



# Temporal integration of optic flow, measured by contrast and coherence thresholds

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## Abstract

We measured, as a function of exposure duration, contrast sensitivity and coherence sensitivity for discerning the direction of motion of random dot patterns moving in circular, radial or translational directions. Contrast sensitivity for these patterns increased linearly with exposure duration, up to about 200–300 ms, consistent with previous estimates of temporal summation of early motion units. Coherence sensitivity, however, showed much longer summation periods, about 3 s. When the stimulus was embedded within 10 s of noise, sensitivity increased with duration up to 2–3 s, approximately linearly, as expected from an ideal integrator. When presented without the noise period, sensitivity also increased, but in a different way. For radial and circular motion the increase tended towards the theoretically predicted square root relationship for the same duration as that found with the embedded noise (about 3 s). For translation, however, the curve was steeper than the theoretical prediction (nearly linear), and the summation estimates of around 1000 ms. When the duration of the target was constant at 200 ms, but that of the flanking noise varied, sensitivity decreased with total duration over a similar interval. We interpret our results to reflect at least two stages of analysis, a threshold-limited early stage of local-motion analysis, with a time constant of 200–300 ms, and a later global-motion integration stage with a much longer time constant, around 3000 ms. There may also exist an intermediate stage, with an integration time of around 1000 ms. © 2001 Elsevier Science Ltd. All rights reserved.

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## 1. Introduction

The visual system does not work on instantaneous information, but integrates over time, presumably to increase signal to noise levels (e.g. Barlow, 1958). Integration occurs both for stationary objects and moving objects, with very similar time constants (Burr, 1981).

Many techniques have been used to study temporal integration, the most common being to measure luminance increments or contrast sensitivity for spots or gratings as a function of presentation duration (e.g. Barlow, 1958; Watson, 1979; Burr, 1981). These techniques typically yield estimates of integration time in the order of 100–200 ms. Similar estimates are ob-

tained for contrast sensitivity of random-dot moving stimuli (e.g. Fredericksen, Verstraten, & van de Grind, 1994a,b). Other performance measures for motion perception, such as speed discrimination, also give estimates of integration times of this order (McKee & Welch, 1985; Snowden & Braddick, 1991). Even quite different techniques, such as measuring the maximum duration over which sequential pattern information can be integrated (Hogben & DiLollo, 1974), or directly sampling the number of visible dots in a random dot field (Ross & Hogben, 1974) give estimates of critical duration of this order.

Under other circumstances, however, quite different estimates can be obtained. For example, Watamaniuk and colleagues have shown that motion coherence thresholds for direction discrimination of random dot patterns improve for over 500 ms (Watamaniuk, Sekuler, & Williams, 1989; Watamaniuk & Sekuler,

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1992). They suggested that these longer integration times reflect properties of higher motion centres that integrate local motion information. Neri, Morrone, and Burr (1998) also found very long integration times, both for simple translation (around 700 ms) and for biological motion (around 2000 ms).

To date no study has investigated temporal summation for optic flow stimuli, the patterns of motion that occur on our retinæ when we navigate through the environment. In this study we have investigated temporal summation for radial, circular and translational motion, by measuring both signal-to-noise and contrast thresholds. The contrast thresholds show relatively short integration times for all types of motion, about 200 ms, consistent with previous studies. However, the signal-to-noise thresholds (that probably tap higher integration areas) show very long temporal integration, of 2000–3000 ms. These results have been reported in abstract form (Santoro & Burr, 1999).

## 2. Methods

### 2.1. Stimuli

The stimuli comprised 200 randomly positioned dots, caused to move coherently along a radial, circular or translational trajectory. Radial and circular motion is best described in polar co-ordinates,  $r$  and  $\theta$ , the radial and angular velocities of the dot (in degrees of visual angle and radians per second, respectively):

$$\dot{r} = v \cos \phi$$

$$\dot{\theta} = (v/r) \sin \phi \quad (1)$$

where  $v$  is local speed ( $4.7^\circ \text{ s}^{-1}$ ) and  $\phi$  defines the type of motion:  $0$  and  $180^\circ$  define expansion and contraction (respectively), and  $90$  and  $270^\circ$  clockwise and counter-clockwise rotation. Note that the local speed does not vary with distance from the origin (as it would for rigid rotation), but is constant for all positions (because of the normalisation by radius) so it can be compared with translation. For translation, each dot moved in the same (vertical) direction at velocity  $v$ . For radial and circular motion, the dots were confined to a  $10^\circ$  diameter circle, with a central hole of  $1.5^\circ$  (to avoid clustering of contracting stimuli). For translation, they were confined to a square  $10$  by  $10^\circ$ . Half the dots were white (increments) and half black (decrements), all subtending  $5$  pixels ( $14$  min arc).

In all cases the dots moved for a limited lifetime of three frames, after which they were reborn in a new random location. One-third of the dots (or more generally, 1 per lifetime) died and were reborn on each frame. If a dot moved outside the confines of the display during its lifetime, it was reborn in a new random position.

Stimuli were generated on the face of a Barco Calibrator Monitor under the control of a Cambridge Research Systems VSG2/4 framestore. The framerate of the monitor was 200 Hz and the mean luminance of the background was  $20 \text{ c deg}^{-1} \text{ m}^{-2}$ . Dots remained in their position for five video frames (25 ms), so the effective framerate of dot motion was 40 Hz.

### 2.2. Procedure

Motion quality was degraded in two ways: by reducing contrast or by reducing coherence levels. For contrast thresholds, all dots moved along a coherent trajectory, and their Michelson contrast varied to home in on threshold. For the motion coherence thresholds, Michelson contrast was held constant at 95%, and the coherence level of the stimuli varied, by causing a portion of the dots (noise dots) to appear at random on each frame, rather than follow the motion trajectory. The total number of dots was always constant (200). The noise dots appeared in new random positions on each frame (lifetime of 1).

Both contrast and coherence thresholds were measured for direction discrimination. The stimulus was presented only once, and subjects had to identify its direction of motion from one of two known opposite motions: expansion from contraction, clockwise from anticlockwise rotation or upward from downward translation. Either the contrast or the proportion of coherently moving dots was varied dynamically by the QUEST routine (Watson & Pelli, 1983), which homed in near threshold. Thresholds were then calculated offline, by fitting probability of seeing curves with a cumulative Gaussian function, and estimating the 75% criterion. In all conditions at least five separate QUEST sessions were run, each with 30 trials.

### 2.3. Subjects

Both subjects were young females (25 years old), with corrected normal vision. LS is an author, while FP was naïve of the goals of the study.

## 3. Results

### 3.1. Contrast sensitivity

Contrast sensitivity (the inverse of Michelson contrast thresholds) for direction discrimination of optic flow motion is plotted as a function of stimulus duration in Fig. 1. The curves on the left refer to discrimination thresholds for vertical translation, in the centre for circular motion and at right for radial motion. The data for both subjects, for all three types of motion are very similar. They first increase steeply, up till around 200

ms, then flatten off. The data of this and the following graphs have been fitted with the twin-limb function of the form:

$$S(t) = \begin{cases} S_0(t/t_0)^p & t \leq t_0 \\ S_0 & t \geq t_0 \end{cases} \quad (2)$$

where  $S(t)$  is sensitivity (in this case *contrast sensitivity* the inverse of the contrast threshold) as a function of exposure duration  $t$ .  $S_0$  is sensitivity for infinite duration (effectively a scaling constant), and  $p$  the slope of the function (on logarithmic co-ordinates) up to the critical summation duration  $t_0$ .

When  $p$  is set appropriately, Eq. (2) describes a simple model of summation up to a critical duration  $t_0$ . For linear summation of contrast thresholds (Block's Law), the slope of the curve must be set to unity ( $p = 1$ ). The parameters  $S_0$  and  $t_0$  were determined by best fit of Eq. (2) to the data of Fig. 1 (simplex procedure). The estimated values of  $t_0$  are indicated by the arrows at the abscissae, and by the white bar graphs of Fig. 4. For both subjects, for all three types of motion, the critical durations were between 200 and 300 ms (geometric mean 246 ms), similar to previous contrast sensitivity estimates of temporal summation for motion discrimination.

### 3.2. Coherence thresholds

We next measured coherence thresholds (minimum proportion of coherently moving dots) as a function of stimulus duration, for the three types of motion. In the first experiment, the stimulus was embedded within

pure random noise, so that the total display lasted 10 s, irrespective of the duration of the stimulus containing the signal. The purpose of the noise was to increase the theoretical dependence on duration (see below), allowing for a more precise estimate of critical duration. The results are shown in Fig. 2, for translation, rotation and radial motion. Sensitivity (inverse of thresholds) increased linearly for a period, before levelling off, as with the contrast thresholds. However, the period of strong summation was much longer than that for contrast thresholds.

To quantify the summation, the data were again fit with Eq. (2). As with the contrast thresholds,  $p$  was set to 1, and  $S_0$  and  $t_0$  were free to vary. The value  $p = 1$  is what is expected from an ideal linear integrator producing constant signal to noise ratios at threshold. As each trial was presented within a 10 s noise interval, the total number of dots for each trial, was always constant. If we assume, as a first approximation, that noise is given by the total number of dots, noise will be constant in this condition and thresholds should be related linearly to the duration of the signal (see Barlow & Tripathy, 1997, for a more detailed theoretical treatment of signal detection predictions for random-dot motion). As with the contrast thresholds, Eq. (2) with  $p = 1$  fit the data well (when  $p$  was allowed to vary, it never deviated from unity by more than 10%). The values for critical duration  $t_0$  of this function (indicated by the arrows on the abscissae) are very high, in the order of 2–3 s, 10 times the estimate for contrast sensitivity.

We performed two further experiments with coherence thresholds, to confirm the lengthy integration periods. Firstly, we measured coherence thresholds as a

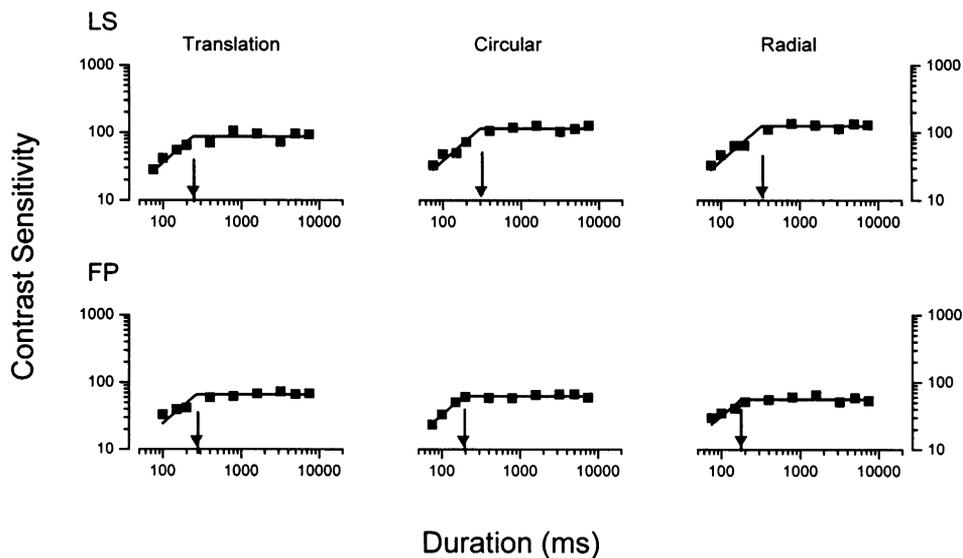


Fig. 1. Contrast sensitivity (inverse of Michelson contrast thresholds) as a function of stimulus duration for direction discrimination of vertical translation (left), rotation (centre) and radial motion (right). Standard errors were about half the size of symbols. The twin-limb functions are the best fit of Eq. (2), with  $p$  set to unity. The values of the critical duration  $t_0$  are indicated by the arrows, and also plotted in Fig. 4. The values of  $\chi^2$  for translation, circular and radial motion were 135, 82 and 106 for LS and 36, 11 and 32 for FP.

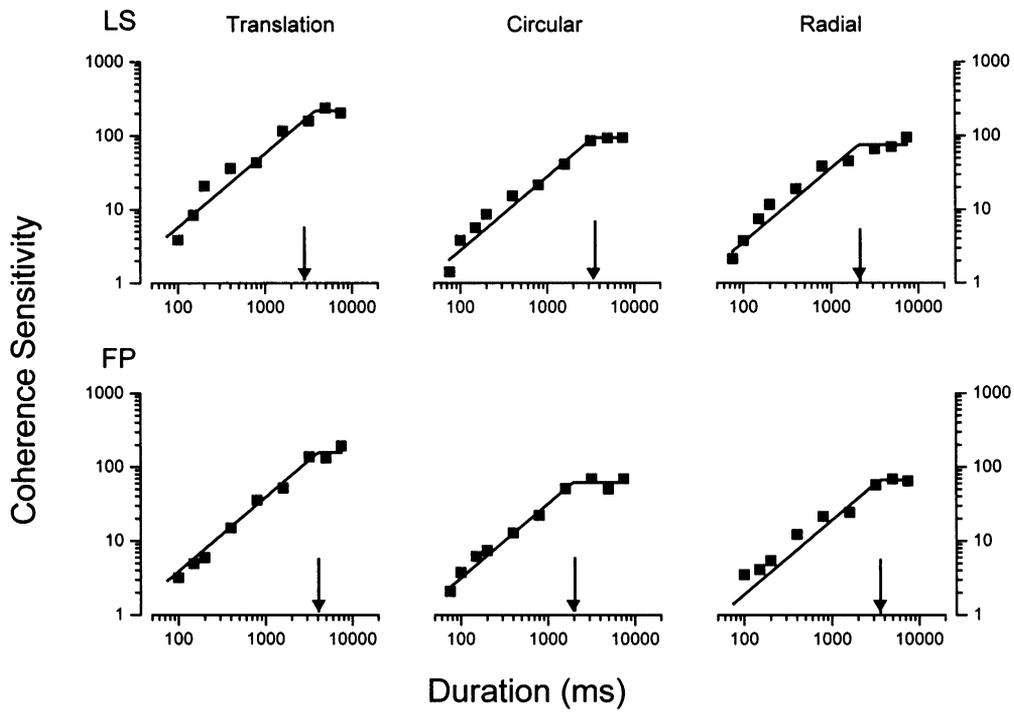


Fig. 2. Sensitivity for motion coherence (inverse of coherence thresholds) as a function of stimulus duration for direction discrimination of vertical translation (left), rotation (centre) and radial motion (right). Each trial was embedded within a 10 s period of noise. Standard errors for this plot, and those of Figs. 3 and 5, were about the size of symbols. The twin-limbed functions are the best fit of Eq. (2), with  $p$  set to unity. The values of the critical duration  $t_0$  are indicated by the arrows, and also plotted in Fig. 4. The values of  $\chi^2$  for translation, circular and radial motion were 484, 5 and 92 for LS and 295, 33 and 16 for FP.

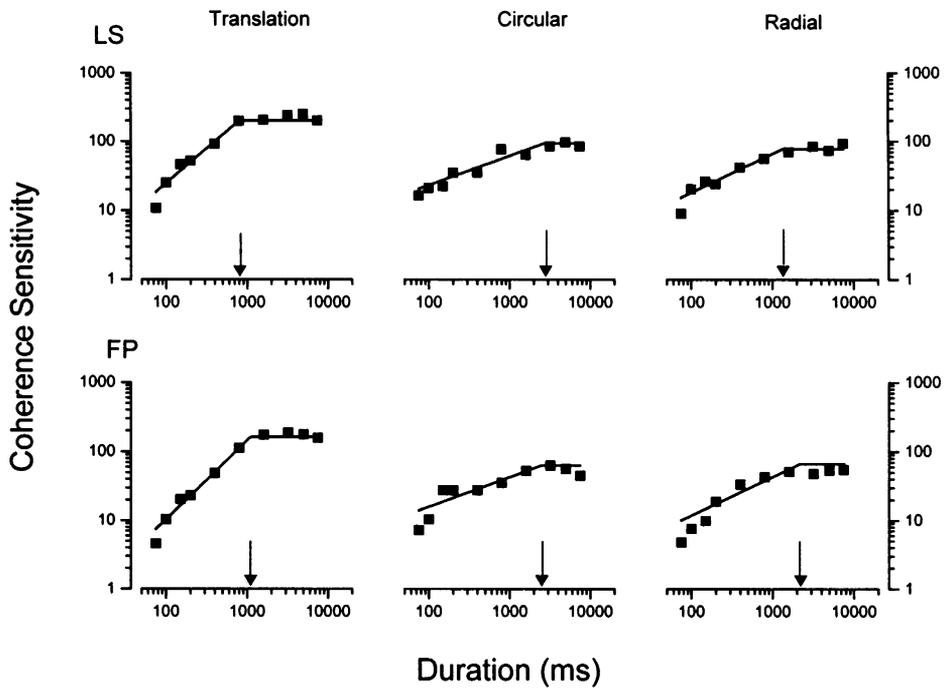


Fig. 3. Sensitivity for motion coherence as a function of stimulus duration for direction discrimination, without the flanking noise. The two-limbed functions are the best fits of Eq. (2), with  $S_0$  fixed from the estimate of Fig. 2, and  $t_0$  and  $p$  free to vary. The arrows indicate the estimates of  $t_0$  (also replotted in Fig. 4). The best-fitting values of parameter  $p$  for translation, circular and radial motion were: 1.00, 0.42 and 0.44 for LS and 1.15, 0.43 and 0.56 for FP.  $\chi^2$  for translation, circular and radial fits was 532, 106 and 50 for LS and 120, 73 and 108 for FP.

function of duration without the surrounding noise, to check that it was not the noise itself producing an artificially high estimate. The results (Fig. 3) show that for all three types of motion, sensitivity increases with duration over an extended period. However, for circular and radial motion, the increase was more gradual than that shown in Fig. 2.

The theoretical predictions are different in this experiment from when the stimulus is encased in noise: here both the number of coherent dots and the total number of dots vary with duration within the integration period, so both the signal and the variance of the noise should increase linearly with duration. As signal-to-noise ratios vary with the standard deviation of noise, thresholds should therefore vary with the *square root* of duration up to the critical duration, implying  $p = 0.5$  in Eq. (2) (see also Barlow & Tripathy, 1997).

For very long stimulus presentations (10 s), the stimuli are physically identical to those of Fig. 2, so  $S_0$  of Eq. (2) should be the same in both cases. We therefore fixed  $S_0$  to the values estimated from Fig. 2, and allowed  $t_0$  and  $p$  to vary. The best fitting values of the slope parameter  $p$  are given in the caption. For radial and circular motion, the values ranged from 0.42 to 0.56 (mean 0.46), quite close to the theoretical prediction of 0.5. For translation, however, the slopes were around unity, 1.0 and 1.1 for LS and FP. Possible explanations for this clear difference will be considered later. The estimates of the integration period  $t_0$  are indicated by the arrows on the abscissae.

Fig. 4 compares the estimates of  $t_0$  for the three conditions reported so far, contrast sensitivity and coherence sensitivity with and without flanking noise. The

dashed lines show the geometric means of  $t_0$  for contrast sensitivity and for coherence sensitivity with surrounding noise. For both subjects the difference was around 1 logarithmic unit. For circular and radial motion, the coherence estimates without noise were similar to those with noise, well within the estimate errors for both subjects. However, the estimates for translation were clearly different, that without noise being around one-third of that with noise, a point to be taken up in the discussion.

The final experiment was designed to test whether sensitivity could decrease as a result of integration. In this case the coherent stimulus was of constant duration (200 ms), embedded within flanking noise of variable duration. If integration is obligatory, the prediction of an ideal integrator is that sensitivity should *decrease* with total duration, following a square root law ( $p = -0.5$ ), as the noise should increase with the square root of the total duration, while the signal remains constant. Provided that subjects cannot learn to ignore the period outside the central signal, the decrease should occur for the entire period of integration.

The results of Fig. 5 show that sensitivity decreased with stimulus duration, over a fairly extensive period. Again, as the curves are quite shallow, making it hard to derive the critical distance, we fixed  $t_0$  with the parameters from Fig. 2, and allowed  $S_0$  and  $p$  to vary. The values of  $p$  are reported in the caption. These values (mean  $-0.44$ ) are slightly less than the theoretical prediction of  $-0.5$  for an ideal integrator, but nevertheless suggest that the noise is compulsorily integrated over an extended period, in the order of seconds.

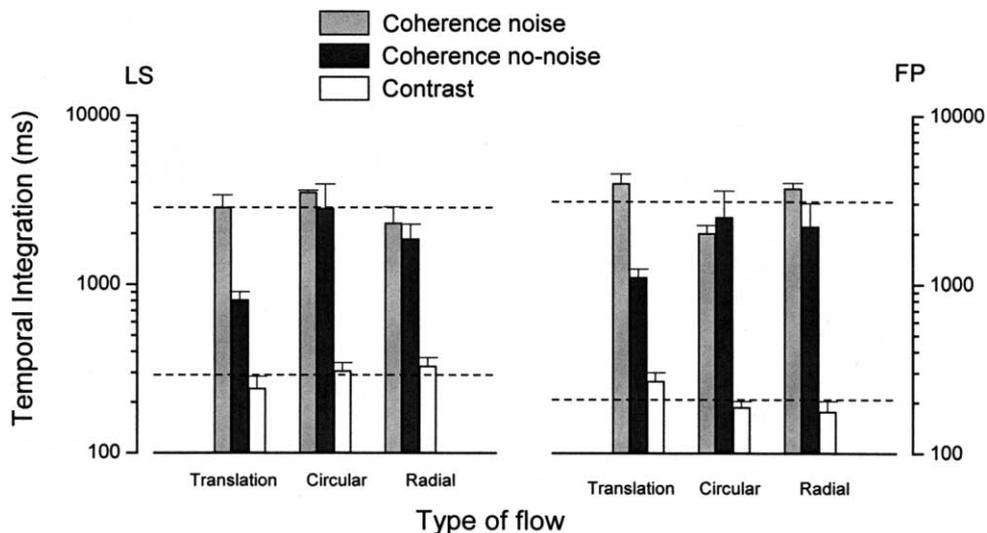


Fig. 4. Estimates of  $t_0$ , the critical duration of summation for contrast sensitivity and coherence sensitivity, for the two observers for the three conditions. The error bars refer to the error of the fit. The dashed lines show the geometric mean for the critical durations estimated from contrast sensitivity and for coherence sensitivity with the flanking noise. For both subjects, critical duration for coherence was about 10 times longer than for contrast sensitivity. The estimates without noise depended on stimulus type. For circular and radial stimuli, these estimates were similar to those with noise, within the range of the error bars. For translation, however, the estimates were near 1000 ms, about a third that estimated with noise.

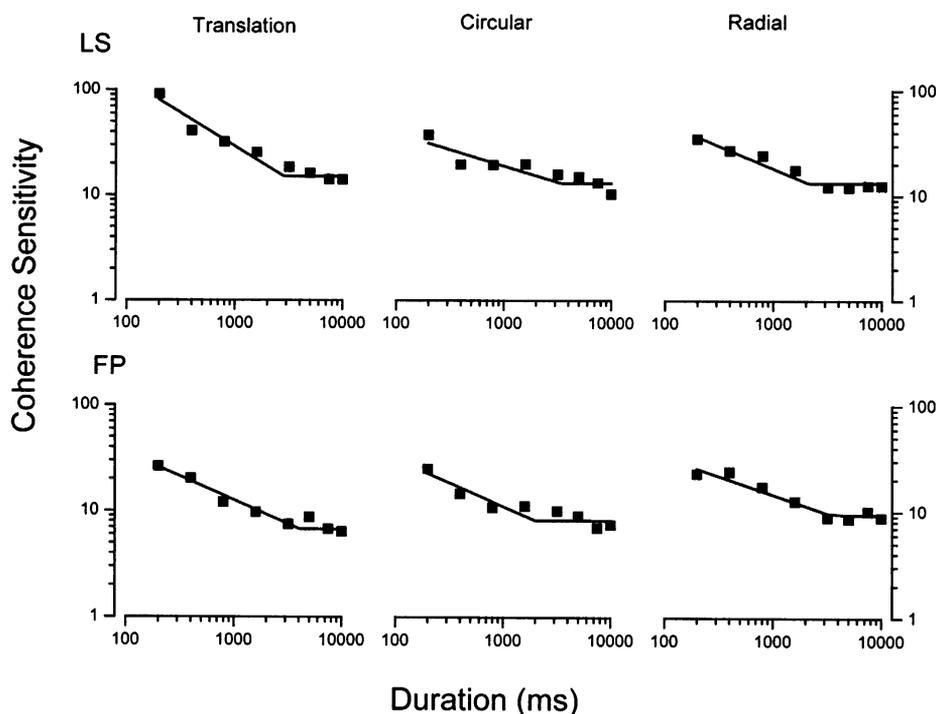


Fig. 5. Sensitivity for motion coherence of a 200 ms presentation of partially coherent stimulus embedded within a period of noise, as a function of total stimulus duration. The curves are the best fit of Eq. (2), with  $t_0$  set to the values shown in Fig. 3, allowing  $S_0$  and  $p$  to vary to minimise residual squares. The best-fitting values of parameter  $p$  for translation, circular and radial motion were:  $-0.66$ ,  $-0.31$  and  $-0.40$  for LS and  $-0.45$ ,  $-0.45$  and  $-0.35$  for FP. These values (mean  $-0.44$ ) are slightly less than the theoretical prediction of  $-0.5$  for an ideal integrator.  $\chi^2$  for translation, circular and radial fits was 35, 16 and 9 for LS and 1, 4 and 5 for FP.

#### 4. Discussion

The major result of this study is that integration times for motion coherence of optic flow stimuli are very long, in the order of seconds, while those for contrast sensitivity are an order of magnitude less. Furthermore, the integration period seems to be obligatory, as highly trained observers could not 'ignore' the leading and trailing noise, even though they knew that the motion signal was always in the middle.

It has been previously argued that motion coherence thresholds may reflect the action of high-level neural mechanisms that integrate local-motion signals (Watanuki & Sekuler, 1992). Contrast thresholds, on the other hand, may be limited more by early local-motion processors. Morrone, Burr, and Vaina (1995) provided very good evidence for this by showing that although coherence thresholds revealed strong spatial integration of optic flow, contrast thresholds showed virtually no summation. However, when noise was added in order to raise the global discrimination thresholds, so the contrast threshold of the local detectors was no longer the limiting factor, strong summation was observed also for contrast sensitivity measures.

A similar argument has been raised for a quite different task, spatial interval acuity (Morgan & Regan, 1987). For small intervals (less than 2.5 min arc), where

the task is thought to be mediated by 'first stage' mechanisms, the judgement depends strongly on contrast. For larger distances, it is thought that the task involves a higher 'second stage' analysis, and these judgements are contrast independent. All these studies are consistent with the notion that contrast sensitivity measures tap first-stage mechanisms, while others may tap second- or higher-stage mechanisms. The very different estimates of temporal integration observed here provide further support that the two techniques tap different physiological levels.

Electrophysiological studies clearly suggest that optic flow is analysed at a high level. Cells selective to the complex flow patterns, such as radial and circular motion, have to date been reported only in the dorsal portion of the medial superior temporal area (MSTd, e.g. Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Graziano, Andersen, & Snowden, 1994). MST receives its primary input from the adjacent motion area MT, which in turn receives input from V1 and V2 (Ungerleider & Desimone, 1986; Boussaoud, Ungerleider, & Desimone, 1990). The properties of the cells in MST suggest that they integrate motion signals from local motion mechanisms at earlier stages. Thus the coherence thresholds may be probing directly the temporal properties of MST neurones. Unfortunately there is little direct information about the temporal integration

properties of these neurones. However, Duffy and Wurtz (1997) have shown that MSTd neurones have a very sustained response, up to 25 s, and that the sustained component of the response provides most information about the flow direction.

A likely candidate for early stage, contrast limited mechanism is V1. The temporal properties of V1 cells (Tolhurst & Movshon, 1975; Duysons, Orban, Cremieux, & Maes, 1985) are consistent with the summation estimates of around 100–200 ms measured here. These cells exhibit contrast thresholds, making them clear candidates for the neural substrate of the summation estimates for contrast sensitivity.

The integration model used to simulate the data was designed to be as simple as possible: perfect integration within a critical period, and no integration thereafter. In reality an actual biological system is unlikely to produce such a discontinuous function. The integrator is likely to have a smooth Gaussian-like envelope, leading to smoother transitions from periods of integration to non-integration; but this should not affect significantly the time constants. One might also wish to allow for a more shallow non-linear summation of the contrast thresholds, typically referred to as ‘probability summation’ (the increased probability that a noisy detector will reach threshold if stimulated for a longer duration: Graham, 1977; Watson, 1979). Allowing for this probabilistic integration (usually a slope of around 0.3 on log–log coordinates) will tend to shorten the temporal summation estimates for the contrast measures (by about 20% on average). However, to allow for a fair comparison with the coherence thresholds (where probability summation is not applicable), and to keep the analysis as simple as possible, we did not introduce this concept here. Other possible effects to consider are those of uncertainty, known to affect thresholds in some conditions (e.g. Cohn & Wardlaw, 1985). Uncertainty effects may be expected to operate in the noise conditions, where subjects may have been uncertain of the exact time of appearance of the stimulus (although it was always in the middle of the display). However, the theoretical effects of uncertainty are small, usually predicting log–log improvements with slopes around 0.25 (e.g. Palmer, 1994; Baldassi & Burr, 2000). As the uncertainty was only partial in these conditions (subjects had a good idea of when to expect the stimulus), the predicted effects are probably even smaller, unlikely to affect the much stronger (linear) effects of integration (the two forms of summation are not accumulative).

In most experimental conditions, the data follow reasonably closely the theoretical predictions of a simple ideal integrator. The predictions of signal detection theory are for a linear increase in sensitivity up to a critical value for contrast sensitivity (where the

noise is essentially internal) and also for coherence sensitivity where the flanking noise of constant duration ensures a constant noise limit. These predictions were upheld for both types of thresholds, for both subjects for all three types of motion. These data clearly point to two ideal integrators with different time constants.

Without the flanking noise, coherence sensitivity should increase with the square root of duration (log–log slope of 0.5), as both signal and noise variance should increase with duration. For circular and radial motion, this prediction was supported by both subjects, with the best fitting log–log slope at 0.46 and small values of  $\chi^2$ . Furthermore, the integration constant in these two conditions was the same as that measured with noise. For the condition of constant signal and variable flanking noise, the prediction is for a square root decrease in sensitivity with duration. Although these data were more variable than the others, none of the conditions violates the prediction.

The only clear violation of the predictions was for translating stimuli without noise flanks (Fig. 3). Here sensitivity increased linearly, and for far shorter durations than for the flow stimuli under these conditions and for all stimuli in the presence of visual noise. It is not at all clear why this behaviour occurs without the flanking noise, nor why it occurs only for translating stimuli. Certainly it suggests that different mechanisms are involved in the analysis of translation and flow stimuli, consistent not only with the physiology (MSTd, e.g. Tanaka & Saito, 1989; Duffy & Wurtz, 1991; Graziano et al, 1994), but also with recent fMRI evidence showing that different areas in the human brain are activated by flow and translational motion (Morrone, Tosetti, Montanaro, Burr, Fiorentini, & Cioni, 2000). Nevertheless, it remains a mystery why the summation for translation should occur at twice the theoretically expected rate. One possible reason may be inhibition between opposing directions of motion, such as that observed in motion area MT (Qian & Andersen, 1994; Heeger, Boynton, Demb, Seidemann, & Newsome, 1999). A brief display of motion contains a wide spread of motion energy, including energy in the opposite direction, that should inhibit the energy in the preferred direction (Anderson & Burr, 1987). This inhibition will be strongest at brief durations, becoming progressively less at longer durations, and may produce a curve that is steeper than theoretical expectations. Perhaps the increase in slope was not noticeable in the noise flanking condition, because the limit there may have been set by the extra flanking noise, and this limit would obscure any additional effects of inhibition. Alternatively, the incoherent motion of the noise-flanked stimuli may have activated motion mechanisms, producing a *hysteresis*, as has previously been reported for motion stimuli

(Williams, Phillips, & Sekuler, 1986; Williams & Phillips, 1987). It is interesting that the steepening of the curve did not occur for circular and radial motion. This may reflect the more linear analysis in MST, that has been reported in the literature (Paolini, Distler, Bremmer, Lappe, & Hoffmann, 2000). A similar argument has been made to explain the functional differences of fMRI responses to translation and flow stimuli (Morrone et al., 2000).

The steeper summation for translation produced an estimate of critical duration that is about one-third that estimated with the flanking noise and that for radial and circular motion under all conditions (Fig. 4). Perhaps this could reflect an intermediate stage of processing, possibly MT, although it is far from clear why this should emerge only under the noise-free conditions. It should also be pointed out that the summation estimates without noise are closer to previous estimates with translation stimuli, such as those of Watamaniuk and colleagues (Watamaniuk et al., 1989; Watamaniuk & Sekuler, 1992) who report summation estimates around 500 ms.

The imaging study mentioned above is interesting in the light of the data reported here, as it showed that continuously rotating or expanding stimuli do not elicit an fMRI response, when measured against locally matched random controls. However, when the direction of flow was inverted every 2 s, either gradually or abruptly, there was a strong response. For translating stimuli, both continuous and inverting stimuli gave a strong response. The fMRI study did not investigate inversions more frequent than 2 s (the integration time suggested by this study), so it did not examine summation. Nevertheless, it is interesting that in similar experimental conditions, one study shows that presentations greater than 2 s reduced the response to flow stimuli, while the current study shows integration up to 2 s.

Very long periods of integration are consistent not only with several other summation studies mentioned previously, but also reaction time studies that point to the existence of a second-stage integration process (Burr & Corsale, 2001). To account for the data, this integration stage must accumulate motion signals for over very long intervals, of the order of 2–3 s, as observed here. What may be the functional advantage of this long integration period? It certainly seems strange that information used for navigation through space should involve such long time constants, as change in the optic flow field should be immediately available, without lengthy integration. The function of integration is typically to improve signal to noise levels. Indeed, in this study, the integration was so efficient that one coherent dot within 200 noise dots was sufficient for accurate direction discrimination at long durations. How that may be of advantage under natural viewing conditions is an interesting problem to speculate about.

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