

Phase is thought to be encoded by even and odd symmetric detectors in the human visual system¹⁹. It has further been shown that the sensitivity of the odd, but not the even, symmetric mechanism is reduced in peripheral vision²⁰. This would account for the disappearance of Mach bands in the periphery, at contrasts well above those required for the independent detection of out-of-phase harmonics.

Although the generally accepted explanation of Mach bands is that they are due to lateral inhibition, several investigators have noted the problem this presents for square waves and sharp edges^{2,5,6,16} and have considered other possibilities. Tolhurst observed that even symmetric receptive fields (which he termed bar detectors) may signal Mach bands¹⁶. He also speculated that for the square wave the response of odd symmetric fields (edge detectors) may inhibit that of the even symmetric fields (bar detectors), so no stripes are seen (see also ref. 6). Watt and Morgan's²¹ general theory of spatial vision also predicts bar signals at the border of a ramp, provided that they are far enough apart. Both these ideas have some similarity to ours, but our results (and simulations to be reported in a fuller paper) suggest that inhibition between edge detectors and bar detectors is unnecessary.

Finally, we note that trapezoids, like square waves and synthetic 'all positive' trapezoids, show zero-crossings at all scales at the mean luminance point. If edges were encoded by align-

ments of zero-crossings, as has been assumed²²⁻²⁴, all should have edges at that point. But trapezoids do not. A model seeking phase congruence as the signature of bars and edges, built on adequate basis functions, can without ambiguity, locate edges and bars where we see them.

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Hysteresis in the perception of motion direction as evidence for neural cooperativity

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When elements of a parallel network, such as the human brain, are extensively interconnected, the network can exhibit 'cooperative behaviour'. Such behaviour, which is characterized by order-disorder transitions, multi-stable states, and a form of memory called 'hysteresis', has been observed in human stereopsis^{1,2} and has motivated models of stereopsis that incorporate cooperative networks³⁻⁶. More recently, cooperative phenomena have also been observed in human visual motion perception⁷. This report strongly supports a cooperative interpretation of motion perception by demonstrating hysteresis in the perception of motion direction. The results agree quantitatively with a mathematical model incorporating nonlinear excitatory and inhibitory interactions among direction-selective elements.

Our stimuli were dynamic random dot cinematograms comprising 512 computer-generated dots. Each dot took an independent, two-dimensional random walk of constant step size (0.9°). The direction in which any dot moved was independent of its own previous displacements and also of the displacements of the other dots⁸.

The direction of motion for each dot was chosen from either (1) one of two uniform distributions, or (2) a mixture of these two distributions. When all dots drew their movements from a uniform distribution extending over 360°, only the 'local random motion' of individual dots was evident. This resembled a detuned television set. However, when all dots drew their movements from a uniform distribution of 180° or less, the dots appeared to flow *en masse* in the direction of the distribution mean—although individual perturbations were still evident. This resembled snowflakes that, although individually perturbed by wind currents, seem to drift in one direction. In all experiments the mean of the signal distribution was upward.

For convenience, we refer to the 180° and 360° distributions as the signal and noise distributions, respectively. When dots drew their movements from a combination of these distributions, each dot's displacement came randomly from either distribution. The resulting perception depended upon the relative proportions of noise and signal.

Two types of trials were run in random order. In one, the direction of motion for each dot was chosen initially from the signal distribution, producing a perception of upward flow. After a random interval lasting up to 12 seconds, the proportion of dots drawing directions from the signal distribution was decreased and the proportion of dots drawing directions from the noise distribution was increased. The observer responded when the cinematogram changed in appearance from upward flow to local random motion. After this response, the proportion of signal continued to decrease for a random interval (up to 6 seconds). The process was then reversed, with the proportion of signal increasing until the subject responded that the upward flow had reappeared. This terminated the trial. For the second trial type, the stimulus sequence was reversed. We started with an initial percept of local random motion, and measured the points of transition to a perception of upward flow and back again to local random motion. These two different trial structures—signal-first and noise-first—were designed to produce different histories of directional exposure and thus reveal any perceptual effects dependent upon the history of stimulation. For both trial types, the signal to noise ratio changed slowly, with the proportion of dots sampling from each distribution changing by just two dots per frame. At the frame rate of our display, 10 Hz, it took a minimum of 25 seconds for the display to shift from complete dependence on one distribution to complete dependence on the other.

Observers used one eye to watch the centre of a circular display 16° in diameter. The dots were presented at twice threshold luminance against a dim background. Over the course of 5 sessions we made 100 measurements of the signal proportion at the two perceptual transitions for each of our three naive observers.

We repeated this experiment with two narrower ranges of signal distribution: 90° and 1°. Each of the three signal distributions generated a different history of exposure. We expected that, as the distribution narrowed, the signal would become

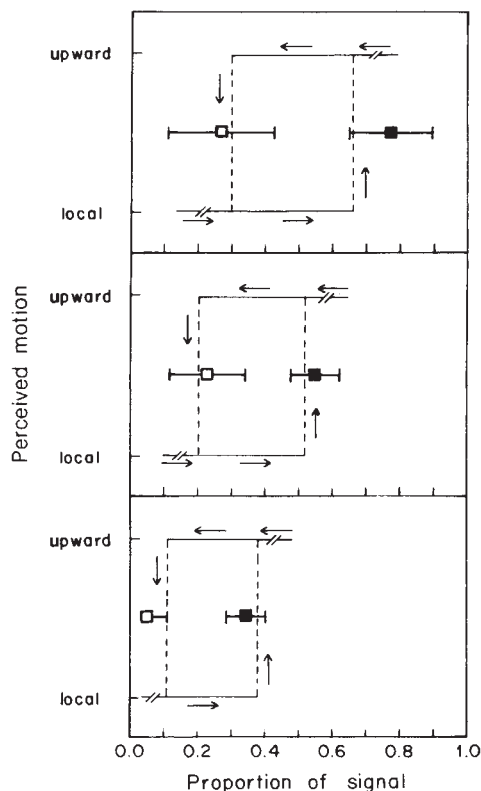


Fig. 1 Perceptual transitions measured under two different histories of stimulus exposure (indicated by arrows) for three signal distributions. The results, for observer J.F., were obtained for signal distributions whose ranges were: top, 180°; middle, 90°; bottom, 1°. Data points show proportion of 'signal' dots required for perceptual transition from local random motion to upward flow (■) and for perceptual transition from upward flow to local random motion (□). Error bars indicate one standard deviation (100 measurements). In each panel the separation between transition points measured with the different exposure histories is an index of hysteresis. The dashed lines mark the transition points calculated from a model incorporating cooperative interactions among direction-selective motion elements.

more effective in stimulating directionally selective visual elements that are tuned to upward motion. As a consequence, the occurrence of a transition between perceived states would require fewer signal dots.

The results for one observer are shown in Fig. 1; similar results were obtained for the other observers. Each panel shows data for a different range of signal. Note that the transitions differ for the three signal ranges. More importantly, the transition from noise-to-upward flow requires a larger number of dots sampled from the signal distribution than does the transition from upward flow-to-noise. For all three signal distributions, the two types of transition occur at significantly different ratios of signal to noise ($P < 0.005$).

Before attributing our results solely to neural hysteresis, a number of alternative explanations were considered and rejected. For example the motion after-effect, or waterfall illusion, did not produce our results as this after-effect would probably have facilitated, rather than retarded, the transition from upward motion to noise. Also, the results were largely unchanged by the use of a fixation point, suggesting that eye movements probably played little or no role. Finally, reaction time could be dismissed given the slow time course for changing the signal proportion.

Before developing a simple network that could describe our results, we needed a fuller account of how spatial parameters

might affect hysteresis. Using a 180° signal distribution, we made measurements (1) with a four-fold decrease in the spatial density of the cinematogram's dots, (2) with a four-fold decrease in the area of the display and (3) with the display shifted horizontally into the periphery of the visual field so that the nearest dot was 4° from fixation. None of these variations produced results that differed greatly from our original measurements. Of course, extreme changes in these display parameters would undoubtedly alter the hysteresis characteristics. However, because of these data and demonstrations suggesting that spatial variables have little effect on the dot interactions responsible for motion in cinematograms^{8,9}, we chose not to treat space explicitly in developing a model network to describe our results.

The model comprises a set of direction-selective mechanisms covering all 360° of motion direction, with each direction-selective mechanism having a gaussian profile for directional sensitivity. Based on previous results from our laboratory, the half-amplitude half-bandwidth of each mechanism's gaussian sensitivity profile was set to 30° (ref. 10). The model, whose mathematical formulation is a modification of the cooperative neural network previously proposed⁴, assumes non-linear excitatory interactions among mechanisms sensitive to similar directions of motion and non-linear inhibition among mechanisms sensitive to different directions. The dynamic response of this cooperative system is represented by a pair of coupled differential equations. For the excitatory activity, E_i , in direction channel i :

$$dE_i/dt = -E_i + (1 - E_i)S\left(P_i + \sum_j a_j E_j - \sum_j b_j I_j\right)$$

where S is a nonlinear function of sigmoidal shape, P_i is the external input to channel i , and a_j , b_j are the excitatory and inhibitory weights, respectively, of channel j with respect to channel i . A similar equation gives the inhibitory activity I_i , in channel i . In general terms, such interactions promote the formation of stable 'coalitions' among similarly tuned elements within the network¹¹. These neural coalitions can in turn produce various cooperative properties, including hysteresis.

The parameters of the model were constrained so that the model behaved in what is defined⁴ as the active transient mode. In this mode the system shows hysteresis, switching between different states of activity. In the model simulation the perception of local random motion is represented by a steady state of uniform activity across all mechanisms. Global upward flow is represented by a steady state in which the activity is localized about the mechanism selective for upward movement. A transition point is defined by the proportion of signal at which the network switches between these two states of activity. The results from the model are shown in Fig. 1. Dashed lines mark the transition points calculated from the model using a single parameter set. It can be seen that the model captures both the leftward shift and narrowing of the hysteresis profile with decreasing signal range. The model's behaviour here is readily explained. With decreasing signal range more activity is concentrated in fewer motion-selective elements arrayed about the upward direction. Consequently, a smaller proportion of signal dots suffices to indicate upward movement. In addition, fewer active elements reduces the opportunity for cooperative interactions in the network, which translates into a narrowing of the hysteresis profile².

If we accept the idea that the perception of motion direction depends upon a cooperative neural network, there may be circumstances outside the laboratory in which this network's cooperativity might be especially useful. Observers must extract a mean direction vector from a scene containing a great many different local vectors in many naturally-occurring situations. For example, we can judge the average direction in which the ocean's surf moves despite the fact that individual waves move along somewhat different paths; or we can judge the average

direction in which the wind blows the leaves of a tree despite the random variation of that movement from one leaf to the next (or for any one leaf over time). Faced with such multivectorial stimuli, a cooperative network like the one embodied in our model would enhance the signal-to-noise ratio and thereby facilitate the perception of the mean direction of motion.

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Inhibitory neurones of a motor pattern generator in *Xenopus* revealed by antibodies to glycine

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Glycine and γ -aminobutyric acid (GABA) are inhibitory transmitters of major importance^{1,2}. Whereas neurones using GABA as the transmitter can be visualized by immunocytochemical methods for glutamate decarboxylase (GAD)^{3,4} or GABA⁵⁻⁸, no comparable techniques have been available for the selective visualization of glycinergic neurones. We have now produced polyclonal antibodies which specifically recognize glycine in glutaraldehyde-fixed tissue. We used these antibodies to investigate the distribution of glycine in the simple central nervous system (CNS) of the *Xenopus* embryo, which contains an anatomically and physiologically defined class of reciprocal inhibitory interneurons, the commissural interneurons⁹⁻¹¹. These interneurons have an important role in the generation of the swimming motor pattern and are thought to be glycinergic¹¹⁻¹³. The glycine antibodies specifically stain these interneurons, revealing their distribution and number in the embryo CNS. This is the first demonstration of the selective localization of glycine-like immunoreactivity in a putative glycinergic class of neurone that has been characterized physiologically, pharmacologically and anatomically.

Evidence for glycine as a transmitter in the vertebrate spinal cord has been based on four types of information: the actions of exogenous glycine^{14,15}, specific blockade by the antagonist strychnine^{14,15}, the depletion of glycine following ischaemic degeneration of spinal interneurons^{16,17} and the demonstration of neuronal uptake of ³H-glycine¹⁸⁻²¹. However, antagonism of an inhibitory postsynaptic potential (i.p.s.p.) by strychnine is not unequivocal evidence that glycine is the endogenous transmitter: the hyperpolarizing actions of β -alanine and taurine (amino acids closely related to glycine; Fig. 1) are also blocked by strychnine². In the absence of further evidence β -alanine

and taurine must therefore also be considered as candidate transmitters. We decided to raise antibodies which could selectively recognize glycine in glutaraldehyde-fixed nervous tissue and could be used to localize glycine in neurones. Modifications of our methods^{5,6} have been used previously by Pourcho and Goebel²² to produce and test a glycine antiserum which marks cells in the cat retina and brain stem.

Glycine was coupled to carrier proteins by means of glutaraldehyde as described previously⁵. As suggested by Seguela *et al.*⁷, the carrier protein was changed, here for each immunization, to avoid boosting the immune response to the carrier protein and any particular configurations of the glycine-glutaraldehyde complex that might depend on the protein (Fig. 1 legend). Unwanted antibodies recognizing glutaraldehyde-treated amino acids and proteins were removed by immunosorbent chromatography on a sequence of columns (Fig. 1 legend). The purified antiserum was initially tested for crossreactivity with a series of compounds conjugated by glutaraldehyde to a total macromolecular extract from rat brain and spotted on cellulose ester filters⁶. The compounds were GABA, taurine, phosphoethanolamine, β -alanine, L- α -alanine, valine, leucine, proline, serine, threonine, tryptophan, tyrosine, histidine, lysine, arginine, ornithine, aspartate, N-acetylaspartate, glutamate, asparagine, glutamine, methionine, cysteine, reduced glutathione, α -aspartylglycine, carnosine, homocarnosine, cadaverine, putrescine, spermine and spermidine. While the glycine conjugate was intensely stained, none of the other conjugates were stained appreciably darker than 'null' conjugates (macromolecular extract treated with glutaraldehyde in the absence of amino acid). The staining was abolished by solid-phase absorption with glycine fixed to ovalbumin or to lysine by glutaraldehyde (Fig. 1 legend).

To check the specificity of these antibodies in the *Xenopus* embryo we made two different sets of conjugates, one of macromolecules from whole embryos and one of macromolecules from the CNS of adult *Xenopus*. To ensure identical conditions for testing and immunocytochemistry, the test filters with these conjugates were processed in the same vessels as the tissue preparations. The tissue consisted of the CNS of *Xenopus* embryos stage 29/30 to 37/38 (ref. 23) raised by induced breeding in Bristol, fixed in glutaraldehyde and shipped to Oslo for dissection and processing⁶ of the CNS.

The results with *Xenopus* conjugates (Fig. 1a) were similar to those with rat brain conjugates. A glycine-glutaraldehyde complex, added to the diluted antiserum (at a final concentration of 100 or 300 μ M with respect to glycine) completely abolished staining of the glycine spots and of the tissue (Fig. 1e, f). Complexes of β -alanine (Fig. 1c, d), L- α -alanine, GABA or reduced glutathione (all at 300 μ M), or a mixture of individual glutaraldehyde complexes of taurine, aspartate, glutamate, glutamine and serine (all at 300 μ M) produced no reduction in the staining of glycine test spots (the converse is seen in ref. 32) or tissue.

The *Xenopus* embryo spinal cord appears on the basis of retrograde horseradish peroxidase (HRP) filling to contain eight anatomically distinct neurone classes⁹. One of these, the commissural interneurons, is defined by the following anatomical features⁹: (1) a unipolar soma in a middle to dorsal position in the cord, (2) a single ventral process bearing dendrites that extend laterally into the marginal zone (lateral tract) and (3) an axon crossing ventrally to ascend and sometimes also descend contralaterally (Fig. 3a). These neurones have been shown by intracellular recording and HRP injection to be active during fictive swimming¹⁰ and to produce mid-cycle i.p.s.ps in contralateral motoneurons¹¹. The mid-cycle i.p.s.ps in motoneurons and the response to exogenous glycine (100 μ M) have a reversal level near the resting potential, depend on an increase in chloride permeability and are unaffected by 10 μ M bicuculline, but are blocked by 1 μ M strychnine^{11,13,24}. The commissural interneurons may therefore be glycinergic.

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