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Dependence of Speed and Direction Perception on Cinematogram Dot Density

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In the present experiments, we find that with abrupt decreases in dot density of random-dot cinematograms, perceived speed decreases, while with abrupt increases in dot density, perceived speed increases. Further, in steady-state conditions, perceived speed is also affected in the same way, but to a lesser degree, by the dot density of cinematograms. Direction discrimination of random-dot cinematograms is enhanced when dot density increases abruptly from one stimulus to the next, but is degraded when dot density decreases abruptly. Finally, speed discrimination remains constant even when density changes abruptly. The perceived-speed and direction-discrimination data are consistent with the Motion Coherence theory which motivated this study, and with models that include a smoothing stage similar to this theory. Of the other models that we consider, most predict that increasing dot density reduces perceived speed. The speed-discrimination data could not distinguish between the different theories.

Perceived speed Velocity discrimination Motion

INTRODUCTION

Spatial and temporal integrations of local motion signals are advantageous for the human visual system. That different features of a single object tend to move together justifies integrating their motion spatially. Such spatial integration can reduce the noise from the motion signal (Yuille & Grzywacz, 1988, 1989). Moreover, by using the knowledge that objects tend to maintain their motion over time, one can simplify the motion correspondence problem (Ullman, 1979; Grzywacz, Smith & Yuille, 1989), which can be stated as: what is the image feature in one instant in time that corresponds to a given feature in another instant? Psychophysical evidence for spatial integration includes the Gestalt's shared-common fate (Koffka, 1935), position independent motion sensitivity (Nakayama & Tyler, 1981), and the phenomena of motion capture (Ramachandran & Anstis, 1983a) and global motion (Williams & Sekuler, 1984; Watamaniuk, Sekuler & Williams, 1989; Watamaniuk & Sekuler, 1992). Support for temporal integration comes from temporal recruitment (McKee, 1981; McKee & Welch, 1985), motion inertia (Ramachandran & Anstis, 1983b; Anstis & Ramachandran, 1987), and the detection of a single translating dot embedded in a field of randomly moving dots (McKee & Watamaniuk, 1991).

Recently, several investigators advanced theories to account for spatial integration of motion in humans (Bulthoff, Little & Poggio, 1989; Hildreth, 1984; Reichardt, Egelhaaf & Schlögl, 1988) and one of these theories, the Motion Coherence theory (Yuille & Grzywacz, 1988, 1989), motivated the present work. This theory divides the computation of motion into the measuring and integration (smoothing) stages. The measuring stage first obtains the local velocity vectors. Then, the integration stage constructs a velocity field over the image. This constructed velocity field tries to follow the local velocity vectors, while being as (differentially) smooth as possible (see Theory).

Application of this theory to a random-dot cinematogram leads to the surprising prediction that global perceived speed increases with dot density until reaching a plateau at the mean speed of the stimulus (see Theory). To intuite this prediction, imagine that the local velocities are like the heights of discrete posts rising from flat ground. Also, imagine that the smooth velocity field is represented by a piece of celluloid film placed over these posts. If there are a lot of posts (high density), then the film's mean height is faithful to the mean height of the posts. Otherwise, the film sags between posts and may even touch the ground. In this case, the film's mean height is smaller than that of the posts.

This posts-film analogy indicates that other motion theories that include a smoothing stage like the Motion Coherence theory's may also account for the prediction above. Yuille and Grzywacz (1989) based on earlier work by Duchon (1979) discussed the formal requirements of such a spatial-smoothing stage. They pointed out that the smoothing must have sufficiently high

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differential order (small values of derivatives higher than second) for it to make the smoothing of random-dot motions well posed. [An example of a model using only a first-order differential smoothing stage was that of Hildreth's (1984) which applied only to contour motions.] Moreover they showed that zero-order differential smoothing (finite integral of the velocity field) was necessary and sufficient for a local velocity measurement not to affect other spatially distant velocities. In other words, zero-order smoothing causes the velocity field "to sag" when the density is low. Therefore, because at least zero- and high-order differential smoothing are necessary, we call this procedure "multiple-order" differential smoothing. [An example of a model using single-order differential smoothing was that of Horn and Schunck (1981) which applies to continuous optic flow, but not to random-dot cinematograms, since it predicts an arbitrarily large distance of interaction between velocity signals.] Theories with multiple-order differential smoothing are not inconsistent with motion-energy models, which are widely used in the psychophysical and physiological literature (Adelson & Bergen, 1985; van Santen & Sperling, 1985; Emerson, Adelson & Bergen, 1992). In essence, one could use these mechanisms to perform the basic local motion measurements and then apply the smoothing stage to these measurements (Yuille & Grzywacz, 1989). Models for the measurement of local velocity from such mechanisms exist (Heeger, 1987; Grzywacz & Yuille, 1990).

However, the prediction above strictly holds only if the theories' parameters are constant over time. As discussed elsewhere (Yuille & Grzywacz, 1989), it might be advantageous for the parameters to vary adaptively to ensure that the performance is independent of density, or more generally, of viewing distance. Nevertheless, even if these parameters vary adaptively, they probably would not do so at an infinitely fast rate. Therefore, if such adaptation existed, then the increase of perceived speed with dot density would be larger in abrupt changes of density than in constant-density conditions.

This prediction is surprising, since one would not intuitively expect velocity perception to depend on density. If the visual system were ideal, then it would adapt "infinitely" fast to changing density, to keep encoding speed correctly. Moreover, we argue that other theories that do not include multiple-order differential smoothing predict quite different results for abrupt density changes. For example, let us consider theories in which the global velocity is just the mean of the local velocity vectors. In this case, any change in perceived speed would have to be due to changes in the local vectors themselves. How do the local vectors change with abrupt changes of density? We argue that on average, the mean of these vectors would decrease with increased density for two reasons: first, with higher densities, mismatch errors would lead to smaller displacements and therefore, slower speeds than those generated at lower densities. Second, at the transition from low to high density, dots are replotted at random positions, leading to new, arbitrary directions of motion, thus reducing the relative strength of the signal in the mean direction. These two arguments are general and should apply to most local detectors proposed in the literature. In particular, these local detectors include the Reichardt detector (Hassenstein & Reichardt, 1956; van Santen & Sperling, 1985), the motion energy detector (Adelson & Bergen, 1985), and the type of detector implied by the Minimal Mapping theory (Ullman, 1979).

A further prediction of the Motion Coherence theory and theories with multiple-order differential smoothing relates to direction and speed discrimination. The variance of the perceived velocity vector should decrease as dot density increases, and thus, direction and speed discrimination should improve (see Theory).

Watamaniuk measured direction discrimination for many different densities of random-dot cinematograms (Watamaniuk, 1990, 1992). He found that this discrimination improved slightly, but significantly as density was increased from 0.64 to 2.56 dots/deg^2. However, his experiment did not address whether transient changes of density have further effects on direction discrimination and whether density affects perceived speed.

Although the dependencies on cinematograms' dot density are not completely known, the literature using them to study speed and direction perception is wide. For example, discrimination of cinematograms' speed has a Weber fraction that is identical to that obtained with other stimuli (De Bruyn & Orban, 1988; Snowden & Braddick, 1991). Moreover, a cinematogram's perceived speed is the mean of the speeds of the cinematogram's dots (Watamaniuk & Duchon, 1992). With regard to direction discrimination, Watamaniuk *et al.* (1989) found that performance is as good when all dots move in the same direction as when the dots' directions are chosen randomly from a distribution spanning 30 deg. They also determined how discrimination falls as a function of the range of the direction distribution.

In this paper, we report on how changes of dot density affect perceived speed, and direction and speed discrimination of random-dot cinematograms. One set of experiments studied the effects of both abruptly increasing and decreasing density. Another experiment investigated whether perceived speed varies with density in a method-of-constant-stimulus procedure. The final experiment measures the effects of abrupt density changes on direction discrimination. In summary, the results show a dependence of perceived speed and direction discrimination on dot density consistent with theories employing multiple-order differential smoothing. The results do not show an improvement of speed discrimination with dot density. This result might imply a failure of these theories or a saturation of the signal-to-noise ratio of the speed signals (Discussion). Before the results of the experiments are reported, we present our theoretical arguments in the next section.

THEORY

This section presents a short mathematical summary of the most studied version of the Motion Coherence theory as applied to random-dot cinematograms. The proofs of the theoretical results are omitted and can be read elsewhere (Yuille & Grzywacz, 1989).

The theory comprises two stages: in the first stage, the system makes local estimates of velocity over the image. For each local estimate, this stage might, for example, combine measurements of motion energy over the population of directionally selective cells over a limited spatial extent. We therefore call this stage, the measuring stage. In the second stage, a new velocity field is built that conforms as much as possible with the local measurements obtained by the measuring stage and simultaneously is as smooth as possible. Even though the measuring stage might provide spatially discrete information on velocity, such as when it is stimulated by a random-dot cinematogram, the new velocity field extends continuously over the entire image. This continuous field is as smooth in the sense that local variations of velocity are small as possible. We call the second stage, the smoothing stage. The theory, as described below, focuses on the smoothing stage and assumes that the measuring stage has already provided local estimates of velocity.

To specify the Motion Coherence theory formally, let the velocity measurement obtained by the measuring stage at point $\vec{r}_i$ be $\vec{U}_i$. This measurement can be adversely affected by neural noise and by disturbances in the transmission of light from the viewed object to the retina. The displays in our experiments, in which dots change direction of motion from frame to frame, mimic and exaggerate the directional component of this noise. To reduce noise, the theory's smoothing stage constructs a velocity field ($\vec{v}(\vec{r})$) such that the following functional is minimized for both components of $\vec{v}$:

$$E(\vec{v}(\vec{r}),\vec{U}_i)=\sum_i[(\vec{v}(\vec{r}_i))-(\vec{U}_i)]^2+\lambda\int\sum_{m=0}^{\infty}\frac{\sigma^{2m}}{(m!2^m)}(D^m\vec{v})^2, \quad (1)$$

where the only two parameters are $\lambda > 0$ and $\sigma > 0$, and where the smoothness operators are $D^{2m}=\nabla^{2m}$ and $D^{2m+1}=\vec{\nabla}\nabla^2$, where $\vec{\nabla}$ is the gradient operator and ∇^2 is the Laplacian operator. The Motion Coherence theory tries to conform with the measuring stage by minimizing the differences between the newly built velocity field and that obtained by the measuring stage as expressed in the first term of the right-hand side of equation (1). Moreover, the theory imposes smoothness by the minimization of the magnitudes of derivatives as seen in the second term of the right-hand side of the equation. Similar forms of smoothing appeared in earlier models of motion measurement (e.g. Horn & Schunck, 1981; Hildreth, 1984).

Therefore, the stronger the theory's parameter λ, the stronger the smoothing imposed on the velocity field.

The parameter σ corresponds to the spatial extent of the smoothing interactions. To see this, one minimizes equation (1) with standard calculus of variations to obtain (Yuille & Grzywacz, 1989).

$$\vec{v}(\vec{r})=\sum_i\frac{\vec{\beta}_i}{2\pi\sigma^2}e^{-(\vec{r}-\vec{r}_i)^2/2\sigma^2}, \quad (2)$$

where the $\vec{\beta}_i$ are solutions of the system of linear equations $(\lambda\delta_{ij}+G_{ij})\vec{\beta}_i=\vec{U}_i$, where $G_{ij}=\exp(-(\vec{r}_j-\vec{r}_i)^2)/(2\pi\sigma^2)$. Hence, equation (2) shows that the constructed field is a superposition of vector fields, which are centered at the points where the local velocity measurements have been made. These fields decay with a Gaussian profile as a function of the distance from these points. Because the standard deviation of the Gaussian profiles is σ, this parameter corresponds to the spatial extent of the smoothing interactions.

When one applies the Motion Coherence theory to random-dot cinematograms, the results depend on λ, σ, and the density of the dots (ρ). Computer simulations demonstrate that to obtain a global-motion percept, the mean number of interacting dots ($\pi\sigma^2\rho$) must be much larger than 1. Under this condition, if one neglects boundary effects (Yuille & Grzywacz, 1989), then the mean of the constructed velocity field is

$$\langle\vec{v}\rangle=\frac{\rho\langle\vec{U}_i\rangle}{\lambda+\rho}, \quad (3)$$

where $\langle\vec{U}_i\rangle$ is the mean of the velocity field obtained by the measuring stage. Figure 1(A) displays the dependence of the mean of velocity on density as expressed in equation (3).

The mean speed increases with density, asymptotically reaching the plateau $|\langle\vec{U}_i\rangle|$.

This particular density dependence holds under the assumption that λ and σ are constant. However, as explained in the Introduction, it would make more sense if they varied adaptively to remove the dependency of the theory on the spatial structure of the image (e.g. density). Therefore, if the experimental density would vary ($\rho=\rho(t)$), then σ should vary to keep the number of interacting dots constant ($\sigma^2(t_1)\rho(t_1)=\sigma^2(t_2)\rho(t_2)$). For the same reason, λ should vary to keep the mean perceived (constructed) speed constant ($\rho(t_1)/(\lambda(t_1)+\rho(t_1))=\rho(t_2)/(\lambda(t_2)+\rho(t_2))$). The theory has not yet been extended to account for the dynamics of σ and λ. However, one expects that if the density change is abrupt, the temporal variations of σ and λ should lag behind it. Thus, a transient change in perceived speed as in equation (3) should occur [Fig. 1(A)].

Finally, from the application of the Motion Coherence theory to random-dot cinematograms, one may calculate the dependence of the variance of the constructed velocity field (Var($\vec{v}$)) on ρ. If, as before, $\pi\sigma^2\rho\gg 1$ and one neglects boundary effects, then

$$\mathrm{Var}(\vec{v})=\frac{1}{2\pi\sigma^2\rho}\left[\log\left(\frac{\rho+\lambda}{\lambda}\right)-\frac{\rho}{\rho+\lambda}\right]\langle\vec{U}_i^2\rangle. \quad (4)$$

Figure 1(B) displays the dependence of the variance of velocity on density as expressed in equation (4). This variance decreases with density, indicating that the variance of perceived direction and speed also decreases with density. Again, the theory makes this prediction with certainty for abrupt changes of densities. However, the theory also allows for the possibility that the prediction holds under steady-state conditions [Fig. 1(B)].

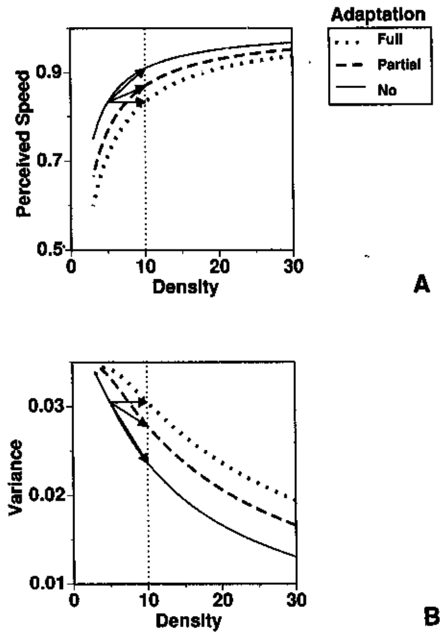


FIGURE 1. Predictions of Motion Coherence theory for mean and variance of perceived velocity of cinematograms as function of density (with perceived-speed axis normalized to physical speed and all other axes given in arbitrary dimensions). Equation (3) underlies (A) and equation (4) underlies (B). The parameters (λ, σ) for the curves labeled with full, partial, and no adaptation are (2, $1/\sqrt{2}$), (1.5, $1/\sqrt{1.5}$), and (1,1) respectively. We start the curves at density = 3 to fulfill $\pi\sigma^2\rho \gg 1$, which was required in the approximations used to develop equations (3) and (4). The arrows indicate the predictions for cases with two-fold increase in density, assuming, arbitrarily, that the solid line corresponds to the initial adaptation state. If the parameters of the theory do not adapt to changes in density, as when density changes abruptly, then perceived speed increases and variance decreases with increasing density (arrows connecting points in the solid curves). If, on the other hand, the adaptation is so complete that the two densities are indistinguishable to the system, then perceived speed and variance are independent of density (arrows connecting solid and dotted lines). We will argue that our data are consistent with a version of the model in which there is partial adaptation.

METHODS

Stimuli

Stimuli were random-dot cinematograms in which each dot took a two-dimensional random walk of constant step size. Each dot's movements, from frame to frame, were chosen from a predefined, rectangular distribution of directions. The rectangular distribution was sampled every 1 deg and the horizontal and vertical increments to create those directions were stored as an array. From this array, the computer randomly chose increment values for the dots' movements. The chosen increments were added to the dots' current positions and the dots' new horizontal and vertical positions were transmitted to the x–y cathode ray tube (CRT) display via digital-to-analog converters. The initial screen location of each dot was randomly determined at the beginning of each new presentation, making it impossible for an observer to use dot pattern information as the basis for his/her judgment.

Apparatus

Stimuli were displayed on a CRT with a fast, P4, phosphor (Tektronix 604) at a constant frame rate of 20 Hz. The observer, viewed the CRT from a distance of 57 cm. A circular mask with a diameter of 8 deg of visual angle was centered over the 10 × 10 deg CRT screen. Each dot subtended about 0.05 deg and had a luminance of about 0.27 cd/m^2.* The background and veiling luminances were 0.03 and 0.07 cd/m^2, respectively.

The height of the CRT was set so that the center of the aperture was approximately at eye level. Observers were required to maintain fixation on a dot located at the center of the aperture. Push buttons connected to a computer initiated each trial and signaled the observer's responses. All experiments took place in a darkened room and, before testing, observers were allowed 5 min for their eyes to adapt.

Experiment 1. Perceived Speed and Rapidly-Changing Density

This experiment investigated how rapid changes in density affect the perceived speed of global motion. Two naive observers participated in this experiment. Both had corrected to normal vision and had previously participated in psychophysical experiments.

Procedure

Stimuli were presented according to a two-alternative forced-choice (2AFC) procedure. In each trial, two different cinematograms were presented, a standard and a comparison, with a blank interstimulus interval of about 200 msec. In one interval, the standard stimulus, which moved with a fixed speed of 6.4 deg/sec (step size = 0.32 deg) and had a density of 1.28 dots/deg^2, was presented. This stimulus was presented every trial. In the other interval, dots could have one of five possible densities 0.64, 0.90, 1.28, 1.81 and 2.56 dots/deg^2 and moved with one of five possible speeds, 5.6, 6.0, 6.4, 6.8 and 7.2 deg/sec (step sizes = 0.28, 0.30, 0.32, 0.34 and 0.36 deg). This stimulus is referred to as the comparison stimulus. Speed and density were completely crossed variables so that 25 comparison stimuli were tested against a single standard. A complete set of standard and comparison stimuli were constructed for each of four direction distributions having directional ranges or bandwidths of 0, 30, 90 and 150 deg. The observer's task was to determine which stimulus moved the fastest. For each trial, the temporal position of the comparison stimulus was randomized so that it appeared equally in the first and second interval over a single block of trials. All stimuli had a mean direction of motion upwards. An inter-trial interval of about 2 sec elapsed before the next trial was signaled.

Although the stimuli were shown at a constant frame rate of 20 Hz, the duration of the cinematograms was varied randomly, from 250 to 450 msec, so that the

*This value was obtained by plotting a matrix of non-overlapping dots (center-to-center spacing was 0.06 deg) at the same frame rate as used in the experiments. The luminance of this matrix was then measured with a Minolta luminance meter.

observers could not base their decision of speed on the distance traveled by the elements. As well, the two cinematograms presented within a trial were forced to have different durations.

Within a single experimental session, observers completed four blocks of 250 trials each. In each block, data were collected for a single directional bandwidth, 10 trials for each of the 25 speed/density conditions. Data were kept separate depending upon whether density increased from the first presentation in a trial to the second or decreased. Thus, within a block, five trials for each of the 25 speed/density conditions were density-increase trials and five were density-decrease trials. The bandwidth of the standard and comparison were always the same within a trial. Before experimental data were collected, each observer had at least 1000 practice trials. Observers completed 16 sessions so that 80 trials for each of the 25 step size/density conditions for each type of trial, density-increase and density-decrease, were collected. Data were recorded as the number of faster judgments for each comparison stimulus. The data were converted to z-scores and plotted as a function of the speed of the comparison stimulus. A least-squares linear fit was made to each of the 32 data sets (4 directional bandwidths × 4 densities × 2 density changes, corresponding to density increase and density decrease conditions*) for each observer. The linear fit was good: mean r^2 for 64 data sets (32 from each of two observers) was 0.89. Figure 2 shows representative data and linear fits for one observer obtained at a single direction distribution bandwidth (0 deg) and density change (decreasing within a trial). The points of subjective equality (PSEs), i.e. the abscissa for z-score = 0, and the precision of speed discrimination (speed increment necessary to reach a z-score = 1.0) expressed as a Weber fraction ($\Delta V/V$), were evaluated from the fitted functions. The perceived speed for each condition was evaluated from the PSE using the following formula:

$$\text{perceived speed} = \left(\frac{\text{standard speed}}{\text{PSE}}\right) \times \text{standard speed}. \quad (5)$$

Because perceived speed and the precision of speed discrimination are independent, separate analyses were conducted on each set of measures.

Equation (5) sets the perceived speed of the standard at its veridical physical speed. This does not mean that the perceived speed of the standard was veridical. The absolute values of perceived speed cannot be determined from the data presented here.

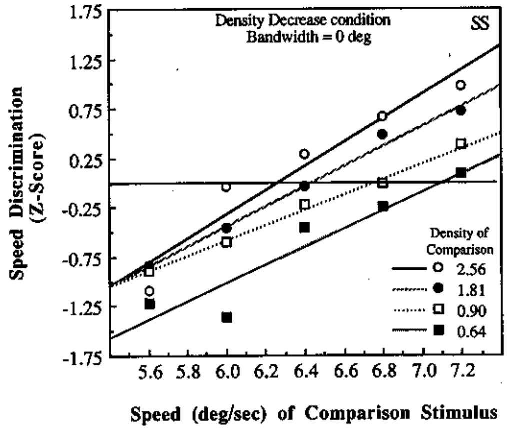


FIGURE 2. Speed discrimination in z-scores plotted as a function of the speed of the comparison stimulus for observer SS. Comparison stimuli were compared each trial to a standard that had a direction bandwidth of 0 deg, a density of 1.28 dots/deg^2 and a speed of 6.4 deg/sec. Data from four comparison densities are shown for one condition, density decreasing from first to second stimulus interval, for a direction bandwidth of 0 deg. The best fitting straight lines have been drawn for each data set. Symbols are as indicated in the legend. Notice that the data shift systematically rightward as the density of the comparison stimulus decreases.

Results

Analysis of perceived speed. In this experiment, we sought to determine whether rapid changes in density affect perceived speed. A three-way analysis of variance (ANOVA) showed that there was a significant effect of the density of the comparison stimulus ($F_{3,32} = 8.362$, $P = 0.0003$). When the comparison and the standard stimuli had the same physical speed, we found the perceived speed of the comparison to be slower (faster) than the standard's when the density of the comparison was lower (higher) than the standard's. This effect can be easily seen in Fig. 3 which plots perceived speed, averaged over all observers and conditions, as a function of the density of the comparison stimulus. The ANOVA revealed that there was no significant difference between direction of density change conditions, density-increase vs density-decrease ($F_{1,32} = 1.889$, $P = 0.179$). This negative effect appears as the similarity between the open and solid circle curves for observer BT† in Fig. 4. In addition, there was no significant difference between directional bandwidth ($F_{3,32} = 1.013$, $P = 0.40$—see Fig. 4).

The main result of lower densities yielding slower perceived speeds has been replicated using different values of densities (0.5, 1.0, 1.5, 2.0 and 2.5 dots/deg^2) on observer BT and three others ($F_{4,60} = 18.136$, $P = 0.0001$). The standard stimulus for this experiment had a density of 1.5 dots/deg^2 and a speed of 6.4 deg/sec. Representative data from one observer are shown in Fig. 5.

Analysis of precision ($\Delta V/V$). An ANOVA on the Weber fraction data showed no significant effects of the direction distribution bandwidth ($F_{3,32} = 2.055$, $P = 0.126$), the direction of density change, increase vs decrease ($F_{1,32} = 1.364$, $P = 0.251$), or the density of the comparison stimulus ($F_{3,32} = 1.361$, $P = 0.272$) on speed discrimination. Thus although the perceived speed of a

*Although five densities were tested, the data for the density of 1.28 dots/deg^2 were excluded from the analysis because this stimulus configuration did not reflect an increase or decrease from the standard stimulus.

†The data for this observer, bandwidth of 150 deg, appear to indicate a three-way interaction between bandwidth, density, and density change. However, this result did not hold for the other observer and did not reach statistical significance overall.

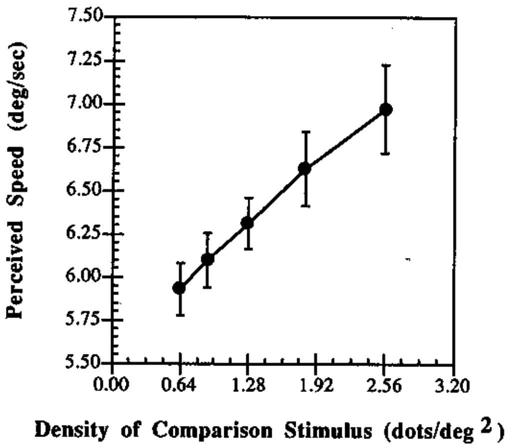


FIGURE 3. Perceived speed in deg/sec plotted as a function of the density of the comparison stimulus. Data, averaged over observers, directional bandwidth and density increase/decrease variation, are plotted along with ±1 SE. There is a clear increase in perceived speed as density increases.

stimulus was affected by dot density, the observers ability to discriminate speeds was not.

Experiment 2. Perceived Speed without Rapidly Changing Density

The previous experiment showed that when there was a rapid change in stimulus density, the perceived speed of the moving dots shifted. We wanted to determine whether this change in perceived speed was entirely due to the abrupt change in density or whether perceived speed depends at least in part on the steady-state value of density. We measured speed discrimination with a different procedure to determine whether the density of a stimulus seen 2 sec earlier would affect perceived speed. One of the authors (SW) and two other experienced psychophysical observers, naive to the purposes of this experiment, served as observers.

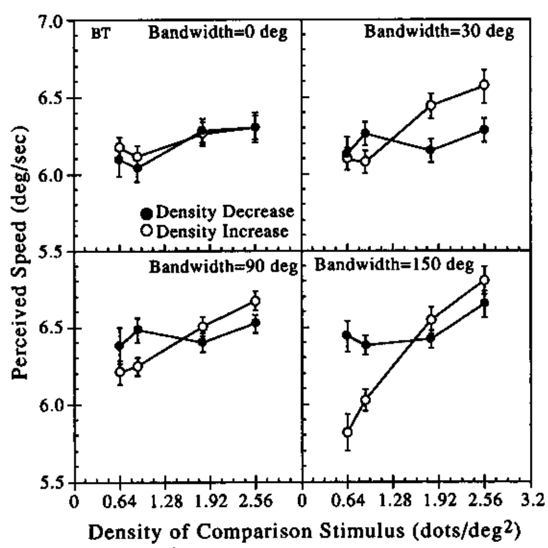


FIGURE 4. Perceived speed in deg/sec plotted as a function of the density of the comparison stimulus for four directional bandwidths. Data for density-increase (○) and density-decrease (●) conditions are shown with ±1 SE for one observer, BT. Data are similar for the two density change conditions for all bandwidths with the exception of the two smallest densities when the bandwidth is 150 deg.

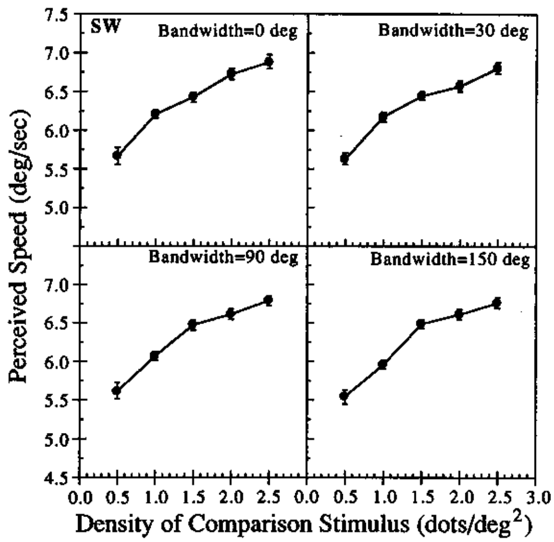


FIGURE 5. Perceived speed in deg/sec plotted as a function of the density of the comparison stimulus for four directional bandwidths. Representative data, averaged over density-increase and density-decrease conditions are shown with ±1 SE for observer SW. Note that the densities of the comparison stimuli are different from those used in Expt 1, but yielded a similar result.

Procedure

Stimuli were presented using a variant of the method of constant stimuli, known as the single-stimulus method (McKee & Welch, 1985). In each trial, one cinematogram was presented. The stimulus moved at one of five possible speeds, 5.6, 6.0, 6.4, 6.8 and 7.2 deg/sec (step sizes = 0.28, 0.30, 0.32, 0.34 or 0.36 deg), and had a density of 0.64, 1.28 or 2.56 dots/deg^2. Speed and density were completely crossed producing 15 unique stimuli. The bandwidth of the direction distribution was fixed at 30 deg. Stimuli were arranged so that pairs of trials had the same stimulus density: if an odd numbered trial had a stimulus density of 0.64, the next trial presented a stimulus with the same density. Density changed randomly from one pair of trials to the next while stimulus speed varied randomly from trial to trial. All stimuli had a mean direction of motion upwards. Although the stimuli were shown at a constant frame rate of 20 Hz, the duration of the cinematograms was varied randomly, from 300 to 600 msec, so that the observers could not base their decision of speed on the distance traveled by the elements. The observer's task was to determine whether the current stimulus moved faster or slower than the implicit mean speed of the stimulus set. This task, though seemingly difficult, is performed easily by the observer and has been used successfully by others measuring speed discrimination (e.g. McKee & Welch, 1985). Observers completed about 600 practice trials before data collection. In addition, 20 practise trials were run before each experimental session to reacquaint observers to the range of speeds that would be appearing in the experiment. After an observer response, a blank interval of 2 sec elapsed before the next stimulus was presented.

Within a single experimental session, observers completed 600 trials: 200 trials for each density. Data were kept separate depending upon whether density had changed from the previous trial or had remained constant. Data were recorded as the number of faster judgments for each stimulus. The data were converted to z-scores and plotted as a function of speed. Because of the way stimuli were presented, an unequal number of trials for each speed/density stimulus were collected for the density change and density constant condition. A least squares linear fit was made to each of the six data sets (1 directional bandwidths × 3 densities × 2 density changes, corresponding to density constant and density change conditions) for each observer. The PSEs and the precision of speed discrimination expressed as a Weber fraction ($\Delta V/V$), were evaluated from the fitted functions. The perceived speed for each condition was evaluated from the PSE as in equation (5).

Results

Analysis of perceived speed. Figure 6(A) plots perceived speed as a function of density for each of the three observers. Data, averaged over the three observers appears in Fig. 6(B). A two-way ANOVA showed that there was a significant effect of the density of the stimulus ($F_{2,30} = 35.021$, $P = 0.0001$) with lower density stimuli yielding slower perceived speeds than higher density stimuli. This effect can be easily seen in Fig. 6(A, B). The ANOVA revealed no significant difference between the density constant and density change conditions ($F_{1,30} = 0.056$, $P = 0.82$).

Analysis of precision ($\Delta 8V/V$). A two-way ANOVA on the Weber fraction data showed no significant effect of density ($F_{2,30} = 0.336$, $P = 0.72$) or density change condition, change vs no change ($F_{1,30} = 0.331$, $P = 0.56$) on speed discrimination. As in the previous experiment, perceived speed was affected by dot density, but the observers' ability to discriminate speeds was not.

Experiment 3. Direction Discrimination with Changing Density

Since changing density affected the perceived speed of our random-dot stimuli, we decided to examine whether such a manipulation would affect direction discrimination. Recall that Watamaniuk (1990, 1993) showed this effect under constant-density conditions. Here, we examine whether abrupt increases and decreases in density produce differential effects on direction discrimination. The two observers from Expt 1 participated in this experiment.

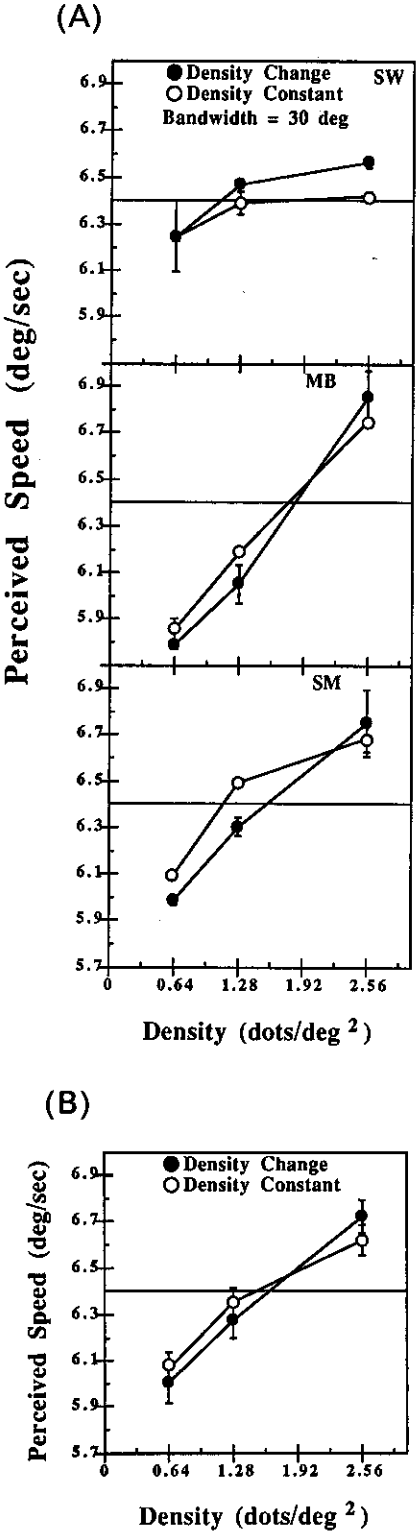
Procedure

A 2AFC procedure, similar to that in Expt 1, was used. In this experiment, instead of the step size changing from one stimulus presentation to the next, the mean direction of the direction distribution was varied. The standard stimulus moved with a fixed speed of 5.6 deg/sec (step size = 0.28 deg) and had a density of 2.56 dots/deg^2. In the other interval, dots had one of five possible densities 0.64, 0.90, 1.28, 1.81 and 2.56 dots/deg^2 and also moved with a speed of 5.6 deg/sec. This stimulus is referred to as the comparison stimulus. The mean direction of the standard stimulus varied from trial to trial but always fell within the range of 72–108 deg. For each of the four directional bandwidths, 0, 30, 90 and 150 deg, a set of comparison stimuli were constructed to produce a difference in mean direction from the standard, both clockwise and counter-clockwise, that would span the range of discriminability.* The differences in mean direction were different for each directional bandwidth. For bandwidths of 0 and 30 deg, mean direction between standard and comparison stimuli differed by 1, 2, 3, 4, 5 and 6 deg. For a bandwidth of 90 deg, mean direction between standard and comparison stimuli differed by 2, 4, 6, 8, 10 and 12 deg. For a bandwidth of 150 deg, mean direction between standard and comparison stimuli differed by 3, 6, 9, 12, 15 and 18 deg. Data were grouped according to only the difference in direction and not the relative direction of the comparison to the standard, clockwise or counter-clockwise. For each trial, the temporal position of the comparison stimulus was randomized so that it appeared equally in the first and second interval over a single block of trials. The observers task was to decide whether the direction of global flow in the second stimulus was to the right or left of the first stimulus. Difference in direction and density were completely crossed variables so that there were 30 stimulus conditions for each directional bandwidth tested. An inter-trial interval of about 2 sec elapsed before the next trial was signaled. Stimuli were shown at a constant frame rate of 20 Hz and the duration of the cinematograms was constant at 350 msec (seven frames).

Within a single experimental session, observers completed four blocks of 240 trials each. In each block, data were collected for a single directional bandwidth, eight trials for each of the 30 direction difference/density conditions. Data were kept separate depending upon whether density increased from the first to second presentation within a trial or decreased. Thus, within a block, four trials for each of the 30 direction difference/density conditions were density-increase trials and four were density-decrease trials. The bandwidth of the standard and comparison were always the same within a trial. Observers completed 12 sessions so that 48 trials for each of the 30 step size/density conditions for each type of trial, density-increase and density-decrease, were collected. Data were recorded as the number of correct direction judgments for each stimulus condition.

Ten direction discrimination psychometric functions (one for each of five densities for each type of density change: increase and decrease) were evaluated for each direction distribution bandwidth. Psychometric functions were fit with a Weibull function and the 75% thresholds and standard errors evaluated as in Quest

*This choice of bandwidth and speed parameters avoids the degradation of direction discrimination, which occurs at speeds slower than 3 deg/sec (McKee, 1981; Pasternak & Merrigan, 1984; McKee *et al.*, 1986; De Bruyn & Orban, 1988). With these parameters, the slowest mean speed of global flow we used was 4.2 deg/sec.



582FIGURE 6. Perceived speed in deg/sec plotted as a function of the density of the stimulus for density-change (●) and density-constant conditions (○). Data were collected with a single direction bandwidth of 30 deg. (A) Individual data for three observers; (B) the data averaged over observers. Error bars in all graphs represent ±1 SE. Notice that perceived speed increases with density in both conditions.

(Watson & Pelli, 1983). Because conditions in which the density of the comparison was equal to that of the standard (2.56 dots/deg^2) could not be classified as density increase or decrease, thresholds for these conditions were excluded from the analyses.

Results

Figure 7 shows thresholds for both observers plotted as a function of the density of the comparison stimulus. Thresholds for density decrease and density increase conditions are plotted on separate curves. Data for each directional bandwidth is presented in a separate panel with bandwidth increasing from top to bottom. One obvious effect evident in these data is the increase in discrimination threshold with directional bandwidth. This effect has been reported elsewhere (Watamaniuk *et al.*, 1989) and therefore we will not address that issue here. In this paper, we are interested in whether the type of density change (increase or decrease) had a significant effect upon direction discrimination. From the plots in Fig. 7, it is apparent that density increase and decrease have different effects depending upon bandwidth. Therefore we performed a separate analysis for each directional bandwidth. The analyses showed that differences between performances under density increase or decrease conditions was only significant for a directional bandwidth of 150 deg ($F_{1,8} = 55.734$, $P = 0.0001$) with increases in density producing lower thresholds than decreases. Although there is a hint of this trend at a bandwidth of 90 deg, this effect did not reach significance ($F_{1,8} = 3.818$, $P = 0.086$).

DISCUSSION

We have presented evidence that dot density of cinematograms affects their perceived motion. The speed of dense cinematograms appears to be faster than that of sparse ones. However, speed discrimination was not compromised by density variations. In contrast, direction discrimination for cinematograms with abruptly varying density was better for density-increase conditions than for density-decrease conditions, but only at large bandwidths.

In the Introduction, we distinguished between two theoretical alternatives for the effects of density: (1) effects due to abrupt density changes and (2) effects occurring in constant-density conditions. Figure 6 demonstrates that perceived speed increases with density even when density does not change from one stimulus to the next. Although not tested here, Watamaniuk (1990, 1992) showed that direction discrimination improves with density for conditions in which density does not change during stimulus presentation. Does an abrupt change in density magnify the dependence of perceived speed and direction discrimination on density? For perceived speed, the data from Figs 5 (30° bandwidth) and 6 (averaged over density increase and decrease) can be compared for only one subject, SW. These data have been replotted along with their linear fits in Fig. 8. The ratio between the slopes of the linear fits was 4.7 (significantly larger than 1, $t_6 = 8.37$, $P = 0.0001$) with the largest slope being obtained with abrupt changes in density. These data show that abrupt changes in density have a larger effect on perceived speed than constant-density conditions, but one must be cautious, since this

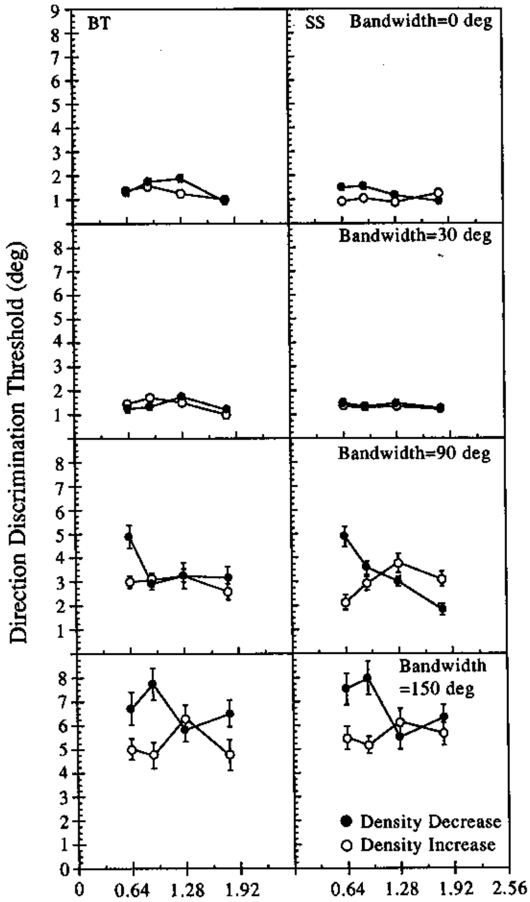


FIGURE 7. Direction discrimination threshold in deg plotted as a function of the density of the comparison stimulus for four directional bandwidths. Data for density-increase (○) and density-decrease (●) conditions are shown with ±1 SE for both observers, BT and SS. Discrimination performance is similar for the density-increase and density-decrease conditions at small bandwidths but not at large bandwidths.

conclusion is based on only one subject. If this conclusion were correct, then it would imply an adaptation of the visual system's parameters in the computation of global motion as discussed in the Introduction. Another piece of evidence for such adaptation is the difference between density-increase and density-decrease conditions in direction discrimination (Fig. 7). Without adaptation, the critical parameters of spatial integration would be constant for these two conditions and therefore should yield similar performances.

The dependence of perceived speed and direction discrimination on density are consistent with the model presented in the Theory section (Motion Coherence theory).* Equation (4), which is represented in Fig. 1 (B), can account for the differential effects of increasing and decreasing dot density on directional discrimination (Fig. 7). While at large bandwidths, the input and output variances are large and thus discrimination can be improved by increases in density, at small bandwidths, these variances are small, leaving no room for improvement. The theory also predicts an improvement of speed discrimination with increases in density. This prediction was not evident in our data. There may be two possible explanations for the failure of this prediction: (1) this theory or theories with multiple-order differential smoothing (see Introduction) are wrong, or (2) this failure might have been due to the high intrinsic noise of the system measuring speeds. On the latter possibility, Watamaniuk and Duchon (1992) showed that speed discrimination for cinematograms with wide distributions of speeds was the same as that for cinematograms in which all dots had the same speed. This independence of performance with stimulus noise suggests that a high level of internal noise limits speed discrimination. Hence, for the stimuli used in this paper, any potential change in speed discrimination due to density variations might have been masked by this putative internal noise.

Can other existing models account for the density effects on perceived speed and direction discrimination? In the Introduction, we argued that theories with a multiple-order differential smoothing stage may also account for these effects. In contrast, we argued that these effects rule out models which compute global velocity as the mean of local velocity vectors. This conclusion is independent of whether these vectors are detected by Reichardt detectors (Hassenstein & Reichardt, 1956; van Santen & Sperling, 1985), motion-energy detectors (Adelson & Bergen, 1985), and the type of detector implied by the Minimal Mapping theory (Ullman, 1979).

A class of models based on temporal frequency also fails to account for the data quantitatively. This class, which was not discussed in the Introduction, applies to textured images and relies on the frequency of texture elements crossing an imaginary line. This temporal

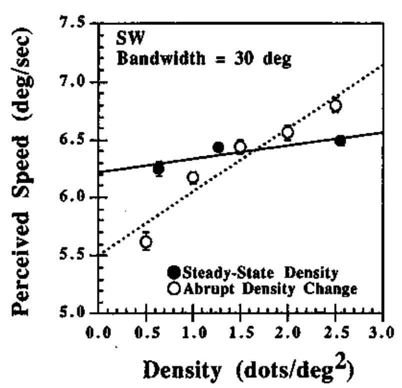


FIGURE 8. Perceived speed in deg/sec plotted as a function of the density. Data, with ±1SE, for a single observer, SW, are shown along with the best fitting straight lines (solid line for the steady-state data and dotted line for the abrupt density change data). The 'steady-state' data (●) are the average of SW's data in Figure 6A and the 'abrupt density' data (○) are replotted from Figure 5. Perceived speed follows a steeper slope when there has been an abrupt change in density compared to when there has not.

*One prediction of the model (Fig. 1) not clearly seen in the data (Fig. 3) is the plateauing of perceived speed at high densities. However, the beginning of such plateauing may be seen in Fig. 5. This hints that the plateauing might be a true feature of the visual system, but that the densities used in this study were not sufficiently high to show this trend clearly.

frequency is proportional to image speed, thus for example, increasing image speed by a factor of two increases temporal frequency by a factor of two. Experimental evidence supports the dependence of perceived speed on temporal frequency (Brown, 1931) and models using this dependence have been advanced (e.g. Watson & Ahumada, 1985). For our stimuli, these models predict that perceived speed should increase proportionally with density, since an increase in density causes a proportional increase in temporal frequency. In other words, increasing density by a factor of two should result in a factor of two increase in perceived speed. However, the data in Figs 3 and 6 do not confirm this prediction. For instance, a four-fold increase in density caused an increase in perceived speed by a factor of 1.12 in Fig. 6(B).

Another class of mechanisms that fails, would postulate that the effect of density on perceived speed is mediated by the dependence of contrast on density. Previous work showed that perceived speed increases with the contrast of sinusoidal gratings (Thompson, 1982; Stone, Thompson & Watson, 1990). However, we argue that regardless how one defines contrast of cinematograms, it does not increase with density. If for instance, the contrast of a cinematogram is the contrast of its dots, then the cinematogram's contrast is independent of density. In another example, if one defines contrast as proportional to the ratio between the luminance's standard deviation and mean (as in the classical definition for sinusoids), then the contrast of cinematograms decrease with increasing density. Even when one considers the Fourier spectrum of windowed cinematograms, the contrast of their Fourier components does not increase with density. (High frequency components of the different dots tend to be summed in random phases and cancel out. Low frequency components add up, but so does luminance, keeping contrast roughly constant.) Hence, contrast does not mediate the effect of density on perceived speed.

Can models that postulate perceived speed increases with the absolute response of directionally selective cells account for the present results? Recent studies found that increasing dot densities of random-dot patterns increases cell responses in V1 and MT (Snowden, Treue, Erickson & Andersen, 1991; Snowden, Treue & Andersen, 1992). Thus, increases in dot density could cause increases in perceived speed. However, a problem with linking perceived speed to absolute cell responses is that it would predict that at high speeds perceived speed actually decreases with speed. This is because cell responses to cinematograms (Hammond, 1979, 1981; Hammond & Reck, 1981) and other stimuli (Movshon, 1975; Mikami, Newsome & Wurtz, 1986; Baker, 1988) first rise to a peak as speed increases and then fall at higher speeds.

However, similar to models with a multiple-order differential smoothing stage, physiologically-based mechanisms might predict an increase in perceived speed with density under steady-state conditions. It has been shown that cortical directionally selective cells with small receptive fields prefer slower speeds than cells with large receptive fields (Mikami *et al.*, 1986). [This is consistent with the psychophysical finding that sinusoidal gratings of spatial frequencies above 2 c/deg appear to drift more slowly than low spatial frequency gratings (Smith & Edgar, 1990). The opposite finding, however, holds for gratings of spatial frequency below 1.5 c/deg (McKee, Silverman & Nakayama, 1986).] Furthermore, cells with small receptive fields may have a sharper spatial sensitivity profile than cells with large receptive fields. Therefore, small individual dots may elicit relatively stronger responses from cells with small receptive fields than from cells with large receptive fields. As a result, in low density cinematograms, small receptive-fields cells, which encode slower speeds, would be relatively more active than cells with large receptive fields. With density increase, cells with larger receptive fields would be relatively more activated, and faster speeds perceived. (The absolute responses of both types of cells would increase with density in agreement with Snowden *et al.*) Despite these physiological based mechanisms accounting for the shift in perceived speed with density, they do not address direction discrimination. Therefore, the Motion Coherence theory provides a more complete account of the effects of density on motion perception.

The increase of perceived speed with density is surprising, since density is not a stimulus variable that one typically connects with speed. Contrast also affects perceived speed in an unexpected way; high contrast sinusoidal gratings appear to move faster than low contrast gratings (Thompson, 1982; Stone *et al.*, 1990). Therefore, for a large set of stimulus conditions, speed is not encoded accurately by the visual system. This observation suggests two non-mutually exclusive possibilities: the visual system is designed to measure absolute speed under visual conditions different from the ones used in this paper, such as at higher densities (see the Motion Coherence theory's prediction in Fig.1) or the visual system might be optimally designed to discriminate small differences in speed.

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