The Effect of Transiency on Perceived Velocity of Visual Patterns: a Case of "Temporal Capture"

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We measured the points of subjective equality of velocity for dynamic unidirectionally moving random-dot patterns with different amounts of transiency. The transiency was changed by varying the time a dot would move before being randomly replotted within the stimulus. The perceived velocity of patterns moving at intermediate velocities (4 or 6 deg/sec) was increased by decreasing the point lifetime while no speedup was observed at high velocities (12 deg/sec). A speedup was also observed when a few *stationary* points of short lifetime were introduced into a stimulus. The non-directional transiency generated by these flickering points seems to be captured by the moving pattern and biases the velocity estimate. We term this phenomenon "temporal capture". The results are in agreement with models that determine velocity by comparing the activity in lower and higher temporal frequency channels. Our stimuli would selectively increase activity in high temporal frequency channels and thus lead to an increase in perceived velocity.

Visual motion   Temporal frequency channels   Velocity   Random-dot patterns   Limited lifetime

INTRODUCTION

The measurement of velocity in the visual image is of great importance. Velocity information is used in image segmentation, structure-from-motion, time-to-collision estimation and other visual tasks (Nakayama, 1985). It therefore comes as no surprise that human subjects have been shown to be highly accurate in velocity discrimination, being able to detect velocity differences as small as 5% (McKee, 1981; Orban, De Wolf & Maes, 1984).

Many cells in the visual cortex are tuned for the direction of stimulus motion. Although they are often also tuned for the velocity of moving bars, this does not represent a true *velocity* tuning, but rather reflects the cells' tuning for spatial and temporal frequencies (Holub & Morton-Gibson, 1981; Movshon, Thompson & Tolhurst, 1978). In other words the activity of a cell will change if one lowers or raises the spatial and temporal frequency of a stimulating grating proportionally even though the velocity of the stimulus has not changed. Furthermore the response of a cell will vary with stimulus contrast. Nevertheless it is generally assumed that these cells form the basis of velocity estimation since as a population they provide the information needed to determine stimulus velocity.

To deconfound the cells' response some models of velocity estimation assume that the visual system compares the activity of cells with the same spatial frequency preference but with different prefered temporal frequencies (Thompson, 1984; Grzywacz & Yuille, 1990). Higher velocities would activate cells tuned for higher temporal frequencies while cells tuned for lower temporal frequencies would respond to slower velocities. This approach resembles the encoding of color through the relative activity of the three cone types. It also fits well with results from psychophysical studies. Thompson (1983) has shown that at threshold just two labeled channels can account for velocity discrimination (with possibly a third channel at higher temporal frequencies).

Such a coding scheme could also prevent changes in contrast and spatial frequency from influencing the perceived velocity since *ideally* such changes would affect all channels equally (see also Adelson & Bergen, 1985). If the visual system indeed uses such an approach it does not seem to work perfectly along these lines since there are reports of a dependence of perceived velocity on stimulus contrast and spatial frequency (Campbell & Maffei, 1979; Thompson, 1982; Smith, 1990).

Further evidence for the crucial role of temporal frequency comes from experiments by Wright and Johnston (1985) who show that the velocity of the motion aftereffect is dependent on the adapting temporal frequency and from Pantle (1974) who showed that the magnitude of the motion aftereffect was determined by the temporal frequency rather than the velocity of the adapting pattern (for review, see Sekuler, Pantle & Levinson, 1978).

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If the visual system indeed encodes velocity as the relative activity between neurons tuned for temporal frequency one would predict that perceived velocity can be altered by stimuli which change the relative activity in the channels involved in velocity discrimination. This is the approach we took in our experiments. We changed the amount of transiency (and thus the temporal frequency content) in unidirectionally moving dynamic random-dot patterns by changing the "lifetime" of individual stimulus points and measured the perceived velocity of the patterns. We did indeed find that for medium velocities the perceived velocity of a pattern is higher when the amount of transiency is higher (i.e. with shorter lifetimes) and that this effect could even be achieved by introducing *stationary* points of short lifetime ("temporal capture"). Furthermore we demonstrate that the effect is much weaker at higher velocities, presumably because the stimulus itself already predominantly activates the high temporal frequency channels.

METHODS

Stimuli

Dynamic random-dot patterns moving within stationary windows were produced prior to an experiment on an AST 386 computer with a Number Nine Sgt. Petter graphics card and displayed on a NEC multisynch XL video monitor at a frame rate of 60 Hz. All patterns contained 100 points moving downward (except for some conditions in Expt 1b where we used stimuli containing 20 points as well as a condition in which some patterns moved upwards). The window sizes were 3.5 horizontal × 4.5 vertical angular deg for Expt 1a and 2.5 × 3.5 angular deg for Expt 1b. Both sizes were used in Expt 2. Points moving over the edge of the window were wrapped around to the other side.

Although subjects were asked to discriminate velocities of two simultaneously presented stimuli the experimental variable in this study was the point lifetime. Lifetime is the time in msec a point moves along a path before being repositioned somewhere within the stimulus window. For a lifetime of 200 msec and a stimulus speed of 4 deg that would result in point paths of 48 min arc traversed by each point during its lifetime. All points in a given stimulus would move at the same velocity and would have the same lifetime (except for the stationary points in Expt 2). The lifetimes of the individual points were desynchronized, i.e. between any two frames only a fraction of the points would be repositioned.* The timing of the experiment was controlled by a PDP11/73

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*Example: when using a lifetime of 166 msec (10 frames) one-tenth of all points are repositioned between any two frames.

†Even though eye position was not measured during the experiment subjects learned quickly (i.e. during the practice sessions) that trying to track the pattern would lower their performance strongly because the short stimulus duration time prevent the consecutive inspection of both patterns. Even if they would have tracked one or the other of the patterns that could not account for the results presented here.

computer which was interfaced with the AST and which also collected the subjects responses.

Procedures

Subjects were seated without restraint 171 cm from the screen in a dimly lit room. Although we used two experimental procedures, the instructions for the subjects and the basic experiment were always the same. Before the beginning of each trial a central fixation would appear. Subjects were instructed to fixate the point† and to move a hand-held computer joystick to begin the trial. Two dot patterns would appear simultaneously for 400 msec on either side of the fixation point (the closer edge of the stimuli being 2 deg from the fixation point). Next the stimuli and the fixation point disappeared and the subjects indicated the pattern which had moved faster by moving the joystick to the right or the left (two-alternative forced-choice, 2AFC). The fixation point then reappeared and the subjects initiated another trial by moving the joystick.

Experimental design and data collection

In every block of trials one movie served as a "standard" and appeared in every trial (randomly on the left or the right of the fixation point). It was paired with a stimulus of another (or occasionally the same) velocity, the "test" stimulus. Within a given block of trials all test stimuli would be of equal lifetime but this "test lifetime" would be different from the lifetime of the standard stimulus. From pilot experiments we decided to keep the difference in lifetime between the test and standard small because otherwise subjects base their response on the saliency of the motion rather than on the perceived velocity.

We used two different data collection procedures:

(a) Method of constant stimuli (MCS). In a random-block design the standard was paired equally often with six or eight different test stimuli. This procedure was used to generate a full psychometric function using a range of velocities for the test stimulus (see Fig. 1) indicating how often subjects chose the standard as being faster.

(b) "Staircase" method. Again subjects were asked to select the faster of two stimuli. We used a modified staircase (Cornsweet, 1962) to determine the threshold for accurate velocity discrimination between stimuli of different point lifetimes (see Fig. 2). In this paradigm the choice of the test stimulus to be paired with the standard for a given trial was determined from the performance of the subject in the preceding trials. The initial stimulus pair was always well above threshold. When the subjects correctly choose the faster stimulus the next stimulus pair would be the same. After five consecutive correct choices the test stimulus velocity was made one step closer to the standard. After every incorrect choice the test stimulus velocity was made one step further from the standard. Using this five down/one up ratio the staircase settled at a threshold of about 83% correct performance. At the beginning of a block of trials, the difficulty was increased with every
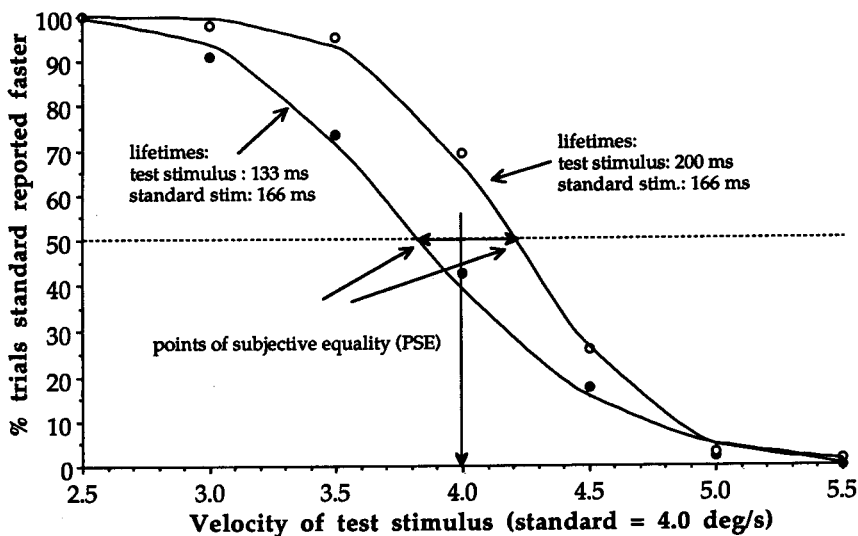
FIGURE 1. Example of two psychometric curves. The frequency at which a subject would report the standard stimulus as being faster is plotted as a function of the velocity of the test stimulus. The standard moved at a velocity of 4 deg/sec and consisted of points with a lifetime of 166 msec while the point lifetime of the test stimulus was either 133 msec (left curve) or 200 msec (right curve). Notice the opposite shift of the two curves away from the center, indicating that for both conditions the subjects overestimated velocity of the stimulus containing shorter lifetime elements.

correct choice in order to converge more quickly towards the threshold level. As soon as the second incorrect response was recorded the five down/one up ration was initiated. Using this approach the threshold was usually reached within a few trials. A single staircase consisted of forty stimulus presentations. The test stimuli were about equally spaced on a logarithmic scale of velocity.

By interleaving two staircases, one starting with the test slower than the standard and the other with the test stimulus faster than the standard, two thresholds were derived from one block of trials. One threshold denotes how much faster than the standard the test stimulus had to be to be reliably discriminated while the other threshold shows how much slower the test stimulus had to be.

This counterbalancing of test speeds made sure that a possible subject bias for or against the standard stimulus (especially in Expt 1b where standard and test stimuli moved in opposite directions) would not affect our results.

Data analysis

The value derived from all our experiments was the "point of subjective equality" (PSE). The PSE is the test velocity which appears the same as the standard velocity. If our lifetime manipulations do not affect perceived velocity the PSE and the standard velocity should be the same. Otherwise the difference between the PSE and the standard velocity is a measurement of the perceived change in velocity created through differences in point lifetime.
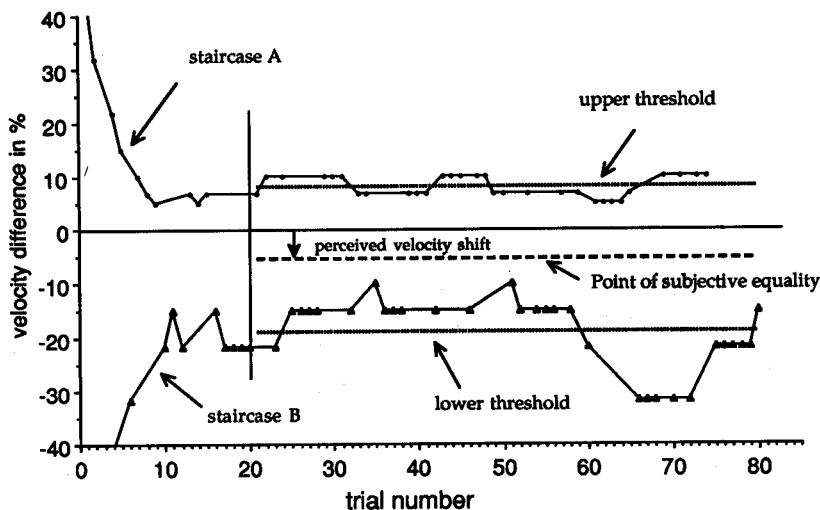

FIGURE 2. Example of a block of trials consisting of two staircase runs. In staircase (A) the test stimulus was always moving faster than the test and in staircase (B) the test pattern was always slower. In this example the point lifetime in the test stimulus was 133 msec. The bottom and top dashed lines denote the respective thresholds while the middle dotted line being equidistant from the two thresholds represents the relative test velocity that appeared of equal velocity as the standard stimulus.

(a) Method of constant stimuli. The percentage of trials in which the standard stimulus was perceived as moving faster was plotted against the test velocity and the data were fitted with a logit function [the integral of a Gaussian (Finney, 1971)] with the log of the velocity as the *x*-axis. The intersection of the psychometric curve with the 50% line is the PSE for the velocity of the standard and the test stimulus. To measure the shift in perceived velocity induced by changing the point lifetime from 133 to 200 msec we added the shifts measured from pairing a stimulus of 133 msec lifetime with one of 166 msec lifetime and the shift measured from pairing a stimulus of 166 msec lifetime with a stimulus of 200 msec lifetime (see Fig. 1).

These lifetimes were also used for the following experiments. They were long enough to allow for good velocity discrimination but short enough to introduce some amount of transiency into the displays. On the other hand the standard and the test pattern lifetimes were always close enough so that naive subjects did not realize that the two patterns presented in each trial had different lifetimes.

Pairing a long lifetime (200 msec) and a short lifetime (133 msec) with an intermediate lifetime (166 msec) allows the measurement of the effect of lifetime for a difference of lifetime too big to be used within one block of trials. Adding the shifts derived from the two conditions enabled us to measure the effect of reducing the lifetime of a pattern by 30% (from 200 msec point lifetime to 133 msec).

(b) "Staircase" method. We measured the thresholds of each of the two staircases by averaging over the last thirty trials of *each* staircase (see upper and lower dashed lines in Fig. 2 for an example). The first ten trials of *each* staircase were ignored so as to allow the staircase to approach threshold. The PSE can be derived by taking the middle between the two thresholds. From blocks of trials using test lifetimes of 133 and 200 msec and standard lifetimes of 166 msec two such shifts can be derived and were added to derive the perceived shift of velocity between lifetimes of 133 and 200 msec.

RESULTS

Experiment 1: effect of comparing stimuli of different lifetimes

(a) Method of constant stimuli. In order to assess the role of point lifetime upon perceived velocity we measured points of subjective equality (PSE) for patterns of different lifetime. The subjects were two of the authors and five naive observers.

The left part of Fig. 3 shows the results using 4 deg/sec as the standard velocity. All subjects show a speedup at shorter lifetimes.

We repeated the measurements for a standard velocity of 12 deg/sec (right part of Fig. 3). Although the apparent speedup is positive in all but two cases the effect is clearly weaker than that observed using a standard velocity of 4 deg/sec.

(b) "Staircase" method. In order to minimize the effects of training, to quickly get data from many subjects, and to replicate our results with another method of data collection we used the staircase method explained in the Method section. Here the standard always moved at 6 deg/sec. We obtained results for two dot densities and a condition in which the standard moved upwards (the test stimulus moved downwards in all our experiments).

Figure 4 illustrates the results from five naive observers and one of the authors. Again we found that decreasing the point lifetime on all tasks increased the perceived velocity and that the effect was stronger with higher dot densities. For some subjects there seems to be a smaller speedup in the condition that pairs oppositely moving stimuli. So far we have no explanation for this aspect of our results.

It is interesting to note that the thresholds for discriminating the velocities of two patterns moving in the same direction and the thresholds for the case of opposite direction of motion were very similar as can be seen in Fig. 5. The thresholds are somewhat higher than those reported by other researchers (McKee, 1981; Orban *et al.*, 1984; Snowden & Braddick, 1991) but it should be
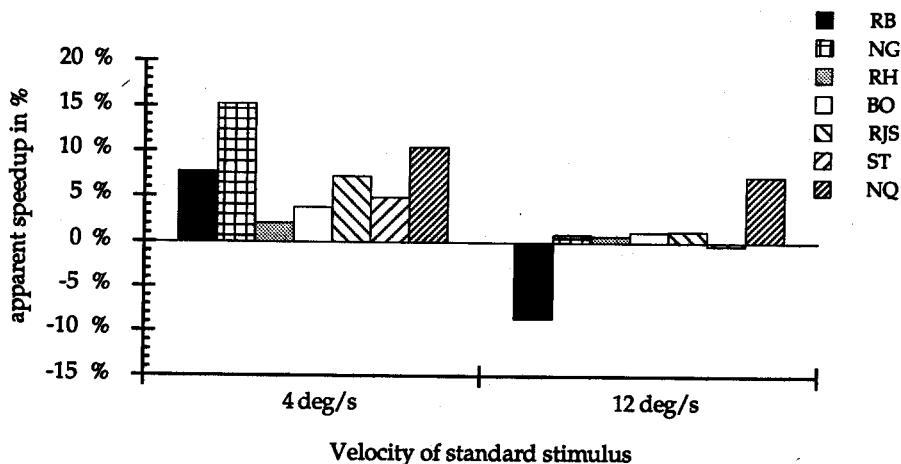
FIGURE 3. Apparent speedup comparing patterns with 133 msec point lifetimes against pattern with 200 msec point lifetime for two standard velocities. Note the much smaller effects for the higher velocity.
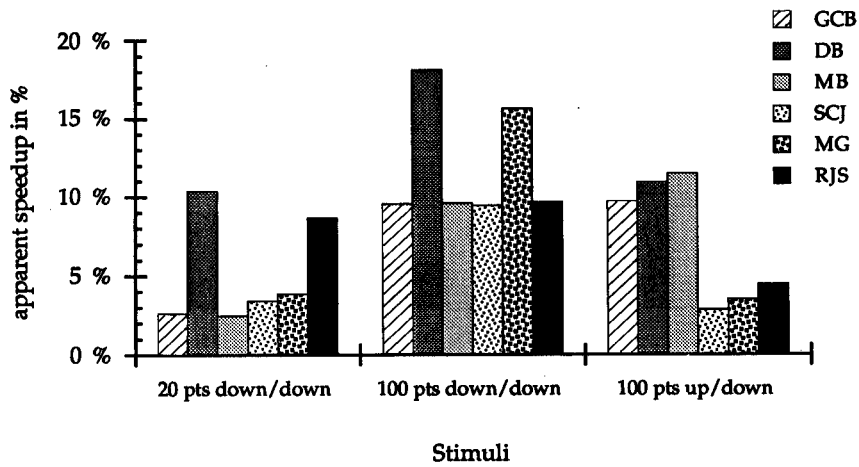
FIGURE 4. Comparison of the speedup observed at two different dot densities and in a condition in which one stimulus moved down while the other moved up. The standard moved at 4 deg/sec in all these conditions.
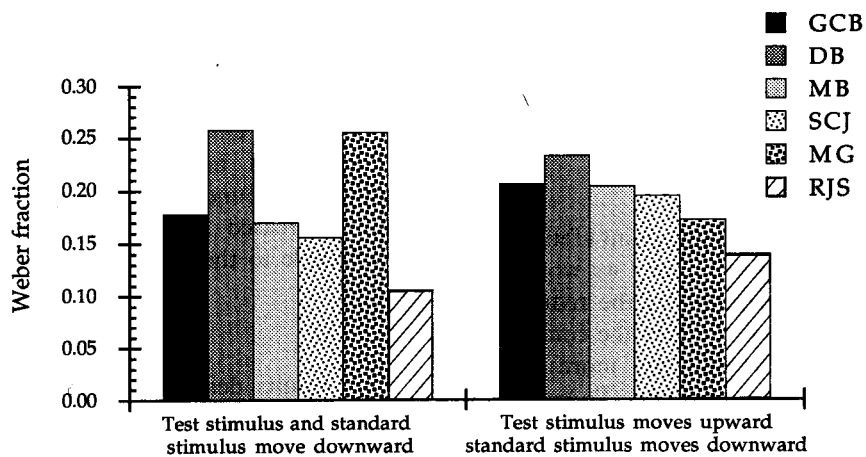

FIGURE 5. Weber fraction for velocity discrimination for the two conditions on the right of Fig. 4. The data on the left were obtained when both the test and the standard pattern moved in the same direction. The data on the right were obtained when the standard and the test patterns moved in opposite directions. The Weber fraction was determined from the logit fit to the psychometric curve (see Fig. 1) by measuring the relative distance from the 50% point to the points where the logit fit crossed the 17 or 83% point.

noted that our stimuli (a) have short lifetimes, (b) are presented simultaneously and in eccentric locations, and most importantly (c) that the subjects received little prior training (except for subject RJS, which also showed the lowest thresholds).

(c) Control. It is conceivable that the observed speedup in our experiments is due to false matches between disappearing and reappearing points in the display. If a point in the display disappears at the end of its lifetime and another point gets replotted at a nearby position the visual system might assume that the disappearing point has moved to the location of the newly appeared point (Minimal Mapping Theory, Ullman, 1979). Such a jump would generally be much bigger than the displacements of a moving point between frames and would thus correspond to a much higher velocity. But since the direction of these matches is random they would tend

to cancel each other resulting in zero net motion. Only if solely those jumps that are in the general direction of overall motion, i.e. down ("down jumps") ("motion inertia", Ramachandran & Anstis, 1983, 1985; Grzywacz, Smith & Yuille, 1989) are considered and somehow incorporated into the overall velocity estimate, patterns containing more jumps (i.e. patterns with shorter point lifetimes) should appear faster. To rule out this explanation for our finding we generated a stimulus variation in which we maximized or minimized the effect a change in lifetime should have (assuming that the above described effect is the basis of our observed speedup). This was achieved by shifting every point when it was replotted at the end of its lifetime by half of the pathlength traveled during its lifetime (i.e. the shifts were between ~16 and 24 min arc depending on the point lifetime used*) in (down) or against (up) the direction of motion. If the "down jumps" are the basis for the speedup then the condition in which all points jump down should lead to a strong speedup while the condition in which all points jump up should minimize the effect of decreasing lifetime on perceived velocity. We

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*Since these values are smaller than the average distance between neighboring points in the display (~27 min arc) it will assure that if false matches indeed play an important role they will be dominated by the points replotted in this manner.
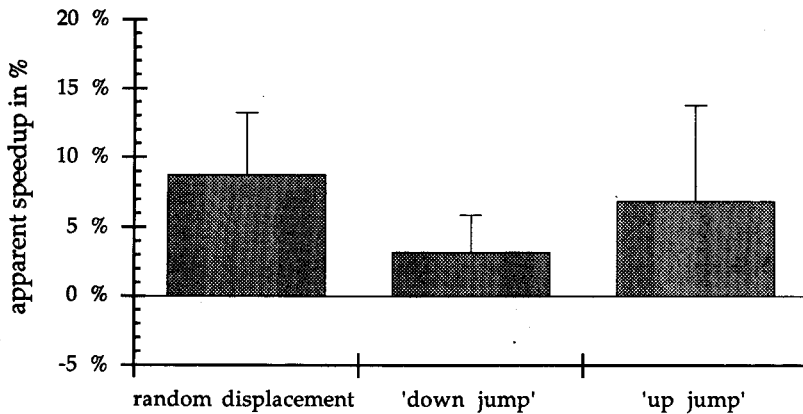
FIGURE 6. Results of a control experiment in which the stimulus elements were not randomly replotted at the end of their lifetime but rather displaced *in* ("down jump") or *against* ("up jump") the direction of overall motion. See text for details. The columns reflect the average result of four subjects and the error bars reflect the standard deviation.

used the method of constant stimuli. The results as plotted in Fig. 6 show no systematic effect of maximizing or minimizing possible false matches. Our results therefore do not support the speedup being due to "false matches".

Experiment 2: "temporal capture"

Having established that decreasing point lifetimes may lead to an increase in perceived velocity we wondered if this effect was directly determined by the reduction in lifetime of the moving points or rather the concomitant increase in "transiency" through the more frequent appearance and disappearance of points. To test this we modified our stimuli by increasing transiency without changing the point lifetime of the moving points.

Specifically, we paired stimuli in which point lifetimes of the moving points were equal but in one pattern the amount of transiency was increased by replacing a few of the moving points with *stationary* ones of very short lifetime (33 msec). Such points introduce a transient signal and we were interested to see if this transient signal would be "captured" by the moving points and incorporated into the velocity estimate.

Again we took care to keep the difference in transiency so low that no difference between the standard and the test patterns was obvious. In order to compare these results with those derived from the previous experiments we chose stimuli whose transiency, i.e. the number of times points would turn off and on during the stimulus duration, was the same as for the experiments using patterns with differing point lifetimes. The stimuli for the two conditions were as follows (note that in each pair the lifetime of the moving points is equal). (a) One stimulus contained 100 moving points of 166 msec while the other contained 90 moving points of the same lifetime as well as 7 stationary points of only 33 msec lifetime;* (b) one

stimulus contained 100 moving points of 200 msec while the other contained 90 moving points of the same lifetime as well as 5 stationary points of only 33 msec lifetime.† The methods were identical to the earlier experiment in all other respects.

The results are shown in Fig. 7. Using both methods we found that the addition of these stationary points increased the perceived velocity by an amount comparable to the results derived from Expt 1.

DISCUSSION

Our results demonstrate that the addition of extra transient information into a display moving at moderate velocity gives rise to an increase in the perceived velocity of that stimulus. This suggests that the perceived velocity of a stimulus is influenced by its temporal frequency spectrum, i.e. the perception of velocity seems to be based upon a global process in which the overall transiency of the stimulus is taken into account. Indeed it is as if the movement of the pattern "captures" the transient information provided by the onset and offset of the points. This is illustrated by the fact that the transiency caused by the addition of brief stationary points is also captured by the moving pattern and used in the velocity estimate. We term this phenomenon "temporal capture" and note its possible relationship to "motion capture" where a coherently moving pattern may capture an incoherent one so that both appear to move together (MacKay, 1961; Ramachandran & Cavanagh, 1987).

The temporal capture phenomena is all the more striking because the points which speedup the pattern can in fact be stationary! Furthermore the temporal energy introduced by the stationary points is non-directional. In models like Adelson and Bergen's (1985) spatiotemporal energy model which oppose motion in opposite directions such a non-directional influence would not pass the opposing stage. It is conceivable though that the non-directional energy introduced by the few stationary points alone is not strong enough to activate the channels for the opposite direction (in our case upwards) and the increased activity in the channel for downward motion gets passed on through

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*We chose this combination since it results in the same number of points being replotted per unit time as in our 100 point pattern with 133 msec lifetime.

†We chose this combination since it results in the same number of points being replotted per unit time as in our 100 point pattern with 166 msec lifetime.
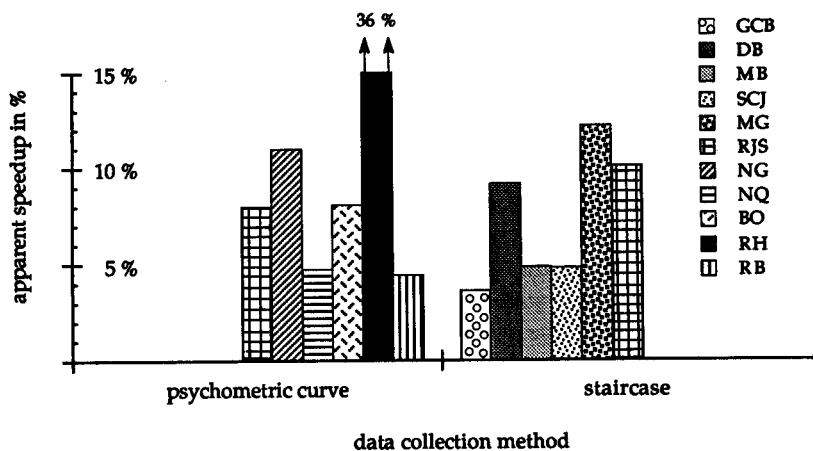
FIGURE 7. Temporal capture: apparent speedup of patterns containing stationary points of very short lifetimes measured with both of the methods employed earlier. Left data collection method is described in Fig. 1 and right method is described in Fig. 2. Arrows denote a bar extending beyond the scale of the graph.

the opposing stage. In this case Adelson and Bergen's model *would* show a speedup.

Another possibility is that the visual system first extracts the direction of motion of a pattern and then compares the activity between channels tuned for different temporal frequencies to extract a velocity measurement. Such a process in which the measured velocity gets "tagged" onto the perceived direction of motion would also account for our results. (These channels might even be influenced by non-directional temporal energy as suggested by our finding of "temporal capture".)

There is some evidence supporting the involvement of non-directional mechanisms in motion/velocity perception. Watson, Thompson, Murphy and Nachmias (1980) report some summation occurring at threshold between gratings that move in opposite directions. Anstis, (1988) reports that following adaptation to a spatially uniform flickering field the drift rate of a moving random-dot field is apparently slowed. He suggests that the adapting stimulus activates transient channels that respond to high temporal frequencies and dynamic visual stimuli (Ferrera & Wilson, 1985). Also Ferrera and Wilson (1991) recently proposed a model for velocity coding that uses non-directional filters as input and predicts an increase of perceived velocity with increasing temporal frequency. Such a speedup albeit small has been observed for moving sine wave gratings by McKee, Silverman and Nakayama (1986).

Grzywacz and Yuille (1990) discuss two implementations of their model for estimating image velocity, the "ridge strategy" and the "estimation strategy". Both try to find a line (plane) in the space of spatial and temporal frequencies which crosses the origin and that is most consistent with the stimulus. The ridge strategy uses a winner-take-all mechanism to determine the image velocity by selecting the velocity tuned cells with the largest response. The estimation strategy on the other hand computes the image's velocity by finding the centers of the motion-energy distribution for several spatial frequencies and fitting a line (plane) through these centers. This strategy is one possible implemen-

tation of the two-channel hypothesis introduced earlier (which could also be implemented with more than just two channels). Since the peak temporal frequency component in the transient component of our stimulus is independent of the spatial frequency the transiency in our stimulus is a horizontal line (plane) in the space of temporal and spatial frequencies. This line (plane) intersects the line (plane) generated by the moving points which crosses the origin and has a slope proportional to the velocity of the moving points. Since the transient component in our stimulus presumably has rather low motion energy the most active velocity cell for any given spatial frequency will be the one responding to the moving component of our stimulus. Thus a system using the ridge strategy might be little influenced by the introduction of transiency into moving patterns. The centre of the motion-energy distribution as computed by the estimation strategy (at least in its simplest form) on the other hand will be shifted by the introduction of transient energy. In fact this strategy would show the strongest speed-up for the lowest stimulus velocities and possibly even a slow-down for very high stimulus velocities. Our results thus suggest that the visual system when faced with a stimulus containing several peaks in its temporal frequency distribution at a given spatial frequency does not just extract the highest peak but is influenced by the other peaks in the spectrum.

A possibly related effect to our findings has been reported by Giaschi and Anstis (1989). These authors found that apparent motion between two points successively displayed appears faster if a blank interval (ISI) is introduced between the illumination of each point by shortening the time the individual points are on. They interpret this result in terms of the "on-time" of each point producing a stationary signal—thus the greater the "on-time" the shorter the time the stimulus appears to move. Their results might reflect a similar mechanism at work as in our experiment since it too can be explained within the framework of combining spatiotemporal frequency channels to extract velocities. By increasing the on-time the amplitude of the low temporal frequency

components will increse and thus the activity in the low temporal frequency channel(s) will increase with respect to the high temporal frequency channel(s) and thus such a stimulus will be interpreted as moving slower.

Furthermore Halpern and Blackstock (1991) report a phenomenon that resembles our observation. They measured the perceived velocity of moving stereoscopic gratings. Perceived velocity of the stereoscopic grating was higher when the points that made up the grating were in random motion than when they were stationary. Since the temporal frequency spectrum of the stimulus containing points in motion is shifted to higher frequencies this result is in agreement with our findings.

The use of temporal frequency channels to extract velocity information might not be restricted to the visual system. There is recent evidence that a similar mechanism might operate in the somatosensory system. Katz, Gizzi, Gardner and Malach (1990) showed that tactile stimuli which were moved over the skin of human subjects were perceived faster when the duration of the movement was shorter.

In summary our results suggest that the transiency of a motion stimulus plays an important role in the determination of its perceived velocity. Such a notion is consistent with recently formulated psychophysical models of velocity perception which include the comparison of activity within at least two temporal frequency channels for any given spatial frequency.

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.

Anstis, S. M. (1988). Models and experiments on directional selectivity. In Elsendoorn, B. A. G. & Bouma, H. (Eds), *Working models of human perception* (pp. 233–249). London: Academic Press.

Campbell, F. W. & Maffei, L. (1979). Stopped visual motion. *Nature, 278*, 192.

Cornsweet, T. N. (1962). The staircase-method in psychophysics. *American Journal of Psychology, 75*, 485–491.

Ferrera, V. P. & Wilson, H. R. (1985). Spatial frequency tuning of transient non-oriented units. *Vision Research, 25*, 67–72.

Ferrera, V. P. & Wilson, H. R. (1991). Perceived speed of moving two-dimensional patterns. *Vision Research, 31*, 877–893.

Finney, D. J. (1971). *Probit analysis*. Cambridge: Cambridge University Press.

Giaschi, D. & Anstis, S. (1989). The less you see it, the faster it moves: Shortening the "on-time" speeds up apparent motion. *Vision Research, 29*, 335–347.

Grzywacz, N. M. & Yuille, A. L. (1990). A model for the estimate of local image velocity by cells in the visual cortex. *Proceedings of the Royal Society of London B, 239*, 129–161.

Grzywacz, N. M., Smith, J. A. & Yuille, A. L. (1989). A common theoretical framework for visual motion's spatial and temporal coherence. *Proceedings of the IEEE Workshop on Visual Motion*, 148–155.

Halpern, D. L. & Blackstock, S. (1991). What determines perceived velocity of stereoscopic motion? *Investigative Ophthalmology and Visual Science (Suppl.), 32*, 695.

Holub, R. A. & Morton-Gibson, M. (1981). Response of visual cortical neurons of the cat to moving sinusoidal gratings: Response-contrast functions and spatiotemporal interactions. *Journal of Neurophysiology, 46*, 1244–1259.

Katz, E., Gizzi, M. S., Gardner, E. P. & Malach, R. (1990). Perceived speed varies inversely with length of the motion path: A multisensory illusion. *Society for Neuroscience Abstracts, 16*, 104.

MacKay, D. M. (1961). Visual effects of non-redundant stimulation. *Nature, 192*, 739–740.

McKee, S. P. (1981). A local mechanism for differential velocity detection. *Vision Research, 21*, 491–500.

McKee, S. P., Silverman, G. H. & Nakayama, K. (1986). Precise velocity discrimination despite random variations in temporal frequency and contrast. *Vision Research, 26*, 609–619.

Movshon, J. A., Thompson, I. D. & Tolhurst, D. J. (1978). Spatial and temporal contrast sensitivity of neurons in area 17 and 18 of the cat's visual cortex. *Journal of Physiology, London, 283*, 101–120.

Nakayama, K. (1985). Biological image motion processing: A review. *Vision Research, 25*, 625–660.

Orban, G. A., De Wolf, J. & Maes, H. (1984). Factors influencing velocity coding in the human visual system. *Vision Research, 24*, 33–39.

Pantle, A. J. (1974). Motion aftereffect magnitude as a measure of the spatio-temporal response properties of direction-sensitive analyzers. *Vision Research, 14*, 1229–1236.

Ramachandran, V. S. & Anstis, S. M. (1983). Extrapolation of motion path in human visual perception. *Vision Research, 23*, 83–85.

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

Ramachandran, V. S. & Cavanagh, P. (1987). Motion capture anisotropy. *Vision Research, 27*, 97–106.

Sekuler, R., Pantle, A. & Levinson, E., Held, R., Leibowitz, H. W. & Teuber, H. (1978). Physiological basis of motion perception. *Perception. Handbook of sensory physiology* (Vol. VIII, pp. 67–98). Berlin: Springer.

Smith, A. T. (1990). Variations in the perception of velocity according to the spatial structure of the image. *British Telecom Conference: "Applying visual psychophysics to user interface design"*.

Snowden, R. J. & Braddick, O. J. (1991). The temporal integration and resolution of velocity signals. *Vision Research, 31*, 907–914.

Thompson, P. (1982). Perceived rate of movements depends on contrast. *Vision Research, 22*, 377–380.

Thompson, P. (1983). Discrimination of moving gratings at and above detection threshold. *Vision Research, 23*, 1533–1538.

Thompson, P. (1984). The coding of velocity of movement in the human visual system. *Vision Research, 24*, 41–45.

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

Watson, A. B., Thompson, P. G., Murphy, B. J. & Nachmias, J. (1980). Summation and discrimination of gratings moving in opposite directions. *Vision Research, 20*, 341–347.

Wright, M. J. & Johnston, A. (1985). Invariant tuning of motion aftereffect. *Vision Research, 25*, 1947–1955.