of an element moving simultaneously in two directions does not depend on whether the two motions are matched in path-length determined affinity; it is sufficient that the activation of detectors responding to each of the two motion directions is above the threshold level required for the motions to be perceived. Implications of the differential activation solution are discussed for the stability of perceived motions once they are established, and the adaptation of perceived and *un*perceived motions.

The correspondence problem in motion perception is concerned with how the visual system establishes pairwise correspondences between the elements belonging to one set of simultaneously presented, discrete elements and those belonging to a subsequent, second set of simultaneously presented elements. The "problem" arises when there is the possibility of different combinations of correspondence matches, and therefore, competing motion paths for each element (Attneave, 1974; Kolers, 1972). The "solution" entails establishing which of the alternative motion paths is perceived. In this study we examined "minimal mapping theory" (Ullman, 1979) as the basis for solving the motion correspondence problem and propose an alternative that depends on the *differential activation* of directionally selective motion detectors that respond selectively to the competing motions.

According to minimal mapping theory, whether or not a match is established between an element ("correspondence token") presented during one time interval and an element ("correspondence token") presented during the following time interval depends on stimulus attributes that affect the affinity of the pair of elements. Some attributes, like interelement distance and element similarity, directly affect affinity. Elements that are near each other have stronger affinity than elements that are further apart, leading to the "nearest neighbor" solution to the motion correspondence problem (e.g., Burt & Sperling, 1981; Hock, Kelso, & Schöner, 1993; Shechter, Hochstein, & Hillman, 1988; Ullman, 1979). Other stimulus attributes neither increase nor decrease affinity. Instead, they "equate" the effects of affinity on correspondence strength that arise from other attributes; for example, long interframe intervals between the presentation of the elements reduce differences in correspondence strength due to differences in the distance between the elements.

The minimal mapping solution to the correspondence problem, the determination of the motion path perceived when more than one path is possible, then depends on local competition (interaction) modifying the correspondence strengths established by stimulus-determined element affinities. Both split competition (when an element presented during one time interval has possible matches with two or more elements presented during the next time interval) and fusion competition (when two or more elements presented during one time interval have the same element as a possible match during the next time interval) affect the ultimate strength of element correspondences. However, the effectiveness of local inhibitory competition depends on there being differences in affinity for the pairs of elements defining the alterna-

---

We thank Gregor Schöner, Cynthia Park, and three anonymous reviewers for their valuable comments. Correspondence should be addressed to H. Hock, Department of Psychology, Florida Atlantic University, Boca Raton, FL 33431 (e-mail: hockhs@fau.edu).

tive motion paths. Without such differences, there is no solution to the correspondence problem; that is, the alternative motions of an element are simultaneously perceived (accompanied by splitting and/or fusion). With the additional constraint that all elements are "covered" (i.e., participate in a correspondence), Ullman's (1979) minimal mapping solution constitutes the set of element pairings that minimizes cost (maximizes correspondence strength) over the entire set of possible element pairings.

The minimal mapping solution is feature based. It assumes that attributes relevant to element affinity are encoded and costs assigned on the basis of the attributes' values. Lower costs are assigned to shorter path lengths on the basis of differences in encoded interelement distances (or speeds), and motion for each element is perceived over the path that is determined by the minimal mapping "decision" to minimize overall cost. Minimal mapping therefore makes no assumptions concerning differences in activation among motion detectors. The choice among alternative motion paths is the result of a decision based on element affinities determined by *explicitly* coded stimulus attributes.

As an alternative to minimal mapping theory, it is proposed that the contributions of different stimulus attributes to establishing motion correspondences are *implicitly* determined by differences in the activation levels of motion detectors that respond selectively to the alternative motions. (There is information in discontinuously as well as continuously displaced stimuli that can activate motion detectors, independent of any process that establishes element correspondences; Adelson & Bergen, 1985; Hock, Gilroy, & Harnett, in press.) Nearest neighbor solutions to the motion correspondence problem then emerge as a result of some motions being perceived (typically those with shorter motion paths) because they produce activation of directionally selective motion detectors above the threshold level required for the perception of motion, whereas other motion directions are not perceived (typically those with longer motion paths) because inhibitory interactions reduce the activation produced by those motions to levels that are below the threshold for perception. In further contrast with minimal mapping, solutions to the motion correspondence problem can emerge as a result of random fluctuations in activation, even when the competing motions have the same path length. That is, random fluctuations can produce differences in detector activation for the competing motions, and inhibitory interactions can "push" the activation levels further apart, the result being that activation is above the perception threshold for one motion direction and below the perception threshold for the other.

Differences in activation among motion detectors with different directional selectivity have been postulated by other investigators. Early psychophysical evidence has come from direction-specific adaptation raising thresholds for the detection of moving gratings (Pantle & Sekuler, 1969; Tolhurst, 1973), differences in detection thresholds between drifting and counterphase gratings (Levinson & Sekuler, 1975a), and activation-decreasing inhibitory interactions among detectors with opposing directional selectivity (Levinson & Sekuler, 1975b; Marshak & Sekuler, 1979). Williams, Phillips, and Sekuler (1986) have shown that a dynamical model involving activation-increasing excitatory interactions and activation-decreasing inhibitory interactions among directionally selective motion detectors can account for hysteresis effects in the perception of motion for random cinematograms, and differences in the activation of motion detectors with different directional selectivity have been proposed as the basis for the relative contributions of two moving gratings to the perception of a coherently moving plaid pattern (Adelson & Movshon, 1982). Significantly for the present study, Burt and Sperling (1981) have argued for differences in motion detector activation (i.e., motion strength) as the basis for solutions to the motion correspondence problem, and a connectionist model developed by Dawson (1991) has demonstrated the computational viability of path-length dependent differences in detector activation as the basis for solving the motion correspondence problem (greater activation for motions over shorter path lengths was implemented by greater excitatory self-feedback).

These findings notwithstanding, there has been no independent evidence to support the critical assumption that motion detector activation depends on the length of the motion path. The first objective of this study, therefore, was to determine whether differences in path length (the distance between "correspondence tokens") result in different levels of motion detector activation for a stimulus for which there is *no* competition between alternative motion paths. Without such differences, it would not be feasible for differential activation to be the basis for nearest neighbor solutions to the motion correspondence problem when there are competing motion paths.

The second objective was to support the differential activation account predictively. The effect of a new stimulus attribute (path luminance) on motion detector activation is tested in the absence of competition, and on this basis, predictions are made regarding its influence on solutions to the motion correspondence problem when there is competition among alternative motion paths.

The third and final objective of this study was to investigate why the visual system sometimes fails to solve the motion correspondence problem; for example, when two motion paths are possible for an element, instead of one path being selected, both are perceived simultaneously (accompanied by splitting and/or fusion). It is here that the minimal mapping and activational solutions can be most clearly distinguished. Minimal mapping specifies that an element is perceived as moving simultaneously in two directions when element affinities and split/fusion competition are the same for the two competing motion directions. In contrast, differential activation accounts for the perception of an element moving simultaneously in two directions on the basis of detector activation for both of the competing motions being above the threshold level required for perception. This distinction between the minimal mapping and differential activation solutions was tested with stimuli for which there were competing motions in two different directions, and these motions were the same or different with respect to path-length determined element affinity (or, alternatively, feed-forward motion detector activation). Consistent with the differential activation solution, but not the minimal mapping solution, it was anticipated that the simultaneous perception of an element moving in two directions would not require equal (or near equal) path lengths for the competing motion directions.

EXPERIMENT 1

As noted, most of the previous evidence concerning the effect of path length (the "nearest neighbor" preference) has been based on paradigms for which there is competition between short and long motion paths. For example, the motion quartet, which was first described by P. von Schiller (1933), is an apparent motion stimulus created by simultaneously presenting a pair of elements corresponding to the diagonally opposite corners of an imaginary rectangle, then presenting another pair of elements corresponding to the other diagonally opposite corners, and so on back and forth (Figure 1a, 1b). Both horizontal and vertical correspondences are possible, the correspondence made depending on the aspect ratio of the quartet (the vertical divided by the horizontal distance between element locations). Vertical motion is typically perceived for small aspect ratios (the vertical path is short relative to the horizontal path) and vice versa for horizontal motion; the two motion directions are never perceived simultaneously (Hock et al., 1993).

Accounting for the influence of relative path length observed for the motion quartet in terms of differences in the activation of directionally selective motion detectors requires demonstrating the activational effect of path length in a paradigm for which motion correspondence is not a factor. Heretofore, such investigations have been based on the measurement of the minimal stimulus onset asynchrony (SOA) required for the perception of standard, single-element apparent motion (i.e., a single element discretely shifted back and forth between two spatial locations). In general, it has been found that the minimal SOA required for the perception of motion is smaller for shorter motion path lengths (e.g., Korte, 1915; Larsen, Farrell, & Bundesen, 1983; Neuhaus, 1930). However, obtaining different SOA thresholds for short and long motion paths is of limited relevance to the motion correspondence problem because it does not logically imply greater activation for the shorter path. Minimum-SOA measurements are more relevant to the question of whether there is a constant speed threshold for the perception of apparent motion (Kolers, 1972).

This and the following experiment are based on the generalized single-element apparent motion stimulus first described by Johansson (1950) and more recently studied systematically by Hock, Kogan, and Espinoza (1997). This paradigm differs from standard apparent motion in that two elements are simultaneously visible at all times. Both elements have luminance values that are greater than the background luminance, and the two luminance values are exchanged during successive frames (illustrated in Figure 2a). Whether or not motion is perceived between the two element locations depends on their background-relative luminance contrast (BRLC), the difference between the two luminance values for each element divided by the difference between the mean luminance of the elements and the luminance of the background (provided that the luminance of one element changes toward the value of the background luminance and the luminance of the other element changes away from the value of the background luminance; Hock et al., in press).[1]

The rationale for Experiments 1 and 2 comes from Albrecht and Geisler's (1991) evidence that the activation of motion-sensitive cortical neurons increases with increased luminance contrast. It can be inferred from these neurophysiological results that if detector activation is relatively weak for long motion paths, more time-varying luminance contrast (higher BRLC values) will be required in order to increase activation to the level required for motion to be perceived as frequently as it is perceived for short motion paths.

Method

Stimuli. A pair of horizontally or vertically separated 6 × 6 min squares was presented simultaneously in the center of a gray rectangular background (3° × 3°; luminance = 6.9 cd/m^2), which was centered on the darkened (luminance < 0.001 cd/m^2) screen of a ViewSonic 15GA RGB monitor. Viewing distance was maintained at 35.8 cm by a head restraint. The luminance values for the two squares were different during each 200-msec frame and were exchanged during successive frames. The pairings of alternating luminance values were selected to give nine BRLC values ranging from 0.1 to 0.9 (Table 1). There were eight frames per trial.

Design. The distance between the two squares (path length) remained constant during each trial at 24, 36, 48, or 60 min (all distances center-to-center) and was varied randomly within separate blocks of trials during which the squares were either horizontally or vertically aligned (so motion was horizontal or vertical). A total of 72 conditions was established by the orthogonal combination of four path lengths, two motion directions, and nine BRLC values. There were four blocks of 216 trials during each of four testing sessions and two blocks for each motion direction (the order of the blocks was counterbalanced both within and between sessions). Each block was composed of six sub-blocks of 36 trials generated by the orthogonal combination of nine BRLC values and four path lengths (trial order was randomized within each sub-block). Each of the 72 conditions therefore was tested on 48 trials over the course of the experiment (eight blocks, six repetitions of each condition per block), so there was a total of 3,456 trials for each participant.

Procedure. Participants were instructed to look midway between the squares and to indicate whether or not they perceived motion of a square through the space between them anytime during the trial. Responses were executed by pressing one of two preassigned computer keys after the conclusion of the trial (participants pressed the spacebar when they were unsure of their response).

Participants. Two of the 8 participants were authors and 6 were undergraduate and graduate students at Florida Atlantic University. The latter were naive with respect to the purpose of the experiment. All had normal or corrected-to-normal vision.

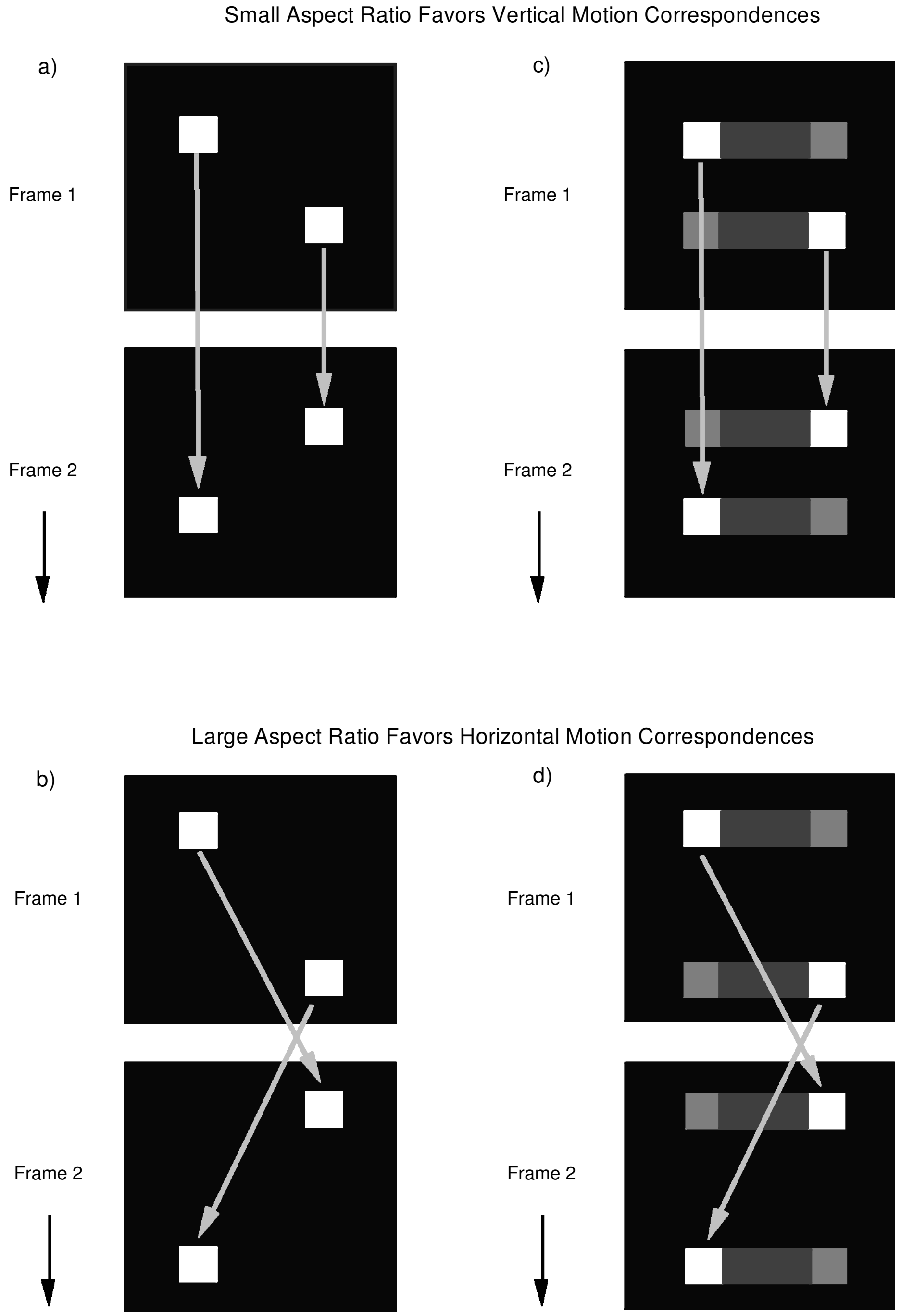

Figure 1. Panels a, c: Two frames of an apparent motion quartet with a relatively small aspect ratio, which favors vertical motion correspondences. Panels b, d: Two frames of an apparent motion quartet with a relatively large aspect ratio, which favors horizontal motion correspondences. These examples are for standard apparent motion (panels a, b) and for generalized apparent motion with a horizontal bar filling the gaps at the top and bottom of the quartet (panels c, d). The latter is illustrative of the stimuli for Experiment 3.

Results

Psychometric functions were obtained by measuring the proportion of trials for which motion was perceived for each BRLC value (averages over all participants are presented in Figure 3; data for individual participants were generally consistent with the averages, but not perfectly so, particularly for the difference between the horizontal and vertical motion directions).

Motion was always perceived more often for larger values of luminance contrast (BRLC), as in Hock, Kogan,

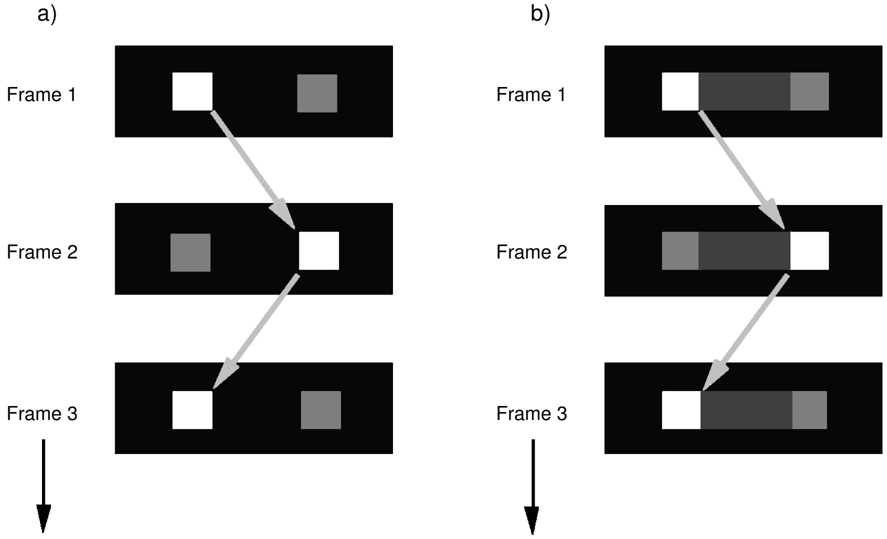

Figure 2. Panel a: Three frames of a generalized apparent motion stimulus, as in Experiment 1. Panel b: Three frames of a generalized apparent motion stimulus with a horizontal bar filling the gaps between the squares, as in Experiment 2 (the luminance of the bar varied).

and Espinoza (1997). The BRLC values required for motion to be perceived for half the trials was determined by probit analysis for each participant in each of the eight conditions (four path lengths by two directions). A within-subjects analysis of variance (ANOVA) based on these 50% thresholds indicated that the effect of motion path length was statistically significant [$F(3,21) = 16.48$, $p < .001$], and the effect of motion direction fell just short of significance at the .05 level [$F(1,7) = 4.39, p = .074$]. The interactive effect of path length and direction on the 50% threshold was not significant [$F(3,21) < 1$]. As can be seen for the regression lines fit to the averaged probit values (Figure 4), the 50% threshold increased linearly with motion path length for both motion directions; the regression lines accounted for over 98% of the variance, with remarkably similar slopes for the two motion directions (.0024 and .0027 BRLC units per arc min).

Table 1
Experiment 1: Alternating Luminance Values and the Resulting Background-Relative Luminance Contrast (BRLC) Values at Each Element Location (in cd/m²)

	Luminance	
BRLC	1	2
.1	71.6	65.4
.2	74.7	62.3
.3	77.7	59.3
.4	80.8	56.2
.5	84.0	53.1
.6	87.0	50.0
.7	90.1	46.9
.8	93.2	43.8
.9	96.2	40.8

Note—The background luminance is 6.9 cd/m^2. BRLC values are determined by the difference between the two luminance values divided by the difference between the mean luminance of the elements and the background luminance.

Discussion

The results provide evidence, for both horizontal and vertical motion directions, that shorter motion paths activate motion detectors to a greater extent than longer motion paths. Motion was perceived at lower values of time-varying luminance contrast (BRLC) for the shortest motion paths, and the BRLC value required to increase detector activation to the level required for motion to be perceived with a particular frequency (e.g., during 50% of the trials) increased as path length was increased. On the basis of Albrecht and Geisler's (1991) evidence that the activation of motion-sensitive cortical cells increases with increased luminance contrast, it can be inferred that detector activation is weaker for long than for short motion paths; more time-varying luminance contrast (higher BRLC values) is required in order to increase activation for long motion paths to the level required for motion to be perceived as frequently as it is perceived for short motion paths. This indication that path length affects motion detector activation is convergent with Anstis, Giaschi, and Cogan's (1985) evidence that there is more adaptation-induced loss of motion perception for longer motion paths. That is, detector activation is more likely to fall below the threshold level required for motion to be perceived when an already low level of activation (for the longer motion paths) is further reduced by adaptation.

The evidence that path length affects motion detector activation provides an empirical basis for the differential activation solution to the motion correspondence problem. That is, when more than one motion path is possible, the shortest path is most likely to be perceived because mo-

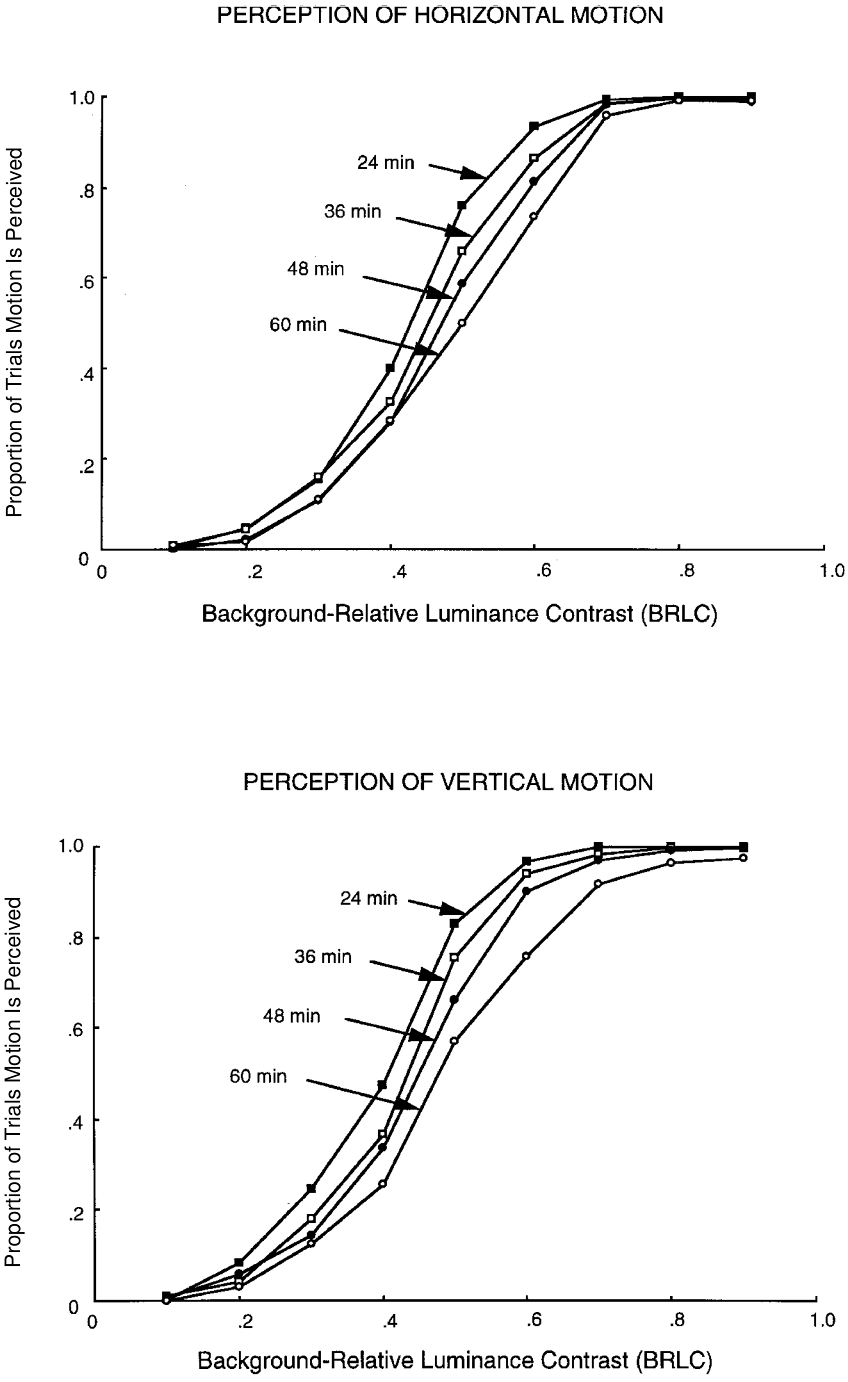

Figure 3. Experiment 1: The effect of interelement distance and background-relative luminance contrast (BRLC) on the perception of motion in horizontal and vertical directions (averaged over 8 participants).

tion detectors are more strongly activated for shorter motion paths. It is alternatively possible that the effects observed in this experiment involved differences in perceived speed; that is, it is conceivable that motion detectors tuned to slow speeds are more activated for a particular BRLC value than motion detectors tuned to faster speeds. This possibility is consistent with Weiss and Adelson's (1998a, 1998b) Bayesian estimation solution to the motion correspondence problem, which is discussed later.

Although the vertical/horizontal difference in BRLC thresholds fell short of statistical reliability, the trend in the results suggests that detector activation may be greater for vertical than for horizontal motion paths of equal length (on average, larger BRLC values were required for hor-

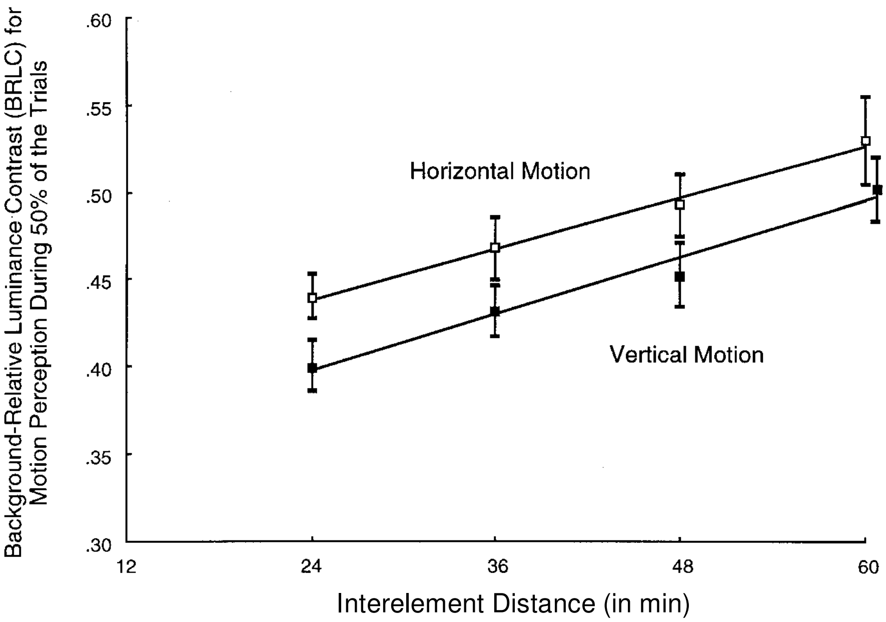

Figure 4. Experiment 1: Probit-determined background-relative luminance contrast (BRLC) thresholds for perceiving motion during half the trials as a function of the interelement distance and the direction of motion (averaged over 8 participants). Standard error bars are based on the average of the standard errors for each participant (which were determined by the 50% thresholds calculated for each of eight blocks of trials).

izontal motion to be perceived as frequently as vertical motion).[2] If further investigation establishes the reliability of this difference, it would support differences in activation as the basis for the bias to perceive vertical motion for motion quartets with equal horizontal and vertical path lengths (Gengerelli, 1948; Hoeth, 1968; Kruse, Stadler, & Wehner, 1986).

EXPERIMENT 2

The purpose of this experiment was to determine whether another attribute of the motion path—namely its luminance—would also produce a change in motion detector activation. If activation is relatively strong for bright motion paths, lower BRLC values for the elements at the start and end of the motion path would be sufficient for motion to be perceived as frequently as it is perceived for less bright motion paths. Evidence for an effect of path luminance on motion detector activation would provide the basis for predicting path luminance effects on motion correspondences in Experiment 3, which follows.

Method

Stimuli. The general viewing conditions and procedure were similar to those of Experiment 1. The stimulus was composed of a pair of 6 × 6 min squares simultaneously presented against a dark background (luminance < 0.001 cd/m^2). The squares, whose luminance varied between two values, were horizontally separated by 36 min (center to center). Filling the gap between the two squares was a 6 × 30 min bar. Its luminance varied randomly from trial to trial—the same as the background (so in reality no visible bar), 3.4 cd/m^2, or 13.7 cd/m^2. The bar was visible for both of the larger luminance values (the luminance of the background was changed from Experiment 1 in order to accommodate the luminance values of the bar). As illustrated in Figure 2b, the bar was presented simultaneously with the two squares at the start of each trial, and its luminance remained fixed for that trial, whereas the luminance values of the two squares were exchanged during successive 200-msec frames (eight frames per trial). Pairs of luminance values for the squares were selected to give nine BRLC values ranging from .1 to .9 (Table 2).

Design. The experiment was composed of 27 conditions determined by the orthogonal combination of three luminance values for the bars and nine BRLC values for the squares. There were three blocks of 162 trials in each of four testing sessions. Each block was composed of six sub-blocks of the 27 trials representing each con-

Table 2
Experiment 2: Alternating Luminance Values and the Resulting Background-Relative Luminance Contrast (BRLC) Values at Each Element Location (in cd/m^2)

	Luminance	
BRLC	1	2
.1	89.7	81.5
.2	94.2	77.1
.3	98.6	72.6
.4	102.7	68.5
.5	107.2	64.0
.6	111.3	59.9
.7	115.4	55.8
.8	119.9	51.4
.9	124.3	46.9

Note—The background luminance is less than 0.001 cd/m^2. BRLC values are determined by the difference between the two luminance values divided by the difference between the mean luminance of the elements and the background luminance.

dition (trial order was randomized within each sub-block). Thus, each condition was tested on 72 trials over the course of the experiment, and there was a total of 1,944 trials for each participant. The participants were 2 authors and a naive undergraduate student at Florida Atlantic University, all with normal or corrected-to-normal vision.

Results

Motion was perceived for lower BRLC values when the space between the two elements at the start and end of the motion path was filled with an illuminated bar (Figure 5). When the bar was relatively bright, less luminance contrast was required to increase motion detector activation (Albrecht & Geisler, 1991) to levels that resulted in motion being perceived as frequently as it was perceived for less bright bars. This evidence that bright bars increase motion detector activation was obtained for all 3 participants (a within-subjects ANOVA indicated that the effect of path luminance was statistically significant [$F(2,4) = 19.20, p < .01$].

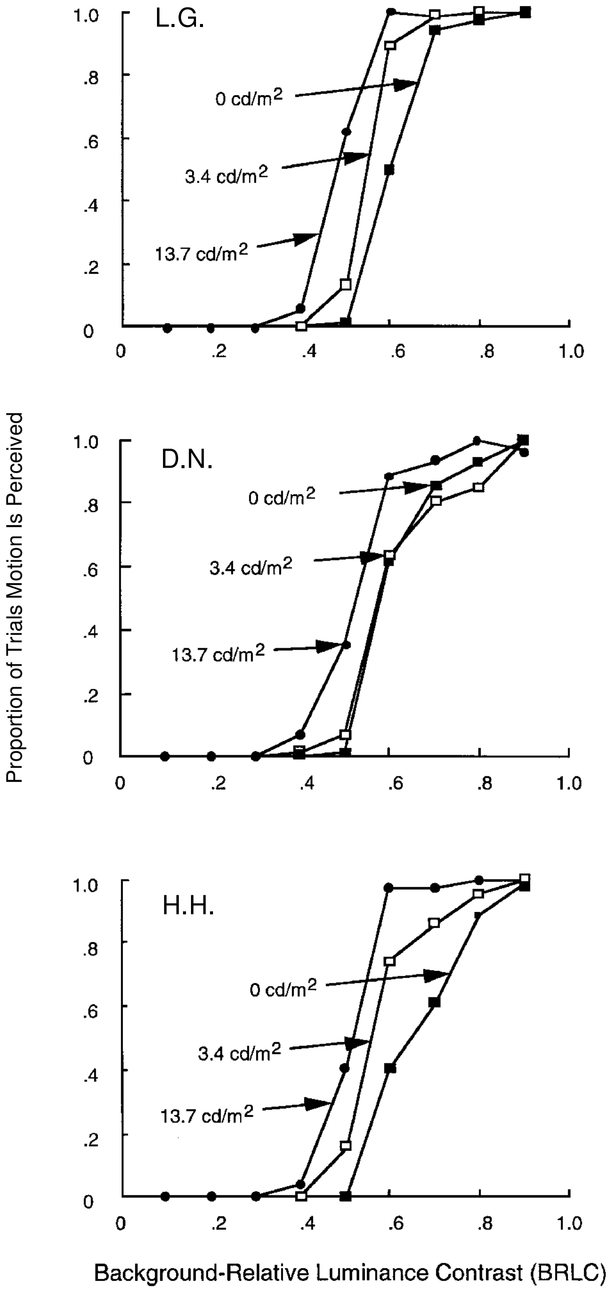

Figure 5. Experiment 2: For each of 3 participants, the effect of the luminance of the motion path and the background-relative luminance contrast (BRLC) on the perception of horizontal motion.

Discussion

Evidence that path luminance affects motion detector activation is consistent with theories of apparent motion perception postulating the presence of activation in the space between the locations of a discontinuously displaced element. The between-element activation was characterized by Grossberg and Rudd (1992) as the sum of two spatially displaced Gaussian distributions of activation, one decreasing in strength (at the start of the motion path) while at the same time the other is increasing in strength (at the end of the motion path). It was characterized by Shepard (1984) as activation spreading across points lying on a representational geometric surface. For both theories, the greater-than-background path luminance could provide a raised "baseline level" of activation for the motion path. When added to the activation resulting from luminance changes of the elements at the ends of the motion path, this could increase the likelihood that activation will be above the threshold level required for the perception of motion. Another possibility, which is supported by recent experimental results (Francis & Kim, 1999; Geisler, 1999), is that the effect of path luminance on motion detector activation is related to interactions between orientation-selective detectors that respond to the static bars, and directionally selective motion detectors that respond to changing luminance at the start and end of the motion path. Further research will be required in order to distinguish among these alternatives.

EXPERIMENT 3

The results of Experiment 2 provided evidence for effects of path luminance on motion detector activation in the absence of competition among alternative motion directions. It could therefore be predicted on the basis of the differential activation solution to the motion correspondence problem that differences in path luminance would influence the motion paths that are perceived when an element can move in more than one direction. Path luminance and path length were covaried in order to determine whether the two variables combine in their effect on the activation of directionally selective motion detectors.

Method

Stimuli. Motion quartets based on the generalized version of single-element apparent motion were presented under the same viewing conditions as in the preceding experiments (background luminance < 0.001 cd/m^2). Small squares (6 × 6 min) were simultaneously visible in all four corners of an imaginary rectangle, and the horizontal gaps between the squares were filled by 6 × 30 min bars (Figure 1c and 1d). As in Experiment 2, the bar luminance was the same as the background (so in reality no visible bars), 3.4 cd/m^2, or 13.7 cd/m^2 for the entire trial.

The bars appeared simultaneously with the four squares composing the quartet at the start of each trial. During each 200-msec frame (there were six per trial), the luminance of the two squares in diagonally opposite corners of the quartet was 124.3 cd/m^2, and the luminance of the squares in the other diagonally opposite corners was 46.9 cd/m^2. These luminance values were exchanged during successive frames, resulting in a BRLC value for each square (.9) that was well above the threshold value required for the perception of motion for all three bar luminances (see results of Experiment 2 in Figure 5). The horizontal center-to-center distance between the squares was 36 min during every trial, and the vertical center-to-center distance was 18, 24, 36, 48, 60, or 72 min. These distances resulted in aspect ratios of 0.5, 0.67, 1.0, 1.33, 1.67, or 2.0, respectively.

Design. The experiment was therefore composed of 18 conditions generated by the orthogonal combination of three bar luminances and six aspect ratios. There were three blocks of 180 trials within each of four testing sessions. Each block was composed of 10 sub-blocks of the 18 trials representing each condition (trial order was randomized within each sub-block). Thus, each condition was tested on 120 trials over the course of the experiment, and there was a total of 2,160 trials for each participant.

Procedure. After each trial, participants pressed one of two preassigned computer keys to indicate whether they had perceived horizontal or vertical motion during the entire trial. On the very infrequent trials for which there was a switch from horizontal to vertical motion (or vice versa), participants were instructed to press the spacebar to reject the trial. (The duration of each trial was kept brief so that the occurrence of such switches would be rare.)

Participants. An author and 2 naive undergraduate students at Florida Atlantic University participated in the experiment. All had normal or corrected-to-normal vision.

Results

Although the effect of aspect ratio was shallow for D.N., the results were typical for motion quartets; that is, for all 3 participants, the proportion of trials for which horizontal motion was perceived increased as the aspect ratio of the quartet was increased (Figure 6). This was consistent with the evidence obtained in Experiment 1 for path length affecting detector activation. That is, the activational advantage of horizontal motion increased with aspect ratio because the activation for vertical motion decreased with increasing vertical path length while the horizontal path length remained fixed. In addition, the proportion of trials for which horizontal motion was perceived increased as the luminance of the horizontal motion path was increased (again for all 3 participants). A within-subjects ANOVA indicated that the effect of aspect ratio was statistically significant [$F(5,10) = 8.54$, $p < .005$], as was the effect of bar luminance [$F(2,4) = 11.78$, $p < .05$]. The significant interaction between aspect ratio and bar luminance [$F(10,20) = 6.91$, $p < .001$] reflected the presence of floor and ceiling effects for the smallest and largest aspect ratios.

Discussion

The experimental results demonstrate the predictive link between inferred effects of a variable (path luminance) on motion detector activation (Experiment 2) and the influence of that variable on motion correspondence (in this experiment). This link also has been established for the effect of path length on both motion detector activation (Experiment 1) and motion correspondence (in many paradigms; replicated for motion quartets in this experiment), and for the effect of element similarity (shape) on both motion detector activation (Hock & Park,

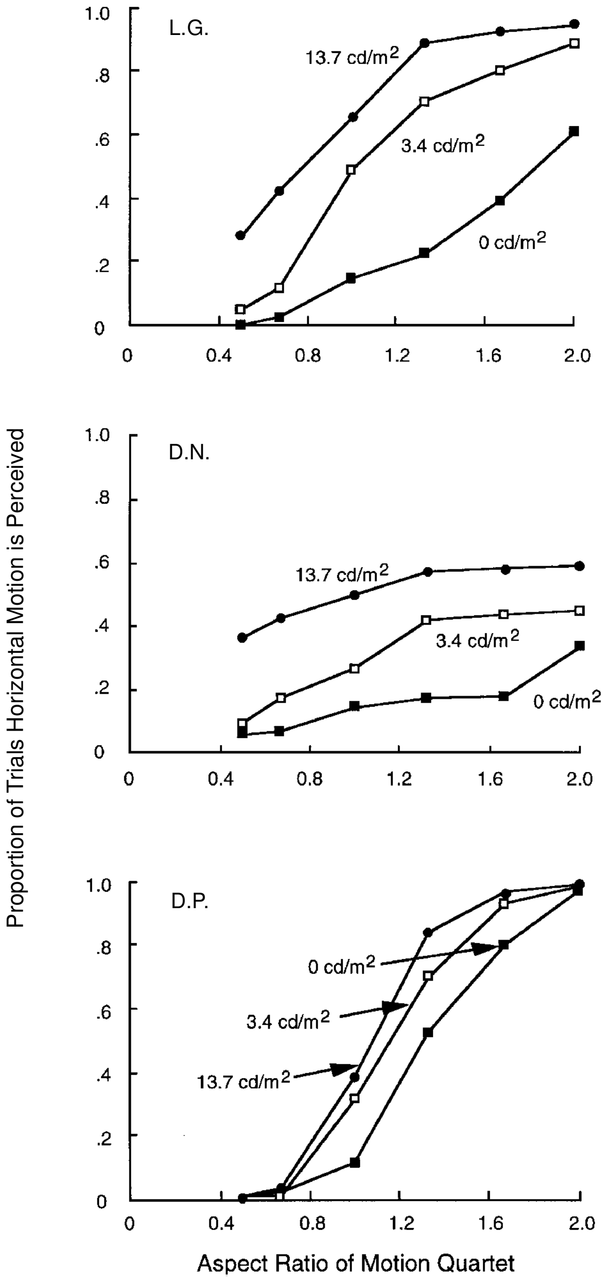

Figure 6. Experiment 3: For each of 3 participants, the effect of the luminance of the horizontal motion paths on the perception of horizontal motion for motion quartets with varying aspect ratio (the vertical divided by the horizontal distance between the squares forming the motion quartet).

1999, using the paradigm of Experiments 1 and 2) and motion correspondence (e.g., Shechter et al., 1988).

In addition to being consistent with the prediction based on evidence for the effect of path luminance on motion detector activation in Experiment 2, the effect of path luminance on motion correspondences in this experiment indicated that the motion detectors affected by path luminance were directionally selective (otherwise, the luminance bars would not have differentially affected the perception of horizontal and vertical motion). Other possible influences of the bars on motion correspondence are suggested by Shepard and Zare's (1983) path guidance effect and Rock and Palmer's (1990) account of "connectedness" as an organizational property. However, neither of these alternatives can also account for the effect of path luminance on motion perception in Experiment 2, when only one motion path was possible.

EXPERIMENT 4

In this experiment we investigated why the visual system sometimes fails to solve the motion correspondence problem; that is, when two motion paths are possible, rather than one path being selected, both are perceived simultaneously (typically accompanied by splitting and/or fusion). According to minimal mapping theory, the perception of an element moving simultaneously in two directions occurs when affinities (and split/fusion interactions) are the same for the competing motions. In contrast, the differential activation solution accounts for the perception of an element moving simultaneously in two directions on the basis of detector activation for each being elevated above the threshold level required for perception for both of the alternative motions. This would be the case regardless of whether or not the path-length determined (feed-forward) activation is the same for the competing motions.

This distinction between the minimal mapping and differential activation solutions to the motion correspondence problem was tested with motion *triplets.* The triplets were created from motion quartets (Experiment 3) by removing the element in the upper right corner of the quartet. According to the minimal mapping solution, vertical and horizontal motion should be perceived simultaneously (with splitting and fusion) for the triplet, but only when path-length determined element affinities and split/fusion interactions are the same. In contrast, it was predicted from the differential activation solution that motion could be perceived simultaneously in two motion directions, even when they differ in path-length determined, feed-forward activation; the requirement is that the activations for each motion lie above the threshold level required for perception (even if they are unequal).

Method

Stimuli. Both motion triplets and motion quartets were presented. For the motion quartets, four small squares (6 × 6 min) were simultaneously visible in all four corners of an imaginary rectangle. The horizontal center-to-center distance between the squares was 36 min. The vertical center-to-center distance was 24, 36, 48, 60, 72, or 84 min, resulting in aspect ratios of 0.67, 1.0, 1.33, 1.67, 2.0, or 2.33, respectively. During each six-frame trial (200-msec per frame), the BRLC was fixed at 1.7 (the luminance of each square alternated between 120.9 and 16.1 cd/m^2; background luminance = 6.9 cd/m^2). The motion triplets were identical except that the square in the upper right corner was not presented (the stimuli are illustrated at the top of Figure 7).

Design. A total of 12 conditions were generated by the orthogonal combination of two stimulus configurations (quartets and triplets) and six aspect ratios. There were a total of four blocks of trials of 120 trials, with each block composed of 10 sub-blocks of the 12 trials representing each condition (trial order was randomized within each sub-block). Over the course of the experiment, there were 40 trials for each of the 12 conditions, resulting in a total of 480 trials for each participant.

Procedure. After each trial, participants pressed one of three preassigned computer keys to indicate whether they perceived just horizontal motion, just vertical motion, or both motions simultaneously. They pressed the spacebar if they were unsure of their response.

Participants. Two authors participated in the experiment, both with normal or corrected-to-normal vision.

Results and Discussion

As can be seen in Figure 7, horizontal and vertical motions were perceived simultaneously for the motion triplet, regardless of its aspect ratio. L.G. perceived simultaneous motion in both directions on every trial with the triplet. H.H. perceived simultaneous motion somewhat less often, the frequency of the percept declining with increased aspect ratio. The results therefore indicated that motion could be perceived simultaneously in two directions for the triplets, even when path-length determined affinities were much different for the two motion directions (the vertical path length was more than double the horizontal path length for the aspect ratio of 2.33).

It might be argued that the path-length differences for vertical and horizontal motion in this experiment were too small to undo the simultaneous perception of horizontal and vertical motion. However, the results of Experiment 1 indicated that these differences in path length were sufficient to affect the luminance contrast (BRLC) required for the perception of motion, and the results for this experiment indicate that the differences in horizontal and vertical path lengths were sufficient to produce substantial differences in the perception of horizontal versus vertical motion for the motion quartets. As in Experiment 3 and Hock et al. (1993), small aspect ratios for the motion quartet favored the perception of vertical motion, and large aspect ratios favored the perception of horizontal motion (Figure 7). Horizontal and vertical motion were not perceived simultaneously for the quartets, even when they were perceived equally often (aspect ratios of 1.0 and 1.33 for H.H. and L.G., respectively). It can be concluded, contrary to minimal mapping theory, that matched, path-length determined affinities are not necessary for the simultaneous perception of an element moving in two directions. Regardless of whether or not there are differences in motion path length, it is sufficient, on the basis of differential activation solution, that

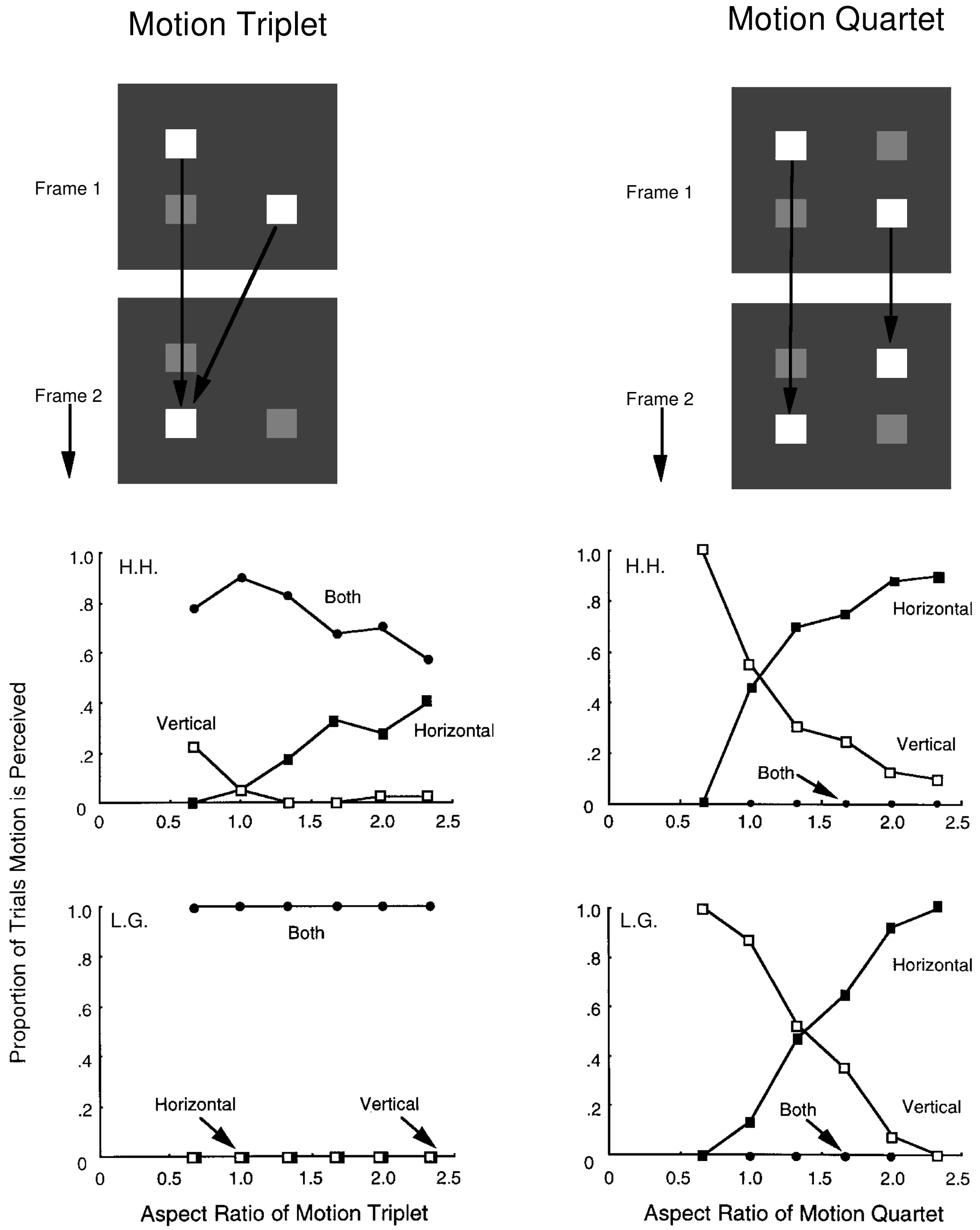

Figure 7. Experiment 4: For each of 2 participants, the effect of aspect ratio on the perception of just vertical motion, just horizontal motion, or both vertical and horizontal motion simultaneously for motion triplets and motion quartets. Also included are illustrations of the triplet and quartet stimuli.

activation lies above the threshold level required for perception for each of the motion directions.

GENERAL DISCUSSION

Ullman's (1979) minimal mapping solution to the motion correspondence problem requires the explicit encoding of all attributes relevant to the competing motion paths and the assignment of an appropriate cost to each encoded attribute value. The motion paths that are perceived are based on the minimization of cost over the full set of potential correspondences. In contrast, the contributions of relevant stimulus attributes to the solution of the motion correspondence problem is implicit in the differential activation account. That is, rather than being explicitly encoded, attribute values of the motion stimulus influence motion perception through their effect on the activation of the directionally selective motion detectors responding to the competing motion paths. The motion paths that are perceived depend on whether the levels of activation for motion detectors responding to the competing motions are above or below the threshold level required for the perception of motion.

Empirical support for differential activation as the basis for the nearest neighbor solution to the motion correspondence problem came from a paradigm for which motion correspondence was not at a factor (Experiment 1). It was found that the length of the motion path affects the time-varying luminance contrast (BRLC) required for the perception of single-element apparent motion. Higher BRLC values are required to increase motion detector activation (Albrecht & Geisler, 1991) for long motion paths to levels that result in motion perception equivalent to that obtained at lower BRLC values for shorter motion paths.

Direct comparisons between the minimal mapping and differential activation solutions are difficult because minimal mapping theory is sufficiently flexible so that it can be modified, post hoc, to accommodate any variable that is found to affect motion correspondence. It needs only to be assumed that values of the variable are explicitly encoded and appropriate costs assigned. However, there is no basis in minimal mapping theory for the a priori prediction of whether or not a new variable will affect motion correspondences. This is not the case for the differential activation solution. The potential influence of a new variable in resolving competing element motions can be predicted from the effect of the variable on the luminance contrast (BRLC) required for the perception of single-element apparent motion. (The rationale, based on Albrecht and Geisler's, 1991, neurophysiological results, is that the required luminance contrast reflects the extent to which the new variable is affecting motion detector activation.) This was demonstrated for path luminance: Effects of path luminance on the perception of single-element apparent motion were observed in Experiment 2, and on this basis, it was successfully predicted that path luminance would influence solutions to the correspondence problem for the motion quartet in Experiment 3.

A further limitation of minimal mapping theory is its difficulty discriminating between stimuli for which there is a solution to the motion correspondence problem (when only one of the two or more alternative motions will be perceived for an element), and stimuli for which there is not a solution (when two or more of the element's alternative motions are perceived simultaneously). Thus, minimal mapping predicts that horizontal and vertical motion will be perceived simultaneously for motion triplets when element affinity is the same for the competing motion paths. By the same reasoning, however, minimal mapping theory predicts that horizontal and vertical motion will be perceived simultaneously for motion quartets with an aspect ratio of 1.0 (element affinities and local interactions are then balanced for the two motion directions). Nonetheless, vertical or horizontal motion is perceived individually for the motion quartet when its aspect ratio is 1.0, or for any other aspect ratio; they are never perceived simultaneously even when the two motion directions are perceived equally often (as in Experiment 4). The absence of simultaneous perception of horizontal and vertical motion for quartets with an aspect ratio of 1.0 cannot be dismissed as a consequence of random influences on encoding that imbalance the "computed" affinities for horizontal and vertical motion. Such random influences would be just as likely to occur for the motion triplets, resulting in vertical or horizontal motion being perceived individually. However, horizontal and vertical motion are almost always simultaneously perceived for the motion triplet.

The inability of minimal mapping theory to account for when competing motions will be perceived simultaneously and when one or the other motion will be perceived individually is reflected in the results of Experiment 4. In that experiment, horizontal and vertical motion were perceived simultaneously for the motion triplets over a range of aspect ratios wide enough for vertical motion to be perceived on every trial (aspect ratio = 0.67) and horizontal motion to be perceived on almost every trial (aspect ratio = 2.33) for the motion quartets. According to the differential activation account, the simultaneous perception of element motion in two directions can occur even if the activation levels for the two motions are different, either because of differences in path length or because of random fluctuations in activation. What matters for simultaneous perception is that activation for both motion directions is above the threshold level required for the motions to be perceived.[3]

As noted, random influences are a problem for minimal mapping. If they prevent affinities from being matched for the motion quartet, they will do so as well for the motion triplet, eliminating the simultaneous perception of element motion in two directions. This is not the case for the differential activation solution. Whether horizontal or vertical motion is perceived for a motion quartet is influenced by random fluctuations, especially when path-length determined feed-forward activations are matched. Horizontal and vertical motion are never perceived simultaneously for the motion quartet because additional inhibitory interactions (compared with the triplet) result from the motion of the element in the upper right corner. This additional inhibition reduces activation sufficiently so that the activation for either horizontal or vertical motion falls below the threshold level required for perception.[4]

Differential Activation and Dynamical Stability

The minimal mapping solution to the motion correspondence problem is concerned with which among two or more possible motion paths is most likely to be perceived when a stimulus is presented, but ignores the stability of the percept once it is established. For example, when a motion quartet is presented, motion is most likely to be perceived in the directions with the shortest path lengths (as in Experiments 3 and 4). However, the correspondences formed upon presentation of the motion quartet are not always consistent with the nearest neighbor solution, and even when they are, there are often spontaneous switches to inconsistent correspondences that are not "favored" by the stimulus (Hock et al., 1993; Hock, Schöner, & Voss, 1997). The differential activation solution can readily account for spontaneous switching in terms of random fluctuations in activation. Such fluctuations can result in greater activation for the longer path length, and the stability intrinsic to each of the competing motions results in the persistence of the "nonfavored" percept over time. As noted, random fluctuations cannot be of significance for minimal mapping since it would break the "balance" required by the theory to account for the perception of splitting and fusion for the motion triplet. Furthermore, minimal mapping cannot account for the systematic inconsistency with the nearest neighbor solution that occurs when the aspect ratio of the motion quartet is gradually increased or gradually decreased and hysteresis is observed; that is, a set of correspondences initially consistent with the nearest neighbor solution is maintained despite changes in relative path length to values that would favor a different set of correspondences (Hock et al., 1993).

An important advantage of the differential activation solution, therefore, is that it provides a principled basis for understanding the dynamical aspects of motion correspondence described above. This is because the key to the occurrence of multistability (i.e., the possibility of more than one set of stable motion correspondences) is the presence of nonlinear inhibitory interactions among competing, directionally selective motion detectors, and the nature of these interactions is readily expressed in terms of differences in activation level (Giese, Schöner, & Hock, 2001; Hock, Schöner, & Giese, 2001; Williams, Phillips, & Sekuler, 1986). For example, the inhibitory effect of horizontal on vertical motion detectors for the motion quartet (when horizontal motion is perceived and vertical motion suppressed) depends on the level of activation of the detectors that respond selectively to horizontal motion; that is, there is more activation-reducing inhibition of vertical detectors when there is more activation of horizontal detectors.

Differential Activation and Adaptation

A further advantage of the differential activation solution to the motion correspondence problem is in accounting for adaptation effects (as in Pantle & Sekuler, 1969). Again, the fundamental principle is readily expressed in terms of differences in activation level: The greater the level of motion detector activation, the greater the proportional decrease in activation as a result of adaptation. (This proportionality is consistent with neural activation decreasing exponentially as a function of time, as shown by Giaschi, Douglas, Marlin, & Cynander, 1993.) Activation-proportional adaptation increases susceptibility to random fluctuations in activation by reducing (though not eliminating) differences in activation among competing motion detectors, so smaller, more probable fluctuations are sufficient to produce changes in motion correspondence (Hock, Schöner, & Voss, 1997). In addition, inhibiting interactions among local detector ensembles (described earlier) can push activation for some correspondences below the threshold level required for motion to be perceived, but the stable, subthreshold level of activation can still be greater than the level that would exist in the absence of stimulation. The presence of this subthreshold activation accounts for both the adaptation of *un*perceived motions and the effect of *un*perceived motions on the adaptation of perceived motion correspondences (Hock, Schöner, & Hochstein, 1996).

Bayesian Estimation

Weiss and Adelson (1998a, 1998b) have recently proposed a Bayesian solution to the motion correspondence problem that multiplicatively combines a priori probabilities reflecting the perceiver's prior knowledge with uncertainty-weighted measurements of motion direction and speed. The nearest neighbor preference is accounted for by an a priori probability distribution in which slow speeds are more probable than fast speeds. Weiss and Adelson's computational model is consistent with a neural implementation based on the differential activation of directionally selective motion detectors, but it is uncertain how it would account for newly discovered variables that influence motion correspondence. In the present study, for example, there is no basis for determining whether path luminance affects motion correspondence through its influence on the uncertainty of motion measurements or through an a priori preference for relatively bright, contrastive motion paths.

Conclusions

The minimal mapping and differential activation solutions to the correspondence problem represent significantly different images of how the visual system functions. Minimal mapping is consistent with the classical information processing view (e.g., Lindsay & Norman, 1977) that perceptual outcomes are governed by an executive process that collects inputs from detecting units that independently encode relevant stimulus features (the so-called neuron doctrine; Barlow, 1972), weighs them according to certain task-related criteria, and makes an appropriate "decision" regarding which among the alternatives is to be perceived. The differential activation solution suggests instead that perceptual outcomes are the result of neural interactions among detecting units whose activation is influenced by many different stimulus variables. Current neurophysiological and neuroanatomical evidence is consistent with this perspective. The response of cortical detecting units is multidimensional (P. H. Schiller, 1996; Stern, Vaadia, Aaertsen, & Hochstein, 1993), and most of the input to these units comes from interaction with other cortical neurons (Braitenberg, 1978; Gilbert & Wiesel, 1990; Kisvárday, Tóth, Rausch,

& Eysel, 1997; LeVay, 1988; Ts'o, Gilbert, & Wiesel, 1986). The results reported in this article provide psychophysical evidence for differences in detector activation within interactive networks as the basis for solving the motion correspondence problem.

REFERENCES

Adelson, E. H., & Bergen, J. R. (1985). Spatiotemporal energy models for the perception of motion. *Journal of the Optical Society of America A*, **2**, 284-299.

Adelson, E. H., & Movshon, J. A. (1982). Phenomenal coherence of moving visual patterns. *Nature*, **300**, 523-525.

Albrecht, D. G., & Geisler, W. S. (1991). Motion selectivity and the contrast response function of simple cells in the visual cortex. *Visual Neuroscience*, **7**, 531-546.

Anstis, S. M., Giaschi, D., & Cogan, A. I. (1985). Adaptation to apparent motion. *Vision Research*, **25**, 1051-1062.

Attneave, F. (1974). Apparent movement and the what–where connection. *Psychologia*, **17**, 108-120.

Barlow, H. B. (1972). Single units and sensation: A neuron doctrine for perceptual psychology? *Perception*, **1**, 371-394.

Braitenberg, V. (1978). Cortical architechtonics: General and areal. In M. A. B. Brazier & H. Petsche (Eds.), *Architechtonics of the cerebral cortex* (IBRO Monograph Series, Vol. 3, pp. 433-466). New York: Raven.

Burt, P., & Sperling, G. (1981). Time, distance, and feature trade-offs in visual apparent motion. *Psychological Review*, **88**, 171-195.

Dawson, M. R. W. (1991). The how and why of what went where in apparent motion: Modelling solutions to the motion correspondence problem. *Psychological Review*, **98**, 569-603.

Francis, G., & Kim, H. (1999). Motion parallel to line orientation: Disambiguation of motion percepts. *Perception*, **28**, 1243-1255.

Geisler, W. S. (1999). Spatial orientation coding of motion direction [Abstract]. *Investigative Ophthalmology & Visual Science*, **40**, S1.

Gengerelli, J. A. (1948). Apparent motion in relation to homonymous and heteronymous stimulation of the cerebral hemispheres. *Journal of Experimental Psychology*, **38**, 592-599.

Giaschi, S., Douglas, R. M., Marlin, S. G., & Cynander, M. S. (1993). The time course of direction-specific adaptation in simple and complex cells in cat striate cortex. *Journal of Neurophysiology*, **70**, 2024-2034.

Giese, M. A., Schöner, G., & Hock, H. S. (2001). *A dynamical neuronal network model of motion perception: Simulations of pattern formation, percepted continuity, and the effects of stability on selective adaptation.* Manuscript submitted for publication.

Gilbert, C. D., & Wiesel, T. N. (1990). The influence of contextual stimuli on the orientation selectivity of cells in the primary visual cortex of the cat. *Vision Research*, **30**, 1689-1701.

Grossberg, S., & Rudd, M. E. (1992). Cortical dynamics of visual motion perception: Short-range and long-range apparent motion. *Psychological Review*, **99**, 78-121.

Hock, H. S., Gilroy, L. A., & Harnett, G. (in press). Counter-changing luminance: A non-Fourier, non-attentional basis for the perception of single-element apparent motion. *Journal of Experimental Psychology: Human Perception & Performance*.

Hock, H. S., Kelso, J. A. S., & Schöner, G. (1993). Bistability and hysteresis in the organization of apparent motion patterns. *Journal of Experimental Psychology: Human Perception & Performance*, **19**, 63-80.

Hock, H. S., Kogan, K., & Espinoza, J. K. (1997). Dynamic, state-dependent thresholds for the perception of single-element apparent motion: Bistability from local cooperativity. *Perception & Psychophysics*, **59**, 1077-1088.

Hock, H. S., & Park, C. (1999). The effect of changing size and shape on motion detection and the formation of global motion patterns [Abstract]. *Investigative Ophthalmology & Visual Science*, **40**, S423.

Hock, H. S., Schöner, G., & Giese, M. (2001). *The dynamical foundations of motion pattern formation: Stability, selective adaptation, and percepted continuity.* Manuscript submitted for publication.

Hock, H. S., Schöner, G., & Hochstein, S. (1996). Perceptual stability and the selective adaptation of perceived and unperceived motion. *Vision Research*, **36**, 3311-3323.

Hock, H. S., Schöner, G., & Voss, A. (1997). The influence of adaptation and stochastic fluctuations on spontaneous perceptual changes for bistable stimuli. *Perception & Psychophysics*, **59**, 509-522.

Hoeth, F. (1968). Bevorzugte Richtungen bei stroboskopischen Alternativbewegungen. *Psychologische Beitrage*, **16**, 494-527.

Johansson, G. (1950). *Configurations in event perception.* Uppsala: Almqvist & Wiksell.

Kisvárday, Z. F., Tóth, E., Rausch, M., & Eysel, U. (1997). Orientation-specific relationship between populations of excitatory and inhibitory lateral connections in the visual cortex of the cat. *Cerebral Cortex*, **7**, 605-618.

Kolers, P. A. (1972). *Aspects of motion perception.* Oxford: Pergamon.

Korte, A. (1915). Kinematoskopische Untersuchungen [Cinematoscopic investigations]. *Zeitschrift fur Psychologie*, **72**, 193-296.

Kruse, P., Stadler, M., & Wehner, T. (1986). Direction and frequency-specific processing in the perception of long-range apparent movement. *Vision Research*, **26**, 327-335.

Kulikowski, J. J. (1978). Spatial resolution for the detection of pattern and movement (real and apparent). *Vision Research*, **18**, 237-239.

Larsen, A., Farrell, J. E., & Bundesen, C. (1983). Short- and long-range processes in visual apparent movement. *Psychological Research*, **45**, 11-18.

LeVay, S. (1988). The patchy intrinsic projections of visual cortex. In T. P. Hicks & G. Benedek (Eds.), *Progress in Brain Research*, **75**, 147-161.

Levinson, E., & Sekuler, R. (1975a). The independence of channels in human vision selective for direction of movement. *Journal of Physiology*, **250**, 347-366.

Levinson, E., & Sekuler, R. (1975b). Inhibition and disinhibition of direction-specific mechanisms in human vision. *Nature*, **254**, 692-694.

Lindsay, P. H., & Norman, D. A. (1977). *Human information processing: An introduction to psychology.* New York: Academic Press.

Marshak, W., & Sekuler, R. (1979). Mutual repulsion between moving visual targets. *Science*, **205**, 1399-1401.

Nakayama, K., & Silverman, G. H. (1985). Detection and discrimination of sinusoidal grating displacements. *Journal of the Optical Society of America A*, **2**, 267-274.

Nawrot, M., & Sekuler, R. (1990). Assimilation and contrast in motion perception: Explorations in cooperativity. *Vision Research*, **30**, 1439-1451.

Neuhaus, W. (1930). Experimentelle Untersuchung der Scheinbewegung [Experimental investigation of apparent motion]. *Archive für die Gesamte Psychologie*, **75**, 315-458.

Pantle, A. J., & Sekuler, R. (1969). Contrast response of human visual mechanisms sensitive to orientation and direction of motion. *Vision Research*, **9**, 397-406.

Ramachandran, V. S., & Anstis, S. M. (1985). Perceptual organization in multistable apparent motion. *Perception*, **14**, 135-143.

Rock, I., & Palmer, S. (1990). The legacy of Gestalt psychology. *Scientific American*, **263**, 84-90.

Schiller, P. H. (1996). On the specificity of neurons and visual areas. *Behavioural Brain Research*, **76**, 21-35.

Schiller, P. von (1933). Stroboskopische Alternativbewegungen [Stroboscopic alternative motion]. *Psychologische Forschung*, **17**, 179-214.

Shechter, S., Hochstein, S., & Hillman, P. (1988). Shape similarity and distance disparity as apparent motion correspondence cues. *Vision Research*, **29**, 1013-1021.

Shepard, R. N. (1984). Ecological constraints on internal representation: Resonant kinematics of perceiving, imagining, thinking, and dreaming. *Psychological Review*, **91**, 417-447.

Shepard, R. N., & Zare, S. L. (1983). Path-guided apparent motion. *Science*, **220**, 632-634.

Stern, E., Vaadia, E., Aaertsen, A., & Hochstein, S. (1993). Stimulus encoding by multidimensional receptive fields in single cells and cell populations in V1 of awake monkey. *Neural Information Processing Systems*, **5**, 377-384.

Tolhurst, D. J. (1973). Separate channels for the analysis of the shape and the movement of a moving visual stimulus. *Journal of Physiology*, **226**, 231-248.

Ts'o, D. Y., Gilbert, C. D., & Wiesel, T. N. (1986). Relationships between horizontal interactions and functional architecture in cat striate cortex as revealed by cross-correlation analysis. *Journal of Neuroscience*, **6**, 1160-1170.

Ullman, S. (1979). *The interpretation of visual motion.* Cambridge, MA: MIT Press.

van Santen, J. P., & Sperling, H. G. (1985). Elaborated Reichardt detectors. *Journal of the Optical Society of America A*, **2**, 300-320.

Weiss, Y., & Adelson, E. H. (1998a). Bayesian common fate [Abstract]. *Investigative Ophthalmology & Visual Science*, **39**, S461.

Weiss, Y., & Adelson, E. H. (1998b). *Slow and smooth: Bayesian theory for the combination of local motion signals in human vision.* (AI Memo 1616, CBCL Paper 158). Cambridge, MA: MIT, Artificial Intelligence Laboratory.

Williams, D., Phillips, G., & Sekuler, R. (1986). Hysteresis in the perception of motion direction as evidence for neural cooperativity. *Nature*, **324**, 253-255.

NOTES

1. Luminance contrast affects the perception of motion for drifting sine gratings (e.g., Kulikowski, 1978; Nakayama & Silverman, 1985), as well as the response of motion energy detectors (Adelson & Bergen, 1985) and elaborated Reichardt detectors (van Santen & Sperling, 1985). When the background luminance is zero, values of BRLC and values of Michelson contrast are equivalent.

2. The observed vertical/horizontal difference might have been unreliable because of variability introduced by uncorrected astigmatism for some of the participants, and because the size of the vertical/horizontal effect might have been reduced by opposing effects due to the vertical–horizontal illusion (vertical distances appear to be longer than matched horizontal distances).

3. Still another limitation of minimal mapping theory is that all interactions are local. Therefore, it does not readily account for long-range excitatory and inhibitory influences on detector activation (Nawrot & Sekuler, 1990; Ramachandran & Anstis, 1985).

4. According to minimal mapping theory, the motion of each element is not perceived in two directions for the motion quartet because of the "minimal cover" property, a preference for "one-to-one" mappings. Ullman (1979) argued that this is achievable purely through local interaction (p. 112).

(Manuscript received December 30, 1999;
revision accepted for publication September 11, 2000.)