
Independent detectors for expansion and rotation, and for orthogonal components of deformation

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Abstract. It is well known that optic flow—the smooth transformation of the retinal image experienced by a moving observer—contains valuable information about the three-dimensional layout of the environment. From psychophysical and neurophysiological experiments, specialised mechanisms responsive to components of optic flow (sometimes called complex motion) such as expansion and rotation have been inferred. However, it remains unclear (a) whether the visual system has mechanisms for processing the component of deformation and (b) whether there are multiple mechanisms that function independently from each other. Here, we investigate these issues using random-dot patterns and a forced-choice subthreshold summation technique. In experiment 1, we manipulated the size of a test region that was permitted to contain signal and found substantial spatial summation for signal components of translation, expansion, rotation, and deformation embedded in noise. In experiment 2, little or no summation was found for the superposition of orthogonal pairs of complex motion patterns (eg expansion and rotation), consistent with probability summation between pairs of independent detectors. Our results suggest that optic-flow components are detected by mechanisms that are specialised for particular patterns of complex motion.

1 Introduction

The array of complex retinal motions that occurs as an observer moves through a structured environment is referred to as optic flow. Within certain constraints, such complex motion can be decomposed mathematically into component vector fields (Koenderink 1985) that would provide the observer with useful information, such as direction of heading (Gibson 1950), time to contact (Lee 1980), and distance travelled (Redlick et al 2001). A growing body of evidence suggests that primate vision contains specialised mechanisms that are well suited to performing the required analysis (eg Gurney and Wright 1996; for a review, see Bex et al 1998).

A stimulus that has been particularly useful in revealing properties of primate motion vision is a random-dot stimulus in which the ratio of signal and noise dots can be manipulated. Methodological details vary between laboratories but, typically, signal dots carry coherent motion and noise dots have either randomised positions, producing a twinkling effect, or move in random directions (Scase et al 1996). Coherence threshold is the lowest proportion of signal dots that can be reliably detected in these stimuli and provides a measure of sensitivity for the visual mechanisms used to detect the coherent motion. In early experiments uniform translation was used as the coherent motion component (Newsome and Paré 1988) to investigate temporal integration (Snowden and Braddick 1989) and the magnitude and direction tuning of the motion aftereffect (Blake and Hiris 1993; Raymond 1993). Later, coherent motion components of expansion, contraction, and rotation were used (Edwards and Badcock 1993; Morrone et al 1995; Harris and Meese 1996; Snowden and Milne 1996), though the speed gradients typical of natural rotating or looming stimuli have not always been included.

For example, Morrone et al's (1995) signals conformed to the direction templates of rotation and expansion (ie the signal dots travelled in multiple directions) but each stimulus dot also travelled at constant speed. Nevertheless, these stimuli drive appropriately selective visual neurons whether they contain speed gradients or not (Tanaka et al 1989), and so might be expected to stimulate related psychophysical mechanisms, even though they produce different percepts (De Bruyn and Orban 1990a).

Of particular interest here is the spatial-summation technique introduced by Morrone et al (1995). In their stimuli, a circular display region (10 deg in diameter) was notionally divided into 16 sectors. Each sector contained noise dots (randomly repositioned on each image frame) plus signal dots that were confined to 2, 4, 8, or 16 of the sectors arranged evenly about the display. They found that direction discrimination (eg clockwise versus anticlockwise rotation) was unaffected by the spatial configuration of the signal dots. In other words, the same number of signal dots was required to achieve discrimination, regardless of their spatial location. This implies detecting mechanisms that can pool appropriately moving dots over a large area (Burr et al 1998). While this provides good evidence that the visual system contains at least some of the processes required to deal with complex motion, we suggest that two further refinements are needed for a complete analysis. First, the analysis should involve further components in addition to expansion and rotation. In particular, Longuet-Higgins and Prazdny (1980) have demonstrated that recovery of information about surface layout is particularly good from deformation stimuli (see also Koenderink 1986; Meese et al 1995; Meese and Harris 1997). Deformation stimuli have received only limited attention in the psychophysical literature (eg De Bruyn and Orban 1990b; te Pas et al 1996) and whether pooling mechanisms exist for this class of stimuli is not known. Second, the mechanisms underpinning the analysis should be independent of each other. Freeman and Harris (1992) and te Pas et al (1996) have provided evidence that the detection of complex motion patterns is largely independent when they are vector summed with other components but, from this, it is difficult to deduce the properties of the visual mechanisms involved.

1.1 *Aims and rationale*

In this paper we (i) use a spatial-summation paradigm (Morrone et al 1995) to investigate the detection of the complex-motion-component deformation and (ii) develop a novel two-component summation experiment to address the question of independence between the detection of components.

The rationale of summation experiments is discussed by Graham (1989), but we sketch a brief outline here. If a detecting mechanism is excited by both of two components in a compound stimulus then it should respond more to that compound stimulus than to either of the components alone. The magnitude of summation of the two components is of particular theoretical interest and is given by what is sometimes referred to as the *threshold ratio*. This is calculated by dividing the detection threshold (or coherence threshold) for one of the components by the detection threshold for that same component in the compound stimulus. If the detection process for the two components involves both common noise and a single common detecting mechanism then a threshold ratio of two (a compound threshold that is half that of its components) is expected. This is because, in this case, the signal-to-noise ratio depends only on the sum of the two signals. In this paper, we refer to this as linear summation and describe the underlying visual mechanism as a *linear integrator* (Morrone et al 1995). This is an example of what is sometimes referred to as *physiological summation* because the two components sum within a single physiological unit. At the other extreme, if the two components stimulate completely different detecting mechanisms then those mechanisms would be no more sensitive to the compound stimulus than to

either of the two components and it might be expected that no summation would occur (a threshold ratio of 1). In fact, in what are thought to be such circumstances, a small amount of summation is often found (typically a threshold ratio of about 1.2). This is conventionally explained by *probability summation*—the rise in probability of detection that accompanies an increase in the number of statistically independent detectors that can be used [for basic, early, and recent discussion of probability summation see Meese and Williams (2000), Graham (1989), and Tyler and Chen (2000), respectively]. An intermediate level of summation is quadratic summation [a threshold ratio of $\sqrt{2}$ (about 1.41)]. One interpretation of quadratic summation is another form of linear physiological summation but one in which the limiting sources of noise are different for each of the components (eg see Burr et al 1998; Tyler 1999; Tyler and Chen 2000). This would occur if noise applied to the output of a summing circuit were negligible compared to that in two independent signal channels providing input. The limiting noise could be external stimulus noise, internal channel noise, or both. In any case, the two independent noise variances are summed ($n_1^2 + n_2^2$) along with the two signals ($s_1 + s_2$). For normalised signals this gives a signal-to-noise ratio of $2s/\sqrt{(2n^2)}$ which is $\sqrt{2}$ greater than the signal-to-noise ratio (s/n) for a single component. However, for the experiments in this paper, several other processes (some of which are discussed later) could result in equivalent levels of summation. Most simply, predictions for quadratic summation can be treated as a gauge indicating a level of summation intermediate between that expected for a linear integrator and probability summation between independent detecting mechanisms.

Conventionally, all of these predictions can be calculated using a Minkowski metric:

$$v_{\text{compound}} = \left(\sum v_i^k \right)^{1/k},$$

where each dimension v_i represents the sensitivity (reciprocal of coherence threshold) for each component, and the exponent k is set to one for linear summation, two for quadratic summation and three or four for probability summation (see Graham 1989 for more details).

In our experiments we investigated summation of complex motion components by constructing compound stimuli made from components that differed either in position (experiment 1), similar to Morrone et al (1995), or in direction (experiment 2), for example, expansion and rotation. In the first experiment, we found summation to be greater than quadratic, and for some observers it was close to linear, suggesting approximately linear integrators for complex motion, including deformation. In the second experiment, we found summation to be close to probability summation, suggesting that the orthogonal complex motion components in our compound stimuli were detected by independent mechanisms. These findings are consistent with a visual system equipped with multiple independent mechanisms suitable for representing multiple components in complex optic flow.

2 General methods

2.1 Overview

In all experiments, observers detected the presence of complex motion components (signal) in noisy random-dot stimuli. In experiment 1, spatial summation was investigated by measuring coherence thresholds for the signal when placed in either the entire circular display region, or when confined to just a single quadrant. In experiment 2, independence of orthogonal complex motion components was investigated by measuring psychometric functions for compound stimuli containing pairs of stimulus components for which sensitivity was normalised.

2.2 *Equipment, stimuli, and task*

Stimuli were displayed on a 120 Hz Eizo monitor by using the framestore of a VSG2/3 stimulus generator under the control of a PC. Stimulus dots were randomly positioned on each trial with equal probability of appearing anywhere within the display region. A two-interval-forced-choice (2IFC) paradigm was used to measure the coherence thresholds for complex motion carried by these dots (Harris and Meese 1996), where the observer's task was to discriminate signal+noise from noise alone (details below). Responses were made by pressing one of two buttons and auditory feedback was used to indicate the correctness of response.⁽¹⁾ For each test interval, up to 440 bright dots (120 cd m^{-2}) were presented on a dark background (11 cd m^{-2}) within an annular window with nominal diameters of 5 deg and 0.25 deg. Dot luminance was ramped linearly at the borders. Both temporal intervals contained a movie consisting of four sequential images each displayed for 9 frames. This produced stimuli that appeared to move smoothly and had a duration of 300 ms.

The stimuli are shown schematically in the insets to figures 3 and 4. Formally, the nominal polar angle of a dot (θ°) is given by $\tan^{-1}(y/x)$, where (x, y) are the Cartesian coordinates of a dot half way through its trajectory, where the origin is in the centre of the display. The directions of signal dots are given by $(\theta)^\circ$, $(\theta - 90)^\circ$, $(90 - \theta)^\circ$, $(-\theta)^\circ$, $(\theta + 45)^\circ$, and $(\theta - 45)^\circ$ for expansion, clockwise rotation, deformation 1, deformation 2, anticlockwise expanding spiral, and clockwise expanding spiral, respectively.

Noise dots were the same as signal dots but had random directions allocated independently on each trial (see, for eg, Scase et al 1996; Snowden and Milne 1996), and those in the signal+noise interval were matched in position and direction to those in the noise interval. In other words, the only difference between the two stimulus intervals was the presence of signal dots in the signal+noise interval, which replaced some of the noise dots contained in the noise-alone interval.

Over the entire movie, each dot travelled linearly through 10% of its nominal distance (d) from the origin, where $d = \sqrt{(x^2 + y^2)}$. Thus, our stimuli contained global speed gradients, though individual dots had constant velocity. This arrangement ensured that, on average, all complex motion stimuli had the same statistical distribution of dot velocities, allowing meaningful comparisons to be made between conditions. (Specifically, dot directions were evenly distributed around 360° , and speed increased linearly with distance from the centre of the display.)

For the translation condition (performed by subjects NJA and CHD), all signal dots travelled in the same direction. They contained no speed gradients and travelled a distance of 0.125 deg. This is the same distance as that travelled by a dot in a complex motion pattern positioned halfway between the centre and the edge of the 5 deg display region. For all stimuli, the algorithm of Georgeson et al (1996) was used to achieve subpixel accuracy. In brief, this technique uses a set of four pixels arranged in a square to represent a single dot. The luminance levels of these pixels are manipulated in a systematic way to control the location of their centroid, which corresponds to the perceived location of the dot (Morgan and Aiba 1985; Georgeson et al 1996).

2.3 *Procedure and observers*

Other than in a control experiment (see below), a three-down, one-up staircase procedure (Wetherill and Levitt 1965; Meese 1995) controlled, in logarithmic steps, the proportion of signal dots contained in the stimulus. All observers were familiar with the stimuli

⁽¹⁾In general, we use a procedure where the response is triggered by the offset of a button press which is recorded only if the other button is not depressed simultaneously. This procedure has the advantage that a sophisticated observer is often able to correct finger errors (pressing the 'wrong' button by mistake) by depressing the 'correct' button before releasing the 'wrong' button, and then finally releasing the 'correct' button.

and were informed of the particular test stimuli being used at the beginning of each experimental session. Furthermore, to remind observers of the appearance of the stimuli, staircases began at high signal levels. For each test stimulus, data were collapsed from a pair of randomly interleaved staircases (Cornsweet 1962), each of which terminated after eight staircase reversals (ie there were sixteen reversals for each stimulus).

Coherence thresholds for discriminating signal+noise from noise alone were measured with probit analysis (Finney 1971) and are expressed as the percentage of signal dots (S) in the stimulus at the 75% correct point. In experiment 1, thresholds were measured for different conditions from interleaved pairs of staircases. In one condition (the 'whole' condition), signal dots were randomly distributed across the entire display, whereas in the other condition (the 'quad' condition), signal dots were confined to just a single quadrant of the display. In experiment 1a, the single quadrant was always the upper quadrant (see schematic inset in figure 1), whereas in experiment 1b, coherence thresholds were measured for all four quadrants. Observers were not cued as to which condition was being presented on each trial, but they were aware of the construction of the different stimulus configurations. For each observer, results are averaged from four or five experimental sessions.

In experiment 2, each experimental session began with a staircase procedure to measure psychometric functions for each of two orthogonal motion signals (component conditions). A pair of staircases was used for each of the two components and all four staircases were randomly interleaved. When this stage was complete, the observer was given an auditory indication that the stimuli were to be changed, and the next stage began when the observer pressed a button. In the second stage ('compound' condition), a pair of randomly interleaved staircases yielded a psychometric function for the superposition (not the vector sum) of the two components used in stage one. The relative contributions (wt_A , wt_B) of the two components were determined by the thresholds (S_A , S_B) for the individual signals as follows: $wt_A = S_A / (S_A + S_B)$ and $wt_B = S_B / (S_A + S_B)$. This arrangement should produce compound stimuli containing signals to which the observer is similarly sensitive. Data were combined from between seven and nine experimental sessions to produce the psychometric functions in figures 3 and 4.

Observers were the authors (TSM and MGH), two postgraduate volunteers (DJH and PAA), and four undergraduate students at Aston University (LED, CK, NJA, and CHD), three of whom completed the experimentation as part of their undergraduate project work. All observers had normal or corrected-to-normal vision.

2.4 Control experiments

2.4.1 Dot-density cues. In an initial control experiment we measured sensitivity to 300 ms presentations of only the final image of the movie sequences, where 25% of the total number of dots were designated signal dots. Performance was around chance (50% correct), indicating that potential position or dot-density cues were not used by our observers. In order to have detected the signal in the moving stimuli investigated in this paper, observers must have integrated stimulus information over a series of image frames.

2.4.2 Effect of second component on noise. In experiment 2 we compared coherence thresholds for stimuli containing a single signal or a pair of orthogonal signals. In the second condition, the distribution of noise dots for component A was skewed towards that of component B because of the simultaneous presentation of component B . Or put another way, we assumed that for the mechanisms that detected component A , component B was equivalent to noise (and vice versa). We tested the validity of this assumption by measuring coherence thresholds for component A , where component B was presented close to detection threshold in both 2IFC test intervals. This simulated the conditions of the test stimulus in experiment 2, but in such a way that component B could not

serve as a detection cue. In this experiment we found component *B* to have little or no effect on coherence thresholds, suggesting that our assumption was reasonable for the experiments reported both here and elsewhere (Meese and Anderson 2001; Meese and Harris 2001).

3 Results and discussion

3.1 Experiments 1a and 1b: spatial summation for complex motion

Coherence thresholds were measured for expansion, rotation, and two directions of deformation referred to as deformation 1 and deformation 2 (see schematic illustrations in figure 3). Results from experiment 1a are shown in figure 1 for four different observers (different panels) and are reported as the percentage of dots in the upper quadrant of the display that carried signal. Figure 1 shows that fewer signal dots were needed in the ‘whole’ condition (dark bars) than in the ‘quad’ condition (pale bars), indicating considerable summation of some kind. The upper and lower bounds of the open boxes in figure 1 indicate predictions for probability summation and quadratic summation amongst the four quadrants respectively (see appendix for further details).

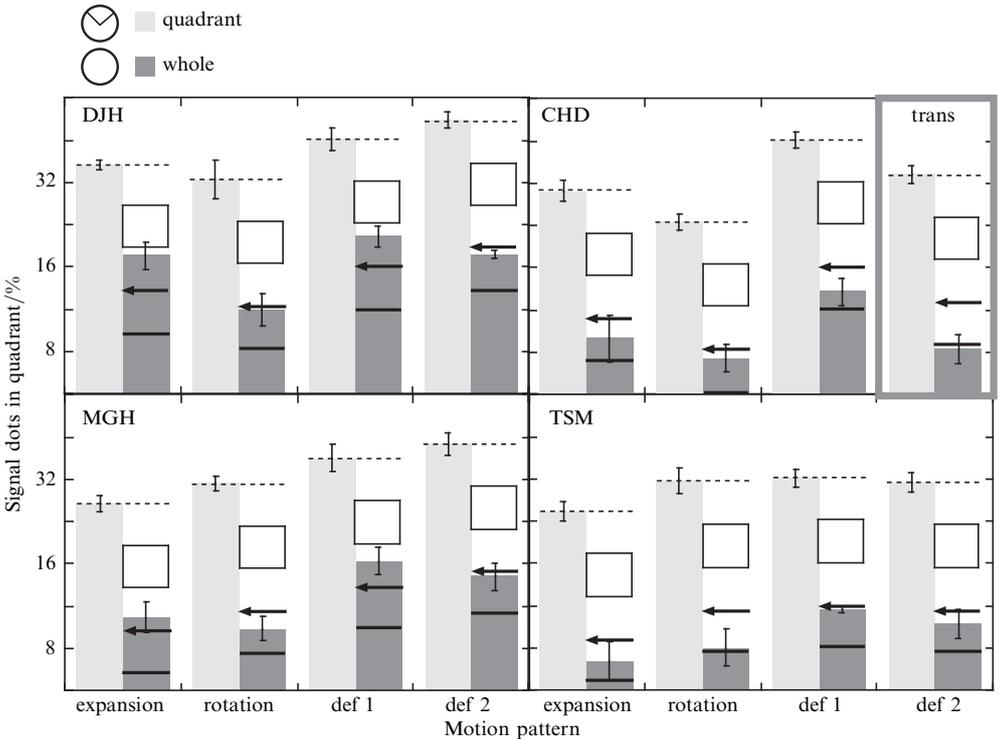


Figure 1. Experiment 1a. Thresholds for detecting complex motion patterns contained in either the whole display (dark bars) or the upper quadrant only (pale bars). Error bars show ± 1 SE. Different panels are for different observers and different columns are for the different motion patterns indicated at the bottom of the figure. An exception is observer CHD who performed a translation condition instead of the deformation 2 condition (bold rectangle). For each condition of motion type, the figure shows five predictions for the ‘whole’ condition derived from the ‘quad’ condition. The dashed horizontal lines are for no summation and the solid horizontal lines are for linear summation. The upper and lower bounds of the open boxes are for probability summation and quadratic summation amongst the stimulus quadrants respectively. The horizontal arrows with the solid arrow heads are for quadratic summation between a pair of detectors that are sensitive to different quadrant pairs (see appendix). On average, the data are closer to the predictions for linear summation than those for probability summation or quadratic summation amongst the four quadrants.

For all observers and stimuli, summation was much greater than the prediction for probability summation. It was also greater than the prediction for quadratic summation and, in 12 of the 16 cases, was closer to the prediction for linear summation indicated by the solid horizontal lines without arrows (we describe the arrows in the next subsection). Furthermore, the differences (averaged across observers) between the data and the linear summation predictions were similar for the different stimulus conditions, being 0.12 logarithmic units ($SD = 0.08$ logarithmic units) for the expansion and rotation conditions and 0.15 logarithmic units ($SD = 0.07$ logarithmic units) for the deformation conditions, suggesting that similar integrative detection processes were involved for all of the patterns of complex motion tested. We note, however, that when signal dots were contained within the entire display (dark bars) thresholds tended to be slightly higher for deformation than for the other stimuli, suggesting a less efficient detection process for deformation. This finding has been confirmed with a fifth observer (PAA; results not shown).

In experiment 1a, equal sensitivity to each of the four quadrants was assumed in our modelling, whereas in experiment 1b, independent estimates of sensitivity to signal dots in each quadrant allowed this assumption to be relaxed. Results are shown in figure 2 for TSM and for the same model predictions as in figure 1. Although there was slight variability in sensitivity for each of the four quadrants (pale bars), the sensitivities and the model predictions were remarkably consistent with those from experiment 1a, which was performed over three years previously. For all stimulus conditions, summation was greater than quadratic and close to linear.

Recall from section 1 that the linear summation model is equivalent to the arithmetic sum of the responses (or sensitivities) to the four quadrants and represents the integration process that would occur within a single detector that responds to both an individual quadrant and the entire display. The quadratic summation model is equivalent

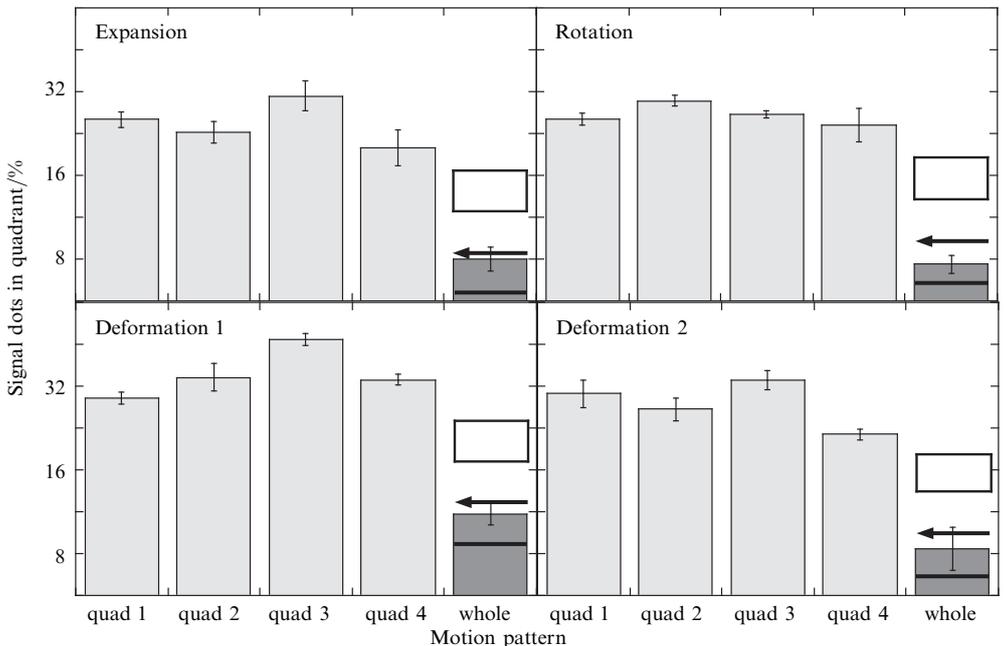


Figure 2. Experiment 1b. Thresholds for detecting complex motion patterns contained in either the whole display (dark bars) or each of four different quadrants (pale bars) for TSM. Different panels are for different motion patterns. Quad 1 is the uppermost quadrant and quads 2–4 are those encountered in a clockwise rotation. The predictions for the whole condition are for the same models as in figure 1. The results are similar to those for the same observer in experiment 1a.

to the square root of the sum of the squared responses to the four quadrants, as might occur for a mechanism that sums the output of each of four independent 'quadrant detectors'. Although our experiments do not address the question of which and how many of the signal dots in each quadrant contribute to detection, both of the above models of physiological summation involve pooling of motion information over direction and space. Because probability summation across the four quadrants cannot account for the data, the strong implication is that our complex motion stimuli were detected by mechanisms that performed the necessary physiological summation. The precise nature of this pooling is unimportant for our second experiment where we investigated the independence of the detecting mechanisms. That global pooling was involved in detecting our stimuli is sufficient to rule out explanations of experiment 2 [and other experiments we have performed (eg Meese and Harris 2001)] in terms of local processes. Nevertheless, in the next subsection we consider why summation might be less than linear for some observers and conditions.

3.1.1 Linear integrators? Even if linear integrators were involved in the 'whole' condition, there are several reasons why the data might show less-than-complete linear summation. First, multiple mechanisms might have been involved when detecting the motion patterns in the quadrant condition, though some of these might not have contributed to the detection of the pattern when it was contained in the entire display. This might occur because (a) the receptive fields of these additional mechanisms were smaller than the size of the display, (b) inhibitory inputs to these mechanisms made them insensitive to the test patterns when they were contained in the entire display (Zhang et al 1993; Meese and Harris 1996), or (c) these mechanisms were sensitive to the quadrant boundary (noise against signal+noise) which was absent in the 'whole' condition. Second, the detecting mechanisms might not have been matched to the stimuli. There are numerous possibilities, but one which straightforwardly makes the point is a pair of mechanisms each sensitive to just two quadrants—for example, the upper and lower quadrants and the left and right quadrants. In figures 1 and 2, quadratic summation between such linear integrators (see appendix) is shown by the horizontal arrows; these predictions are fairly consistent with some of the data. No doubt, combinations of other pooling mechanisms that are suboptimal for our stimuli (eg Meese and Harris 1997, 2001), would also make similar predictions. Different levels of summation shown by different observers, reported here and elsewhere (Burr et al 1998), might reflect differences in threshold sensitivity for all of these different types of mechanisms.

3.2 Experiments 2a and 2b: independent detectors for complex motion

In experiment 2, the aim was to assess the independence of the pooling mechanisms established in experiment 1. Psychometric functions were measured for detecting (i) individual signals (signal *A*, signal *B*) from the three pairs of complex motion patterns shown in figure 3, and (ii) compound stimuli made from the superposition of the signals in each pair. Results are shown for three different observers in figures 3 and 4. In experiment 2a (figure 3), signal dots were placed randomly and approximately evenly across the entire display, whereas in experiment 2b (figure 4), the display was notionally split into 16 radial sectors. In this second case, signals were randomly allocated to either odd or even-numbered sectors on each trial and, for compound stimuli, signal *A* and signal *B* were allocated to spatially alternate sectors. This technique was intended to lessen the possibility of local spatial interactions between individual signal dots from the two different motion patterns (either in the display, or within the visual system). In both figures, results are plotted as a function of the percentage of signal *A* dots on a logarithmic axis. (The results for signal *B* are normalised to these levels—see figure legend.) The 75% correct points on the psychometric functions typically fall between 8% and 16% signal dots, consistent with those of experiment 1.

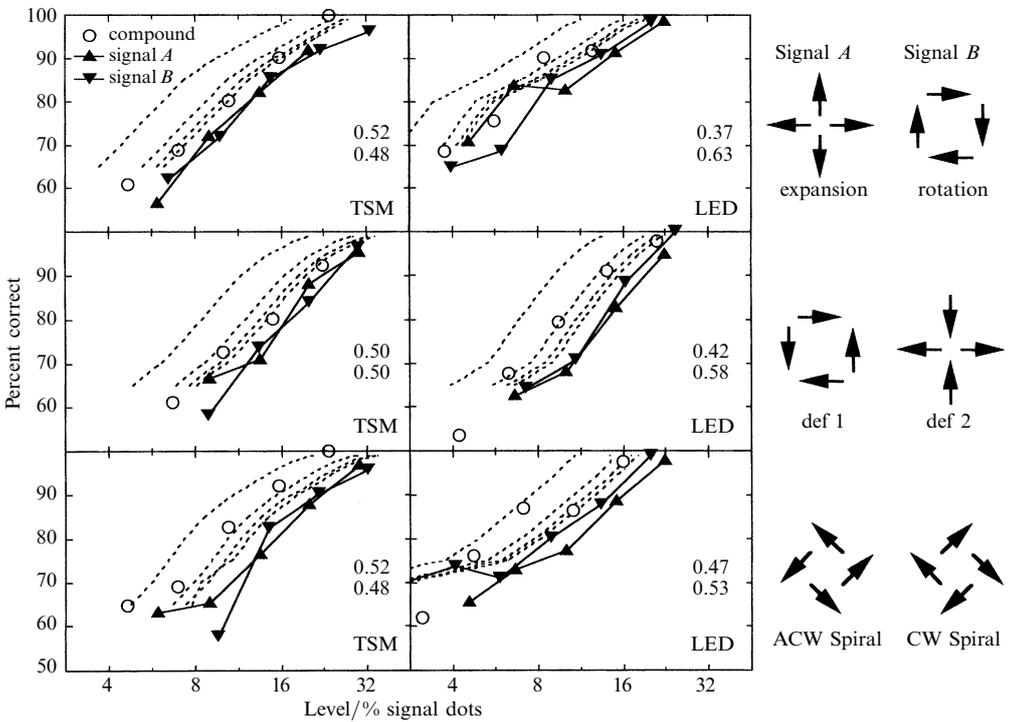


Figure 3. Experiment 2a. Psychometric functions for orthogonal two-dimensional motion patterns and their compound. Results are for two observers (left panels—TSM; right panels—LED) and the stimulus types are illustrated schematically down the right-hand side. Filled symbols are for individual signals and open symbols are for compound stimuli made from a weighted superposition of the signal pairs where the numerals inset within each panel indicate the average weights (wt_A and wt_B). The abscissa indicates the percentage of signal-*A* dots for the psychometric functions for both signal *A* and the compound stimulus. For signal *B*, the psychometric functions were normalized by shifting them laterally by $\log_{10}(wt_A/wt_B)$. Most data points are for at least 50 trials, and those towards the centre of the psychometric functions are typically for well over 200 trials; a typical psychometric function represents data gathered from 700 to 800 trials. The dashed curves are predictions for different levels of summation ($k = 1, 2, 3, 4$ from left to right; see appendix). In no instance does the compound psychometric function fall near the linear-summation prediction ($k = 1$), though typically it falls close to the widely used probability-summation predictions ($k = 3$ or 4).

In general, the compound data (open symbols) fall on, or slightly to the left of, the component data (filled symbols), indicating that coherence threshold for signal *A* was similar, or slightly lower, when it was presented in the compound stimulus than when it was presented alone. In further conditions (results not shown), a fourth observer's (NJA) sensitivity was measured for (a) vertical and horizontal translation, (b) left and right oblique translation, (c) contraction (opposite to expansion) and rotation, and (d) a pair of contracting and expanding clockwise spirals. For this observer, sensitivity to the compound signal was similar to the component signals in all cases.

3.2.1 Independent detectors. In figures 3 and 4, the dashed curves are predictions for different models of summation with different indices in the Minkowski metric ($k = 1, 2, 3, 4$ from left to right; see appendix). In no instance does the compound psychometric function fall near the linear-summation prediction ($k = 1$), though typically it falls close to the widely used probability-summation predictions ($k = 3$ or 4). These results are consistent with the idea that different complex motion mechanisms were independently involved in detecting different stimulus components and that observers

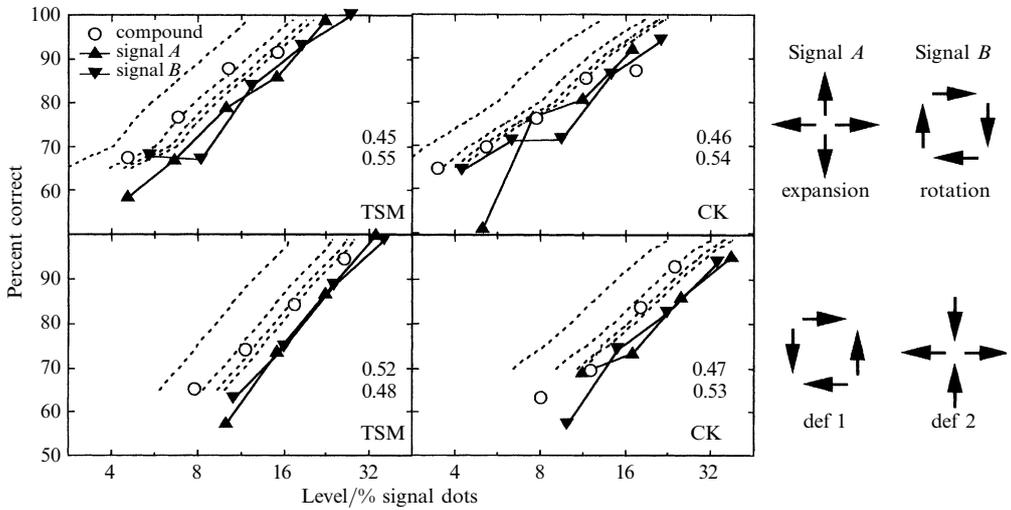


Figure 4. Experiment 2b. Psychometric functions for motion patterns where orthogonal components were placed in adjacent sectors. The format is similar to figure 3 [observers were TSM (left panels) and CK (right panels)], but component signal dots were presented in only the eight odd or even-numbered display sectors. This meant that for the signal+noise test interval, when the stimulus was a single component, a given sector would contain either noise alone or signal+noise. When the stimulus was a compound, all sectors contained noise, and signal-*A* and signal-*B* alternated between sectors. The results are similar to those shown in figure 3, indicating that it was not important whether the dots from the two components were placed in the same or different signal sectors. Note that, for TSM, the sensitivities for expansion, rotation, and deformation did not depend upon the number of sectors that were permitted to contain the signal (compare figure 3 and figure 4, left columns). This is consistent with the results from experiment 1, which suggested approximately linear integrators for these patterns for this observer.

were able to monitor the outputs of different mechanisms (eg expansion and rotation) simultaneously (or in rapid sequence), causing a slight improvement in performance for the compound stimuli.⁽²⁾ This contrasts with results from suprathreshold experiments (De Bruyn and Orban 1993) where observers were unable to identify the directions (eg expansion versus contraction) of each of a pair of briefly presented (83 ms) superimposed stimuli (eg expansion and rotation). However, whether the critical difference here is the task or stimulus duration remains unclear.

For some stimulus conditions (eg spirals for TSM), summation was a little greater than that usually found for probability summation. This might be taken to indicate a lack of independence between detecting mechanisms, though it is not a sufficiently prominent feature of our data to cast serious doubt on the hypothesis of independent detectors in general. Nevertheless, we briefly discuss why this summation might have occurred. One possibility is that detection might have been mediated by mechanisms that are not matched to the stimulus. For example, so long as mechanism bandwidths are sufficiently broad, as has been suggested on both theoretical (Zhang et al 1993) and empirical grounds (Ball and Sekuler 1979, 1980; Rodman and Albright 1987; Graziano et al 1994; Meese and Harris 1996, 2001; Snowden and Milne 1996), expansion and rotation detectors might be used to detect spiral stimulus patterns (Cavanagh and Favreau 1980; Morrone et al 1999; Burr et al 2001). In this particular case, linear summation

⁽²⁾The results of NJA (not shown), revealed no summation. However, his data are consistent with the independent detector hypothesis if it is supposed that efficient monitoring of multiple mechanisms did not take place (Graham 1989). An absence of probability summation has also been reported in the spatial-contrast domain for components with spatial frequencies that are far apart (Olzak and Thomas 1981).

of orthogonal spiral stimuli with the expansion detector would result in summation greater than if detectors were matched to the signals in the stimulus. There is recent psychophysical evidence both for (Burr et al 2001) and against (Meese and Anderson 2001) this hypothesis. Another possibility is that the visual system contains multiple mechanisms, selective, for example, for expansion, rotation, and spirals (Meese and Anderson 2001). In this case, performance would be dominated by mechanisms matched to the component signals but, even so, if bandwidths were sufficiently broad then linear summation would also take place in the intermediate mechanisms. If probability summation took place between all relevant mechanisms then this would result in greater summation than that expected from an optimally placed pair of independent mechanisms only [eg see the modelling in Meese and Harris (2001)]. Under this hypothesis, variations between observers and conditions might reflect variations in observer strategy (Graham 1989).

3.2.2 Independent noise? We have interpreted the small amount of summation in experiment 2 as probability summation. However, this makes an implicit assumption that there is no correlation between the limiting noise sources for each stimulus component. Physiological evidence indicates that correlation is either weak or absent for cortical cells (Zohary et al 1994), suggesting that the assumption is reasonable for internal (detector) noise, but the stimuli used here prompt further consideration because of the use of external stimulus noise. A potential problem in experiment 2 is that the same dots served as noise for both of the two components and so the noise is not strictly independent. A formal analysis is difficult because the details of how noise influences the detectability of (complex motion) signals are not yet clear (eg Watson et al 1997). Nevertheless, a given noise pattern might result in detector stimulation, detector suppression (Snowden et al 1991), or correspondence noise (Barlow and Tripathy 1997) for both detectors of the two components, neither of them, or just one. This is because the broad-band (in the senses of 'direction' and 'position') noise masks used in our experiments contain multiple narrow-band components, each important for different detecting mechanisms. It is likely, therefore, that the conditions necessary for probability summation have been met.

4 Concluding remarks

The data in this paper suggest a visual system containing multiple detectors each selective for different patterns of complex motion at threshold. Results from our laboratory suggest that the direction selectivities of these mechanisms are fairly broad (Meese and Anderson 2001; Meese and Harris 2001). Whether these psychophysical mechanisms are used in computations of observer motion, object motion, or both remains unclear, though we note that cells have been identified in the dorsal stream of monkey that are responsive to stimuli of the type used here. For example, in MSTd, single cells have been found that are selective for expansion and rotation (Tanaka and Saito 1989; Duffy and Wurtz 1991; Orban et al 1992) and spirals (Graziano et al 1994). In this area, cells that respond to deformation are rare (Orban et al 1992), though MT cells that respond to speed gradients (Allman et al 1985; Treue and Andersen 1996) would presumably also respond to our deformation patterns. In the human brain, magnetic evoked responses have been recorded that are stronger for complex motion (expansion, rotation, and noise) than for lateral translation (Holliday et al 1998; Holliday and Meese 2001).

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APPENDIX

Summation predictions

In all experiments, we employed a widely used Minkowski metric to make summation predictions (Quick 1974; Robson and Graham 1981; Graham 1989). In experiment 1, the first implementation of the formula was:

$$v_{\text{whole}} = \left(\sum v_i^k \right)^{1/k}, \quad (1)$$

where v is reciprocally related to coherence threshold ($1/S$, where S is the percentage of signal dots in a single quadrant at threshold) and subscripts $_{\text{whole}}$ and $_i$ are for the 'whole' condition and the 'quad' conditions ($i = 1$ to 4). In experiment 1a, local sensitivity was assumed to be the same for signal dots contained in each of the four quadrants of the display, so v_i was the same for all i . In experiment 1b, independent estimates of sensitivity were available for each of the four quadrants. For the upper and lower bounds of the boxes in figures 1 and 2, $k = 4$ and $k = 2$, respectively. These values represent predictions for probability summation and quadratic summation between the four stimulus quadrants in the 'whole' condition (Graham 1989; Tyler and Chen 2000). The region within the box represents summation for intermediate values of k , and encompasses other values that have been used to model probability summation (eg $k = 3$). The solid horizontal lines (without arrow heads) in the data panels of figures 1 and 2 are for linear summation, where $k = 1$.

The predictions indicated by the horizontal arrows in the data panels of figures 1 and 2 were given by

$$v_{\text{whole}} = [(v_1 + v_3)^k + (v_2 + v_4)^k]^{1/k}, \quad (2)$$

with $k = 2$. This represents quadratic summation between a pair of detectors performing linear summation over just two quadrants (one to the upper and lower quadrants, and the other to the left and right quadrants). With $k = 4$ in equation (2), predictions are about half way between the horizontal arrows and the bottom of the open boxes in figures 1 and 2.

In experiment 2, the formula was

$$v_{\text{compnd}} = (v_{\text{signal-A}}^k + v_{\text{signal-B}}^k)^{1/k}, \quad (3)$$

where the sensitivities (v) are for the compound stimulus and the normalised levels of signal A and signal B . Figures 3 and 4 show predictions for $k = 1, 2, 3$, and 4.