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"Integration across directions in dynamic random dot displays: Vector Summation or Winner Take All?"

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These are preliminary lecture notes, intended only for distribution to participants.

Integration across directions in dynamic random dot displays: Vector Summation or Winner Take All?

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Introduction

The analysis of visual motion is based primarily on neural signals from a functionally specialized pathway in the visual cortex. This pathway, which originates in striate cortex and extends to the cortex of the inferior parietal lobule, is characterized by a large proportion of direction selective neurons (Zeki, 1974, Zeki, 1978). Direction selectivity is especially prominent in the extrastriate middle temporal area (MT or V5) and medial superior temporal area (MST or V6). Neurons in MT are organized in a columnar fashion: neighboring neurons tend to have similar preferred directions of motion as well as largely overlapping receptive fields (Albright and Desimone, 1987, Albright, et al., 1984). Each cortical column, therefore, encodes a direction of motion in a specific region of the visual field. The preferred direction of motion varies systematically from column to column, so that a topographic representation of all directions of motion exists in area MT.

There are several strong indications that the neural activity in MT and MST contribute to the perception of motion. (1) Lesions of MT selectively impair motion-based visual capacities such as motion direction discrimination or accurate smooth pursuit eye movements (Newsome and Paré, 1988, Newsome, et al., 1985). (2) Recordings from awake, behaving monkeys have shown that the sensitivity of single cells in MT and MST is comparable to the performance of the monkey in a direction discrimination task (Britten, et al., 1992, Celebrini and Newsome, 1994). (3) Significant trial to trial covariation between the monkeys' decision and the neuronal firing rate can often be observed when the animal performs the discrimination task at near threshold conditions: neurons in MT and MST tend to fire at higher rates when the monkey makes a correct judgment of the direction of motion and at lower rates prior to a wrong decision for presentations of the same visual stimulus on different trials (Celebrini and Newsome, 1994, Newsome, et al., 1989). (4) An improvement of the monkey's psychophysical performance during the course of an experiment is mirrored by a comparable average increase in sensitivity of neurons in MT and MST both in magnitude and in time course (Zohary, et al., 1994). Finally, (5) local microstimulation of clusters of direction selective neurons in area MT or MST during the performance of the direction discrimination task at near threshold conditions often biases the monkey's decision in the preferred direction of the activated neurons (Murasugi, et al., 1993, Salzman, et al., 1992).

All these lines of evidence support the view that the activity of neuronal populations in areas MT and MST plays a direct role in the judgment of the direction of motion. But how is the information about motion represented across the *population* of neurons? Is the activity of all neurons irrespective of their preferred direction weighted and pooled to obtain an accurate estimate of the direction of motion, or is there a competition between different direction specific channels, so that decisions are cast in favor of the channel generating the largest signal?

Abstract

Recent studies have clearly demonstrated that the activity of directionally selective neuronal populations in the middle temporal (MT) and medial superior temporal (MST) cortical areas plays a direct role in the judgment of the direction of visual motion. However, the way in which the information is derived from a population of neurons remains unknown. Two principal models have been suggested in the past: The Vector Summation model suggests that the responses of neurons encoding all directions of motion are weighted and pooled to obtain an accurate estimate of the mean direction of motion; The Winner-Take-All model is based on a competition between different direction specific channels, so that decisions are cast in favour of the channel generating the strongest directional signal. To discriminate between these two models we generated random dot stimuli that contained an asymmetric distribution of directions of motion. Human subjects were asked to adjust the global direction of motion to the upward vertical direction. When the directional signals were of similar strength, subjects tended to perceive global motion in the mean direction of motion (corresponding to vector summation), but as one directional signal became more prominent, most subjects' settings diverged from the mean towards the modal direction of motion. Some subjects could either match the mean or the modal direction of motion in the display depending on the task instructions. These results suggest that the perceptual judgment of direction of motion is not based on any rigid algorithm generating a single valued output. Rather, human observers are able to judge different aspects of the distribution of activity in a cortical area depending on the task requirements.

Key Words

Motion perception, Global motion, Direction perception, Population coding.

Running Head

Integration of directional signals

In the case of motor control, strong experimental evidence suggests that the direction of a voluntary limb movement or saccadic eye movement is encoded by a neuronal population vector in the motor cortex and the superior colliculus, respectively (Georgopoulos, 1990, Georgopoulos, et al., 1986, Lee, et al., 1988).

In the case of visual motion perception, human psychophysical studies have shown that the percept of a global, coherent motion can result when many different localized motion vectors are combined (Williams and Sekuler, 1984). This experiment utilized dynamic random dot displays whose elements took independent, random walks of constant step size with the directions of displacement drawn from a uniform distribution. When the range of directions used was less than 180°, observers saw the pattern flowing in the general direction of the mean of the distribution, even though they were aware of the variations in individual dot directions of motion. These experiments suggest that in some experimental conditions vector averaging mechanisms might underlie the perception of visual motion. However, the percept of global motion was critically dependent on the presence of local motion vectors whose directions were similar to the direction of the mean vector. When these motion vectors were absent, coherent perception of unidirectional flow was abolished. This result, and the fact that we can perceive motion transparency when two distinctly different moving dot patterns are superimposed (Marshak and Sekuler, 1979), suggests that vector summation is not the *exclusive* algorithm used to compute the direction of motion.

The neuronal pooling mechanisms responsible for the perception of motion have recently been studied at the physiological level. An experiment examining the interaction of visual stimulation and electrical microstimulation suggests that motion direction perception is based on a "winner-take-all" mechanism (Salzman and Newsome, 1994). When the preferred direction of the electrically stimulated neurons is perpendicular to the direction of the visual motion signal, and the monkey can select one of eight directions of motion spaced at 45°, the animal usually chooses a direction corresponding to one or other of the two competing neuronal signals rather than the vector average of the two signals. It may be argued that the experiment was the physiological analogue of superimposing two dot patterns moving in perpendicular directions, and so electrical microstimulation in these particular conditions may create a subjective impression similar to motion transparency. Salzman and Newsome discount this possibility on the grounds that "the perception of a second transparent dot field would almost certainly require intricate patterns of activity in V1 and other extrastriate areas that microstimulation in MT cannot replicate".

The above experiments, taken together, strongly suggest that when a distribution of motion directions exists in a random dot pattern, at least two kinds of operations on the motion signals are possible. When the distribution of motion directions is uniform or Gaussian over a wide range, the perception is that expected from vector summation, but when the distribution is bimodal, motion transparency may ensue. However, to test

whether vector summation is indeed determining perceived direction, rather than some form of peak detection, one must create an experimental situation in which the mean of the distribution of motion directions is different from its mode. We therefore investigated human subjects' perception of direction when directions of motion in the stimulus were distributed *asymmetrically*. A winner-take-all algorithm would predict that under such conditions the subjects should see motion in the direction of the strongest directional signal (the mode) whereas vector averaging mechanisms would lead to the perception of motion in the mean direction. We have also studied how the perceived direction of motion depended on the relative strength of the most prominent motion signal in the distribution.

Methods

Subjects

Five subjects participated in this study. All subjects had previous experience in psychophysical experiments. Three of them were the authors and the two others were naive to the experiments' purpose. All subjects had normal or corrected to normal vision.

Visual stimuli

Two hundred computer generated dots, each subtending approximately 0.1° , were plotted on an X-Y cathode ray tube (CRT) with P31 phosphor. The CRT screen was viewed binocularly at eye level from a distance of 60 cm. A mask with a circular aperture of 5° in diameter covered the face of the CRT, so that on average 50 visible dots were presented at any one time. The dot density was 2 dots per square degree of visual angle. The dot luminance was approximately 2 log units above detection threshold. The refresh rate of the display was 60 Hz, but to give an optimal impression of motion each dot was plotted in the same position for three consecutive frames before repositioning, so that the effective frame rate of the dots was 20Hz. The duration of each presentation was 500 msec. The initial position of each dot was randomized from trial to trial, and each dot's lifetime was limited to two successive positions on the screen, to eliminate the possibility of determining the overall direction of motion from the extended course of individual dots within the display. The displacement of each dot was controlled by a predefined distribution of directions stored as an array of specific X and Y increments. Fine spatial precision of our display could be achieved by the use of 16-bit digital-to-analog conversion. The dot displacement was 0.25° ; at an effective frame rate of 20Hz this corresponds to a speed of $5^\circ/\text{sec}$.

Experimental procedure

We used an adjustment method described below, in which the subjects had to align the direction of motion of the display with the vertical axis. In the first experiment, the

dots were distributed among four directions of motion spaced at 30° steps, giving a total range of 90° . (Our subjects found considerable difficulty in making a satisfactory judgment of global direction with distributions wider than 90° .) The distribution among the four directions varied from a uniform distribution to the case where 70% of the dots moved in one of the two extreme directions ("0°" or "90°")¹ while the rest of the dots were homogeneously distributed between the other three directions of motion. Besides the uniform distribution, there were five different asymmetric distributions, with 70, 55, 46, 40, and 31 percent of the dots moving in the modal direction. The mode could either be in either of the two extreme directions ("0°" or "90°"). Trials of each kind were blocked (in counterbalanced order), so measurements with the uniform distribution were included within each kind of block. Thus there were a total of 12 conditions. Figure 1 illustrates histograms of some selected distributions, and depicts the linear relationship between the average direction of motion and the percentage of the dots moving in the modal direction across the different conditions of this experiment. Eight adjustments were performed per stimulus condition so that in total 96 matches were performed within an experimental session.

Figure 1 about here

The experiment was initiated by the subject pressing a button. This led to a presentation of a random dot stimulus whose directions of motion were drawn from one of the preselected distributions in that block of trials, with a random angular offset of the distribution as a whole between -60 and +60 degrees. By pressing the right push-button the subject could initiate a new presentation of the stimulus with the whole distribution shifted clockwise by 5° . Pressing the left push-button led to a similar counter-clockwise shift of the distribution. Subjects were instructed to adjust the global direction of the display until it was perceived as vertical upward motion. Two dots, each subtending approximately 0.1 degrees, were continuously visible 3° above and below the center of the display, and served as end points of a virtual vertical line connecting them. These target dots were designed to assist the subject's judgment of vertical upward motion. When the subjects were satisfied, they pressed a third button that led to storage of the offset of the distribution in the trial, and the presentation of the next stimulus condition. No feedback to the accuracy of judgment was given. Each experimental session lasted approximately 30 minutes.

Results

Experiment 1

The performance of subjects in this matching task was examined with reference to two alternative possibilities for computing global direction computation. On a winner-take-all algorithm, the adjusted direction of motion should match the mode of the distribution. On the other hand, vector summation should lead to the adjusted direction of motion following the mean of the motion vectors. Figure 2 shows the average matched direction of motion as a function of the mean direction of the distribution, for each of the five subjects that participated in the experiment². Since there is a linear relationship between the percent of dots in the modal direction and the mean direction of motion in the display (see Figure 1), the data also show the average matched direction of motion as a function of the percent of the dots in the modal direction (upper scale in Figure 2).

Figure 2 about here

The open symbols in Figure 2 are data from the initial run in which subjects were instructed to set to vertically upwards the global direction of motion in the display. The circles and squares are data points for the cases where the mode was at 90° and 0°, (i.e. the most counterclockwise and the most clockwise direction in the display) respectively. Each data point reflects the average direction setting of 16 adjustments over two sessions. The error bars indicate the standard error of the means.

While subjects could make consistent settings of the global direction, they could also perceive that the dot motions were not homogeneous. In later test sessions, therefore, four of the subjects were asked to match the direction of the strongest motion signal in the display. These results are shown by the solid symbols in Figure 2.

Several features are apparent from these results:

- (i) When the distribution of directions is uniform, matches are close to the mean of the distribution, although some individual biases are apparent. This result is consistent with previous studies using uniform distributions (Watamaniuk, et al., 1989)
- (ii) When asymmetry was introduced into the distributions, there were clear and consistent individual differences between subjects. Three subjects (MS, JK and EZ) made settings that diverged from the mean towards the modal direction as the mode became increasingly prominent. This can be described as a kind of compromise between a vector averaging and a winner-take-all result. These results were consistent across the two sessions, and within

sessions showed no trace of a bimodal distribution of settings; thus there was no support for the idea that on some trials they were following a winner-take-all rule and on others a vector average. The other two subjects (OB and JZ), when required to adjust the global direction of motion (Fig 2, open symbols), made settings that remained close to the mean across the range of distributions tested, and so appeared to behave as vector averagers.

(iii) One of the two subjects who showed this vector-averaging behaviour (OB) could generate a completely different pattern of results when instructed to set the direction of the strongest motion signal. Provided that the mode was at least twice as strong as the other directions, his settings approached the true modal direction quite closely (Fig 2, filled symbols). Other subjects show much smaller effects of the alternative instructions, but generally in the same direction.

The differences between subjects imply that different pooling strategies for neural directional signals are potentially available. The existence of flexibility within at least one subject, suggest that at least in this case perceptual judgment cannot be *rigidly* based on a simple summation or competition between neuronal directional signals, or on any algorithm generating a single-valued output.

Figure 3 about here

Experiment 2

Experiment 1 showed that many subjects give an increasing weight to the modal direction compared to the other directions of motion as the mode becomes more prominent. Is this shift in behaviour governed by the absolute strength of the modal motion signal (i.e the number of dots moving in the modal direction), or is it determined by the ratio between the strongest motion signal and the other directional signals? To distinguish between these two possibilities, we designed a second experiment in which the percentage of dots in the modal direction remained constant while the rest of the dots were distributed evenly between a variable number (2-6) of directions (see example histograms in Figure 3). To allow more scope for varying the stimulus within the regime where coherent motion is perceived, directions spaced at 15° intervals were used in this experiment. Figure 3 depicts the relationship between the range of directions and the calculated mean direction of motion in these stimuli. Since the percent of dots moving in the modal direction was kept constant in all stimulus conditions, this experimental design had a useful feature: The difference between the mean direction and the modal direction of motion increases as the range of directions is enlarged. Thus, it allows better discrimination between mean- and mode-sensitive algorithms.

Figure 4 (open symbols) shows the data from three subjects (those who in the first experiment gave increasing weight to the modal direction of motion as the distributions became less uniform). All three subjects closely matched the mean direction of motion when the range of directions was only 30°. However, when the range of directions of motion was expanded further, two of the subjects (EZ, JK) deviated significantly from the mean towards the modal direction of motion (see Figure legend). This suggests that the dominance of the modal direction of motion does not depend on the absolute strength of the motion signal, but rather is determined by the relationship between the strongest motion signal and the remaining directional signals.

Figure 4 about here

The third subject showed only small deviations from the mean towards the mode when the mode was at 0°, and none at all for a 90° mode. This subject repeated the experiment with the instructions to set the strongest direction of motion (MS, filled symbols in Figure 4). In this situation, his responses were closer to the mode across all values of the range of directions in the stimulus. As for OB's results in experiment 1, this is evidence that the computation of motion direction can be task dependent.

Discussion

The visual system can integrate a stimulus containing many different local motion vectors to achieve a global motion percept (Williams and Sekuler, 1984). Subjects can accurately discriminate between two similar global directions of motion. Discrimination thresholds are typically only a few degrees even when the direction of global motion is derived from a Gaussian distribution spanning many tens of degrees (Watamaniuk, et al., 1989). Finally, human observers do not distinguish a display containing only eight directions of motion spanning 180° from a uniform distribution of directions over the same range (Williams, et al., 1991). The authors concluded from these experiments that the output of direction selective mechanisms spaced about 30° apart are combined non-linearly to produce the percept of motion in the direction of the mean of the component directions. However, experiments on the perceived direction of symmetric distributions of motion cannot readily distinguish an algorithm that computes the mean of the distribution from one based on competition between channels in which the strongest signal prevails.

In this study we used asymmetric distributions of directions to test which of these two algorithms might be used by the visual system. The result shown by the majority of subjects in experiment 1 implied an intermediate rule; the mode became progressively more dominant as the proportion of dots moving in that direction increased, but not to the level of a pure winner-take-all algorithm. These results might be described by a model in which directional signals were averaged following a non-linear transformation (e.g. a power-law with exponent greater than one). However, in the second experiment the strength of the motion in the modal direction was constant, but its contribution to perceived direction still increased as the remainder of the distribution was varied. This argues against any simple fixed rule for combining the outputs of directional channels.

The argument against any fixed combination rule is strengthened by the variation between and within subjects. The results encourage the view that the human visual system is remarkably versatile in the way motion signals are interpreted. They suggest that the full distribution of activity from the set of directional channels may be potentially available for perceptual analysis. When required to make a single judgment of global direction, subjects apply strategies for abstracting information from this distribution which may differ between individuals, and in at least one subject can be apply different rules for different versions of the experimental task.

This approach is similar to a suggested model for the analysis of depth judgments based on the activity of neurons tuned to stereo disparity (Lehky and Sejnowsky, 1990). The authors point out that the pattern of activity across the population of neurons cannot be reduced to a single parameter but must be treated as a characteristic representational "spectrum" across different disparity tuned channels. This representation is analogous to the 3-dimensional representation of a coloured light by the activity across three cone types. Depth matches may require the observer to abstract from two different distributions some measure of their similarity. Similarly, we propose that observers' information about the distribution of directions of motion in our display is not restricted to a single parameter. Different aspects (such as the mode or the mean of the distribution) can contribute to judgments depending on the requirements of the task.

Comparison with global speed perception

Our experiments, in which the displays contain a range of motion directions at the same speed, can be compared with a recent analogous experiment which studied the integration of speed information in random dot displays containing various speeds in a single direction (Watamaniuk and Duchon, 1992). This study concluded that human observers always based their discrimination on the *mean* speed of the stimulus, and that

manipulations of the mode of the distribution were not detectable if the mean was kept constant.

The contrast between this result and ours may be explicable in terms of the organization of motion information in area MT. The columnar organization in MT is based on the direction of motion, not the speed of motion. Consequently, neurons within a single direction column share a similar preferred direction of motion but have a wide range of preferred speeds. Thus averaging of motion signals within a column could lead to Watamaniuk and Duchon's findings that perceived speed followed a global mean for a stimulus containing a wide range of speeds (2 octaves), and showed discrimination thresholds very similar to those for stimuli with uniform speed. On the other hand, the computation of motion direction of motion would be based on averaging of the neuronal signals within a relatively limited bandwidth; the neurons' preferred direction within a single column vary by no more than 30-40 degrees, corresponding to the restricted range for which we found consistent perception of the global mean direction. Vector averaging of neuronal signals within a direction column can also explain the observation that the behavioral effect of electrical microstimulation in MT showed directional tuning that was usually substantially narrower than the tuning of single neurons at the stimulation site (Salzman and Newsome, 1994).

An alternative explanation for the apparent averaging across relatively wide range of speeds and a small range of directions is that this simply mirrors the typical bandwidth of neurons in the motion pathway. According to this view, averaging results from the summation of different directional (or speed) components in the response of individual neurons, rather than combination of information across populations tuned to different speeds or directions of motion. Although summation of different motion signals within a single neuron has not been tested directly, the tuning characteristics of MT neurons could fit well the observed psychophysics. MT neurons are typically broadly tuned for speed, with an average bandwidth is roughly 2.5 octaves (full width at half maximal rate), while their direction bandwidth is approximately 80° (Maunsell and Van Essen, 1983, Rodman and Albright, 1987).

Motion transparency

If the entire distribution of directional channel activity is available for perceptual analysis, this can provide a basis for perceiving more than one direction of motion simultaneously in the display. We restricted the directional range to 90° because with wider ranges, our subjects found it difficult to assign a single direction of motion. It is clear that the 'coherent global motion' reported by (Williams and Sekuler, 1984) using broader

distributions does not necessarily imply a perception of uniform motion (see footnote on p. 938 of Watamaniuk & Duchon, 1992). We conclude that subjects' judgment of global motion as present or absent in Williams and Sekular's experiment required a less stringent criterion than the directional settings required in our experiments (our dot density and step size were close to Williams and Sekular's optimum).

We do not yet know the conditions under which two or more transparent motions are explicitly extracted from the distribution of directional activity. Watamaniuk & Duchon, (1992) suggest that perception of transparency is task-dependent. They propose that the same distribution of speeds can be averaged when a global speed judgment is required, but segregated into separate planes for a three-dimensional structure-from-motion judgment – a proposal which is clearly consistent with the flexibility in processing velocity distributions that is apparent in our results.

The perception of transparency raises the issue of the spatial extent over which a description of motion is computed. Qian and Andersen (1994) report that when superimposed dot patterns moving in opposite directions are locally balanced, transparency is not perceived; that is, at a sufficiently local level, the representation of motion is single-valued, but different local motion signals from neighbouring locations can be integrated into a global perception of transparency. The properties of single neurons in MT are consistent with local combination to a single motion signal (Qian and Andersen, 1994, Qian, et al., 1994, Snowden, et al., 1991). Thus it is possible that the flexible global integration processes studied in this paper are associated with the requirement to combine information over an extended area, and that the processing of the directional distribution arising from a single location depends on more specific neural interactions such as the mutual suppression of directions implied by the results of Snowden et al. (1991)

In conclusion, a full account of these phenomena needs to consider several possible levels of interaction: (a) the summation of signals within the tuning bandwidth of single neurons, and interactions between neurons with overlapping receptive fields that determine the activity of these neurons; (b) computations carried out independently within the bandwidth of directions and speeds handled by specific motion channels (possibly corresponding to direction columns in MT), that determine motion averaging and possibly transparency effects; (c) the processing of patterns of activity across a range of direction columns and spatial locations. In the latter case at least, the visual system appears to use an adaptable algorithm to compute global motion, which cannot be simply described as winner-take-all or vector averaging. In particular, it seems clear that observers can pay attention to different aspects of the distribution of activity depending on the requirements of the task they perform.

Footnote

1. In describing the distributions, 0° and 90° refer to the relative angles among the directional components, and not to any absolute direction. The absolute direction at the beginning of each adjustment was randomized as described, and at the end of the adjustment was determined by the subject's setting.
2. The mean direction of motion as computed in Figures 1-4 is the weighted scalar mean of the angles rather than the vector average. However, with the relatively narrow distributions of directions used in these experiments, the difference between this weighted scalar mean and the direction of the vector average would never exceed 1° .

Figure Legends

Figure 1: The linear dependence of the calculated mean direction of motion on the percentage of dots moving in the modal direction, for the stimulus set used in Experiment 1. The stimuli contained four directions of motion in which a certain percentage of the dots moved in the modal direction (25-70%) while the rest of the dots were distributed evenly between the other three directions of motion. The histograms depict a few example cases of the distributions of directions of motion used in this experiment (range, 0°-90°; see footnote 1). The mode was at either of the two extreme directions. Filled and empty squares denote the conditions in which the mode was at 0° and 90°, respectively.

Figure 2(a-e): The perceived direction of motion as a function of the calculated mean direction of motion in the stimulus for five subjects in experiment 1 (see Figure 1 for stimuli). The data can also be interpreted as a function of the percent of the dots in the modal direction (upper scale). If a Winner-Take-All algorithm is implemented by the visual system the perceived direction of motion should match the mode of the distribution (following the step function), whereas vector summation should lead to matches of the mean direction of motion in the visual stimulus (following the main diagonal). Circles and squares correspond to matches when the mode was at 90° and 0°, respectively. Open symbols are the average settings when the subjects attempted to match the global direction of motion, filled symbols are average settings for attempting to match the most dominant direction of motion. Symbols represent the average of 16 settings per data point across two sessions. Error bars denote standard error of the mean.

Figure 3: The mean direction of motion as a function of the range of directions in the visual stimulus for the stimulus set used in Experiment 2. The percentage of dots in the modal direction was 50% in each of the distributions shown. The directions of the rest of the dots were distributed evenly between a variable (2-6) number of directions, spaced at 15° intervals. The histograms depict a few example stimuli in a similar fashion to the ones shown in Figure 1. Filled and empty squares denote the conditions in which the mode was at 0° and 90°, respectively.

Figure 4: The perceived direction of motion as a function of the calculated mean direction of motion in Experiment 2 (see Figure 3 for stimuli). The data can also be interpreted as a function of the range of directions in the visual stimulus (upper scale). Again, Winner-Take-All algorithms would predict a match to the mode of the distribution (following the step function), whereas vector summation should lead to matches of the mean direction of motion in the visual stimulus (following the main diagonal). Symbols represent the average of 10 settings per data point. Error bars denote standard error of the mean. The percentage

of the dots in the modal direction was set at 50% for subjects E.Z. and J.K. (a,b). Statistically significant deviations from matches following the mean direction of motion are denoted by asterisks; (* = $P<0.01$; ** = $P<0.001$, unpaired t-test). In initial tests with the same set of stimuli, subject M.S. set the matches close to the mean direction of motion. We therefore repeated the experiment with even a more prominent directional signal in which 70% of the dots moved in the modal direction. The results of this experiment are shown by the open symbols in (c). M.S. repeated the experiment trying to match the most prominent direction of motion. These data are depicted by the filled symbols in (c).

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To Add: Celebrini & Newsome JND (1995)
"Microstimulation of extrastriate area MST influences performance on a direction discrimination task"

Fig 1







