Vision Res. Vol. 27, No. 4, pp. 547–554, 1987
Printed in Great Britain.

0042-6989/87 $3.00 + 0.00

PERCEPTION OF RANDOM-DOT SYMMETRY AND APPARENT MOVEMENT AT AND NEAR ISOLUMINANCE

TOM TROSCIANKO*
Universitäts-Augenklinik, Schleichstr 12, D-7400 Tübingen, F.R.G.

(*Received* 19 *June* 1986; *in revised form* 18 *August* 1986)

Abstract—There have been conflicting reports on whether apparent movement in random-dot kinematograms is abolished at isoluminance. The present results suggest that it is, provided that dynamic (uncorrelated) surrounds are used, and the subject has to report the shape of the target rather than the presence of movement in an isolated portion of the target. On the other hand, perception of random-dot symmetry is still possible at isoluminance. The reason for this difference appears to be the need for exact-position informatin in movement but not symmetry perception. Control experiments suggest that the effects are not due to artefacts such as chromatic aberration in the eye.

INTRODUCTION

The literature on what happens to vision at "isoluminance" has been expanding in recent years. The theoretical impetus for this work has been varied. Some, such as Gregory (1977), argue that vision with pure colour contrast can be a means of finding out how the brain treats colour information: the psychophysicist's answer to Zeki's (1978) and other physiological and anatomical mapping of the brain by functional specialisation. An example here is the argument by Ramachandran and Greogory (1978), Srinivasan (1985), and others, that motion detectors may be insensitive to wavelength.

There has been another approach, seeking to explain isoluminant phenemena by means of peripheral organisation of receptive fields and consequent frequency bandpass characteristics. An example here is the work of Mullen (1985), who measured csf's at a variety of luminance contrasts including isoluminance. The findings (that isoluminance gives superior low spatial frequency detectability but worse acuity) are explained in terms of post-receptoral opponent channels. Further, Mullen and Baker (1985) argue that, if care is taken to eliminate artefacts resulting from, say, chromatic aberration, "the preliminary conclusions that motion-detecting mechanism(s) fail or function poorly at isoluminance . . . must be reconsidered." Thus, it is argued, it is sufficient to consider two low-level explanations of the phenomena: one dealing with post-receptoral opponent processes, and the other with the difficulty of actually producing an isoluminant stimulus on the retina.

Since there is fundamental disagreement about something as basic as whether motion is actually seen at isoluminance, a theoretical understanding of the phenomena is made difficult. Ramachandran and Gregory (1978) argue that apparent motion in random-dot kinematograms disappears; Cavanagh *et al.* (1985) say that it is still visible but that the boundaries of the moving figure become indistinct; Cavanagh *et al.* (1984) and Moreland (1980) show that isoluminant real movement appears considerably slower than with even small amounts of luminance contrast; but Mullen and Baker (1985) show that movement aftereffects from such gratings are just as strong. A similar level of disagreement is found in the literature on stereopsis, with Lu and Fender (1972) claiming that stereopsis is abolished at isoluminance, but DeWeert and Sadza (1983) showing that 2AFC performance always remains above chance, and Grinberg and Williams (1985) showing that stereopsis, both of the random-dot variety and of the line variety, is still possible under conditions when only blue (non-luminance) receptor channels contribute to the percept. Thus, the reader is left with a dilemma: does anything (except consensus between investigators) actually disappear at isoluminance?

The purpose of these experiments was to investigate two visual tasks at and near isoluminance. A differential effect can be expected to provide a richer understanding of the under-

*Present address: Brain and Perception Laboratory, Department of Anatomy, University of Bristol, Bristol BS8 1TD, England.

lying mechanisms than an isolated experiment. One of these tasks was the perception of apparent movement in random-dot patterns (Braddick, 1974), and the other was the perception of mirror-symmetry, also in random-dot patterns (as in Barlow and Reeves, 1979). The reason for selecting apparent movement is that, although so much disagreement still surrounds the perception of AM at isoluminance (see above), most investigators agree that the percept is much weaker; symmetry perception was studied because earlier work (Troscianko, 1984, 1985) suggested that symmetry is still seen at isoluminance. However, this earlier work on symmetry (and much of the work on AM) was susceptible to the criticism that artefacts such as chromatic aberration may have affected the results. Thus, it was felt that a direct comparison of the two processes should yield revealing data, particularly if control experiments were to suggest that artefacts were not of primary importance.

METHODS

The stimuli were generated using a colour graphics system described in detail elsewhere (Troscianko and Low, 1985). Basically, a monochrome, non-interlaced computer-graphics image, in this case generated on a British Broadcasting Corporation microcomputer, is transformed to a two-colour image, where the (white) foreground is transformed to Colour A and the rest of the screen to Colour B, where both colours are 8-bit selectable in each of the R, G and B channels. Thus, a palette of some 16.7 million colours is available for both the foreground and the background. It is then relatively simple to vary only the luminance of one of the colours while keeping its chromaticity approximately constant.

The coloured stimuli were presented as yellow foreground on a green background. Chromaticity coordinates were yellow $u' = 0.20$, $v' = 0.55$; green $u' = 0.13$, $v' = 0.56$ (as measured on a Bentham Instruments spectroradiometer). The luminance of the green background was kept constant at 270 cd/m^2 (SEI photometer). The luminance of the yellow foreground was adjusted to lie at, and on either side of the isoluminant point. The latter point was determined by counter-flicker photometry at 12.5 Hz.

A Digivision CD14 R, G, B monitor was used. Viewing distance was 1 m. Viewing was monocular through the dominant eye, with an artificial pupil of either 1, 2 or 5 mm diameter. The artificial pupils were matched for retinal illuminance by the provision of suitable ND filters on the two larger sizes.

Stimulus presentation time was 0.5 sec in the case of symmetry perception and 1 sec in the case of apparent movement. This difference in presentation times was designed (a) to lessen the chances of eye movements in the symmetry task, and (b) to allow more than 1 cycle of the apparent movement (and since perception of AM is impaired, a longer presentation time should only improve performance). In each case, an auditory warning was given shortly before each presentation, and auditory feedback followed a correct response.

Screen subtense was 15.7 deg (h) by 11.7 deg (v). For all experiments, a central fixation point was provided, surrounded by an opaque black disc subtending 2.9 deg. This was (a) in order to eliminate foveal vision which has a somewhat different isoluminant match point from the rest of the near periphery (probably due to macular pigmentation), and (b) to provide a large and readily visible negative afterimage in the case of eye movements, which were thus more readily avoided. This disc was affixed in the centre of the display screen for all the symmetry experiments. For the apparent movement experiments, it was affixed 3 deg below the centre of the screen.

Stimuli for symmetry consisted of two displays each containing 80 small squares (subtense 0.29 deg), the centre of one display being 3 deg above, the other 3 deg below the fixation mark. One of these was symmetric about a vertical midline axis, the other one was random. Both displays lay within an area of 8 deg (h) by 3.4 deg (v). The subject had two response push-buttons and had to press one of them to indicate whether the symmetry was at the top or at the bottom of the display. The computer scored correct responses and reaction time. Auditory feedback was given after a correct response.

The apparent movement stimuli consisted of random-dot kinematograms of the kind used by Braddick (1974). The surround consisted either of dynamic (i.e. uncorrelated) squares or static (correlated) squares and the central stimulus was a rectangle subtending 3.2×1.6 deg. The correlated components of the rectangle moved in apparent motion in a horizontal direction, with an amplitude of 0.2 deg. The duration of each stationary phase of the cycle was 200 msec, with an ISI lasting only a few milliseconds (screen blanking interval). The substance of the whole kinematogram was 9.5 deg^2. The target rectangle was in the centre of the screen, thus it was seen 3 deg above fixation. In half of the stimuli it was oriented with its long axis vertical, in the other half the long axis was horizontal. Subjects had to respond "vertical" or "horizontal" by pressing one of two pushbuttons. In the case of dynamic surrounds, the task involved perceiving not just the isolated movement of one or few component units, but knowing the shape of the embedded stimulus. Auditory cueing and feedback were the same as in the symmetry experiments. As in the case of the symmetry experiments, the computer counted correct responses and reaction time.

Two subjects took part in the experiments. One was the author (male, aged 33, normal vision), the other was naive to the purposes of the experiment (male, aged 28, normal vision).

In all experiments, 160 stimulus presentations were given per condition (e.g. contrast level). These were grouped into eight blocks of 20 presentations. Each block gave a mean correct score and mean reaction time. Each data point in the next section is a mean of these eight values, with error bars denoting ± 1 SE. The order of conditions was randomised.

RESULTS

Apparent movement

Figure 1 shows the results of the apparent movement experiment, in which the subjects viewed the display through a 2 mm dia pupil with a 25% transmittance ND filter fitted to the pupil: see the next section. It can be seen that performance on the 2AFC task at isoluminance is not significantly above chance, but rises to above-chance levels at all other contrast values.

When the same experiment is repeated with a static (correlated) surround, there is still a decrease in performance at isoluminance but the proportion of correct respnses remains above chance. This is shown in Fig. 2.

Symmetry

Compared to the apparent movement data, the effect of isoluminant presentation on performance is much reduced: see Fig. 3. Viewing conditions were the same as for the movement experiments.

At all luminance contrast levels, performance remains above chance and the curve appears to be more broadly tuned than the apparent movement data.

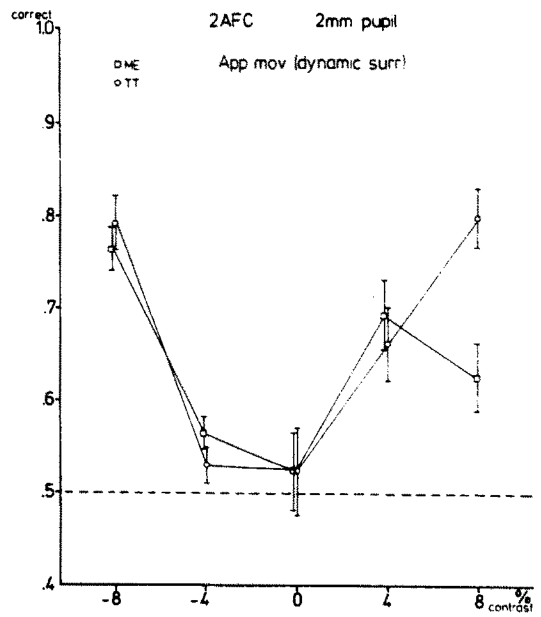

Fig. 1. Performance in 2AFC apparent movement experiment. Subjects had to distinguish between a horizontal and vertical target rectangle which was moving in short-range apparent movement with an amplitude of 0.2 deg. Surround was dynamic (uncorrelated). Zero contrast refers to each subject's isoluminant point, as measured by counterflicker photometry at 12.5 Hz. Chance performance level is indicated by dashed line at 0.5 ordinate. Monocular viewing through 2 mm diameter artificial pupil.

Reaction-times in both experiments were almost always shorter with better performance, thus arguing against a speed-accuracy tradeoff.

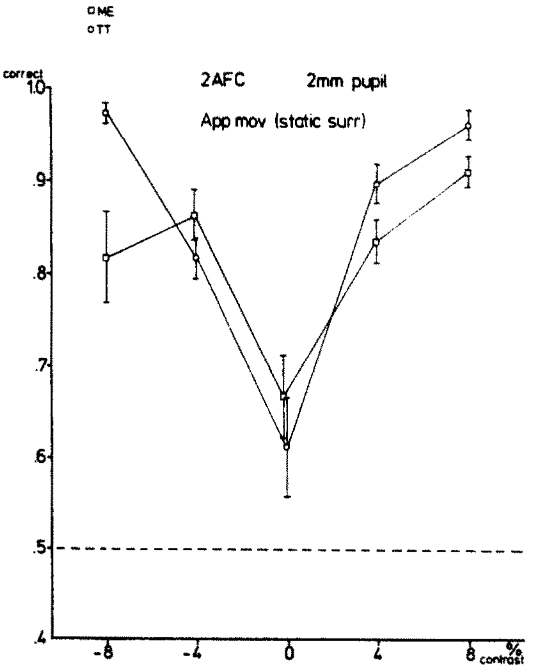

Fig. 2. As Fig. 1 but with a static (correlated) surround.

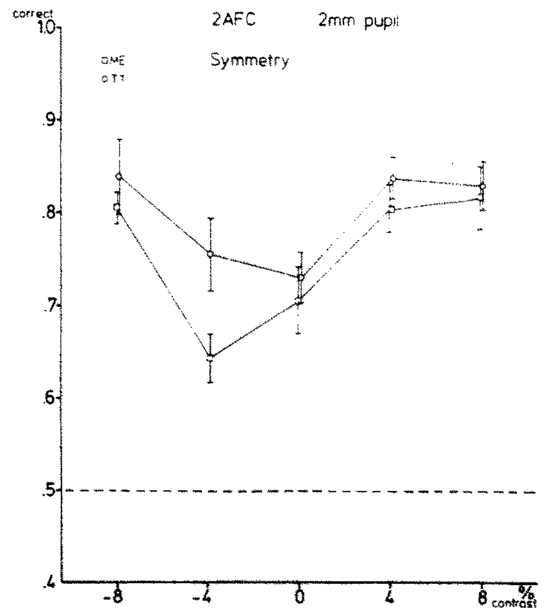

Fig. 3. Performance in 2AFC mirror-symmetry detection experiment. Subject's task was to say whether the symmetry was in the top or the bottom part of the screen. Viewing conditions were the same as in the apparent movement experiments.

CONTROL FOR CHROMATIC ABERRATION

It has been suggested (e.g. by Mullen and Baker, 1985) that attempts to measure the perceptual effects of isoluminant viewing are confounded by an inability to remove the effects of chromatic aberration known to prevail in the eye. One attempt to reduce the size of any artefact in the present data is viewing through a 2 mm pupil. The effects of this are to reduce the blur circle diameter on the retina compared to viewing the display through a natural pupil (diameter >5 mm). However, it might still be argued that chromatic aberration contributed to the results. Thus, a series of control experiments was performed to measure the likely effect of chromatic aberration in the present conditions.

Chromatic aberration renders the eye increasingly myopic with decreasing wavelength (e.g. see Wyszecki and Stiles, 1967). The resulting differences in blur as a function of wavelength can be expected to affect retinal illuminance in a way which depends on the accommodation of the lens. Attempting to focus one wavelength leads to a reduced illuminance in another, defocussed wavelength. Clearly, one can paralyse accommodation and include an achromatising lens in the system; but the former is uncomfortable for the rather time-consuming 2AFC experiments, and the latter is expensive and in some cases of dubious value. It should be simpler to compare performance when viewing through several artificial pupils matched for retinal illuminance but varying in diameter. The larger the diameter, the greater the expected effects of chromatic aberration.

Note that this applies to longitudinal chromatic aberration. There is also transverse aberration, i.e. a sideways shift of the image, which will be unaffected by pupil size. Another function of these control experiments was therefore to try to distinguish between these two mechanisms.

To look for longitudinal aberration effects, the apparent movement and symmetry experiments were repeated in part, when viewing the display through pupils having diameters of 1, 2 or 5 mm. These were matched for retinal illuminance by attaching appropriate neutral density filters to the discs containing the pupils (which were inserted into a trial frame). The 2 mm pupil/ND filter combination was the same as in the main experiments. Only the +8%, 0 and −8% contrast levels were used, and only the dynamic (uncorrelated) surrounds were used in the random-dot kinematograms. The same two subjects participated in these experiments. Subject T.T. was run on all three pupil sizes; subject M.E. only received the 2 and 5 mm sizes.

If chromatic aberration significantly contributes to performance, it is to be expected that there will be an effect of pupil size. Specifically, one would predict:

(a) that the apparent movement data, where a small contrast change away from isoluminance results in a large change in performance, should show a big effect, particularly for isoluminant presentations,
(b) that any effect on symmetry perception should be smaller, and
(c) that the larger the pupil size, the higher the performance level should be.

Figure 4 shows the results of the apparent movement control experiments, and Fig. 5 the corresponding data for the symmetry experiments. It is readily apparent that none of the predictions (a)–(c) above is upheld. Note that the apparent movement performance is not significantly different from chance at all three pupil sizes. There may be some indication that the 5 mm pupil allows slightly above-chance performance, possibly due to a very small aberration effect (a luminance contrast of some

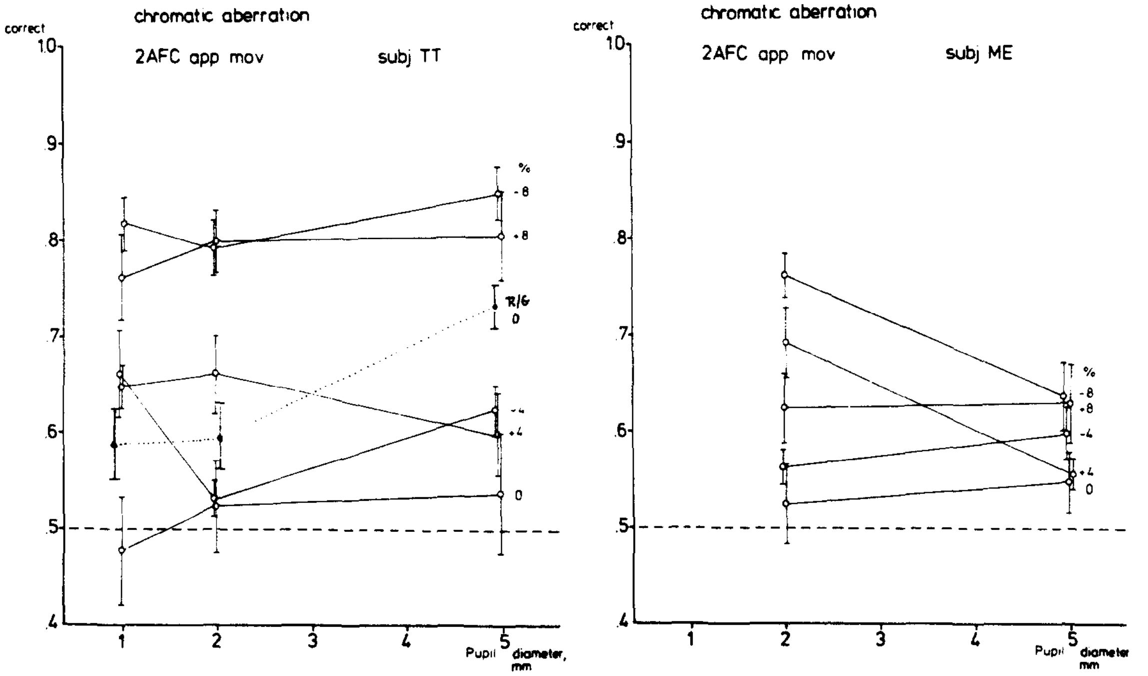

Fig. 4. Performance in the apparent-movement shape discrimination task as a function of increasing artificial pupil diameter (all pupils were matched for retinal illuminance using ND filters). Results for subject T.T. on left, for subject M.E. on right. If chromatic aberration has a significant effect one would expect the graphs to show a significantly positive slope. The dotted line for subject T.T. shows results with an isoluminant red-green, rather than a yellow-green image.

0.5% would give a similar improvement in performance).

The lack of a positive gradient in the isoluminant apparent movement data may simply indicate that it is the transverse chromatic aberration which is more important, and thus we need to show that the pupil-varying method can, in principle, give a positive-gradient func-

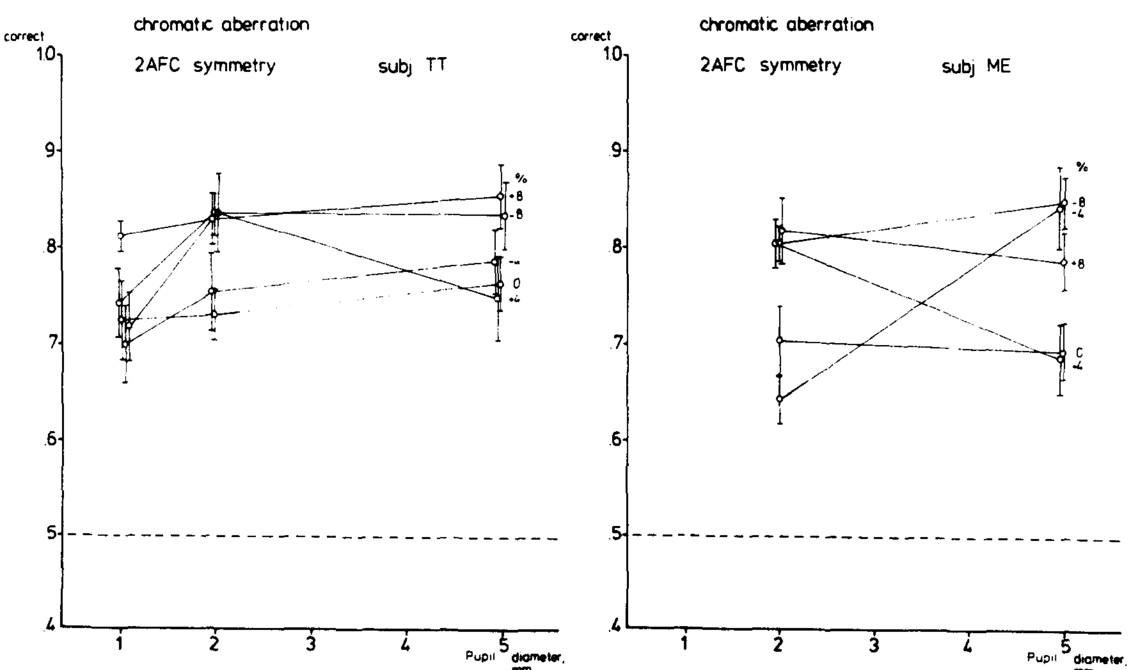

Fig. 5. As Fig. 4, but showing data on the symmetry perception task. Again, there is little effect of pupil diameter.

tion. Clearly, it is useful to look at performance with stimuli having a greater chromatic modulation and therefore more aberration effects. Data were therefore obtained for one subject (T.T.) using an isoluminant red-green, instead of yellow-green, apparent-motion display (red chromaticity $u' = 0.42$, $v' = 0.53$). This stimulus would be expected to be more susceptible to aberration artefacts. The dotted line in Fig. 4 gives the results. Two points should be noted: first, there is a clearly discernible improvement in performance with increasing pupil size, and secondly the performance for the 1 and 2 mm pupils is still above chance. Thus, this kind of stimulus seems to exhibit both longitudinal aberration effects (giving a positive gradient) and transverse effects (giving a baseline above 50% ordinate). This suggests that such red-green stimuli should be avoided unless some effective means of removing aberration is found. The yellow-green stimuli used in the present experiments, on the other hand, are relatively immune from aberration effects because of the smaller chromatic modulation.

It could still be argued that some other artefact exists which produces a retinal luminance contrast where there should be none. Can such an artefact account for the present experimental results (that global apparent movement perception is abolished but symmetry perception persists)? In that case, one would have to argue that a small (low-contrast) retinal luminance artefact is sufficient to allow symmetry perception but insufficient to allow apparent movement perception: ie, the contrast threshold for symmetry perception should be lower than that for apparent movement perception.

The two contrast thresholds were measured, using a green stimulus whose background was the same as that in the other experiments. Performance was measured for a variety of low-contrast presentations (in random order) and the lowest contrast value at which performance was better than chance with $P < 0.05$ was defined as the threshold. Table 1 gives the results.

It can be seen that the contrast necessary to perform above chance in the symmetry perception experiment is 50–100% greater than that required to see the shape of the apparent-movement stimulus. Thus, these data make it unlikely that the present experimental results are due to any low-contrast luminance artefact.

These results suggest that the lack of chromatic-aberration artefacts applies only to

Table 1. Contrast thresholds

Subject	Symmetry	Apparent movement
T.T.	5.6%	3.7%
M.E.	7.5%	3.7%

Contrast thresholds for above-chance performance ($P < 0.05$) on symmetry perception and apparent-movement shape discrimination tasks. A monochrome (green) display was used. More contrast is needed to see symmetry than for the apparent movement task.

the chromaticities and stimuli used in these experiments, and cannot be generalised to other data. In particular, the choice of yellow/green stimuli in these experiments serves to reduce aberration artefacts, since there is a relatively small (<0.5 D) difference in power between the two dominant wavelengths of these stimuli. Other investigators have used red/green or other stimuli and aberration effects may well have been greater, as suggested by the dotted line in Fig. 4.

DISCUSSION

The results show that isoluminant presentation has little effect on performance in a mirror-symmetry detection task. On the other hand, given a kinematogram with a dynamic surround, it becomes impossible to discern the shape of an embedded target. If one accepts that this is unlikely to be accounted for by chromatic aberration or other artefacts (and the control experiments suggest that this assumption is correct) then it may be possible to use this divergence of movement and symmetry results to further our understanding of what happens to vision at isoluminance.

The apparent movement results suggest that what is rendered impossible to see is the shape of the target area when the latter is described by cooperative movement alone. If we view a kinematogram with a static surround and moving target, the shape is still discernible, but not necessarily on the basis of a global apparent-movement mechanism. In this type of stimulus, it is possible to see the shape simply because it is the only region which is dynamic. Also, the results do not mean that it is impossible to see movement of individual parts of the display. Indeed, Cavanagh *et al.*'s (1985) data suggest that subjects always report some movement in the stimulus (unless the ISI is increased). Cavanagh *et al.* suggest informally that it is indeed the exact shape of the target which suffers, but we should remember that they used a stimulus with a static surround in which even the shape remains visible.

To explain why symmetry may be seen but apparent movement may not, it is useful to consider some findings relating to monochrome symmetry perception. Barlow and Reeves (1979) found that small local image perturbations have little effect on symmetry perception in stimuli rather similar to the ones used here. Thus, introducing a small error into the exact position of each dot has little effect on performance. I have suggested (Troscianko, 1984; Troscianko and Gregory, 1985) that the main effect of isoluminance may be an introduction of a small positional uncertainty into the neural representation of the stimulus. If this hypothesis is true, then we would expect the extraction of shape information about the embedded target in a random-dot kinematogram to be severely affected by positional uncertainty of the elements, but symmetry perception to be much less affected. A simple experiment suggests that this is indeed so.

Four subjects (three of them naive) were presented with a high-contrast black and white image of dots which were mirror-symmetric and in which a central column moved in apparent motion. Both symmetry and the shape of the column were clearly seen by all subjects. Then, instead of each dot being stationary or moving left-right (in the case of the dots forming the column), a progressively larger random "jitter" was introduced in the location of each dot. The subjects were asked whether they could still see (a) the shape of the moving column, and (b) the overall symmetry. Figure 6 shows the results of this experiment.

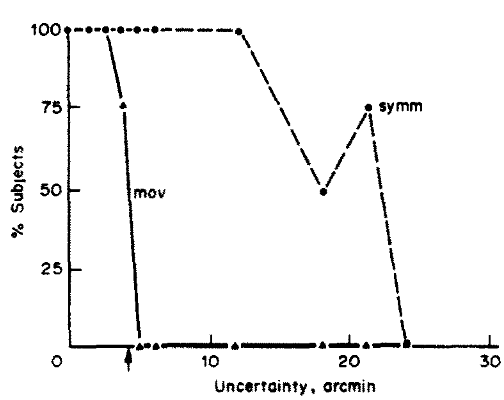

Fig. 6. Four subjects' subjective estimates of visibility of global apparent movement ("mov": solid line) and overall symmetry ("symm": dashed line) in a monochrome display. The independent variable plotted on the abscissa is the amplitude of dynamic "jitter" superimposed on the position of each of the constituent dots. The arrow indicates the amplitude of the apparent movement (4 arcmin). Symmetry is reported to be visible for much larger "jitter" amplitudes than global apparent movement.

It can be seen that subjects report the disappearance of the column for "jitter" amplitudes much smaller than those which finally abolish the percept of symmetry. Thus, the cooperative global process underlying the extraction of the shape of a moving stimulus cannot "average out" random movement components superimposed on the global motion. In the case of symmetry perception, such perturbations are ignored.

Another explanation given for isoluminant effects is a greater neural blur. Anyone who has observed such stimuli is, however, impressed by the difference between introducing optical blur into the image and making it isoluminant. Furthermore, in the brief experiment reported here, the introduction of positive blurring lenses (approximately equivalent to low-pass filtering) at the point where it was hard to see the shape of the moving column resulted in the column being easier, not harder, to see. Thus simple blur is not sufficient as an explanation. Positional uncertainty, whatever its exact neural origin, is a better descriptor.

Both tasks involved here (movement and symmetry) are "global" in the sense that many comparisons must be made across a substantial extent of the visual field. But the present data suggest that they may best be differentiated on the basis of exact-position representation: global movement perception needs such exact representation, while symmetry perception does not. Isoluminance can simply be seen as a means of introducing small positional errors into the image. This suggests a fairly peripheral locus to the effect of isoluminance, in distinction to those who argue (e.g. Ramachandran and Gregory, 1978) that isoluminance has its effect by the differing specificity of various areas of the brain. The positional uncertainty postulated here may well have its origins in the difference in receptive-field organisation for chrominance and luminance coding. Neither is it necessary, therefore, to postulate a lack of colour input to motion-detecting units, as does Srinivasan (1985) for example. Taken together, the studies of Cavanagh *et al.* (1984), Mullen and Baker (1985), and now these results, suggest that colour-only information does indeed feed into a motion-detecting system. It is the extraction of the global shape of the moving stimulus which suffers.

If we assume that isoluminance does in fact isolate colour channels, it may still be true that these channels may selectively be routed to some cortical mechanisms rather than others, in spite of the peripheral explanation given above. As the psychophysical results stand at present, it is not possible to say that colour information does not feed into a motion system. It may do so to a lesser extent than luminance, but the data do not prove this. Perhaps the strongest point to emerge from this study is the concept of positional uncertainty in colour information, and the extent to which that (rather than colour or luminance) is differentially fed into various cortical mechanisms.

CONCLUSIONS

The results of this study suggest that isoluminant presentation abolishes the ability to discern the shape of a target moving in global apparent movement, but the perception of mirror-symmetry is relatively unimpaired. It is suggested that the implications of this are (a) that isoluminance introduces a small positional uncertainty into the neural representation of the image; and (b) that extraction of shape of a stimulus in global apparent movement therefore needs exact-position representation. This hypothesis assigns a rather peripheral locus to the effects of isoluminance, perhaps at the level of post-receptoral receptive fields. This is in distinction to those explanations which seek to account for isoluminance by postulating that specific areas of the cortex may or may not receive colour information, or that motion-detectors are colour-blind. Rather, the most interesting feature of isoluminance may be its ability to distinguish between mechanisms (such as global movement perception) which depend on knowing the exact position of all constituent elements, and other mechanisms (such as symmetry perception) which are immune to such spatial perturbation.

Acknowledgements—The author's research was funded by a Research Fellowship from the Alexander von Humboldt Foundation. Some of the preparation of this work was done in U.K. with funding from Medical Research Council. Much of the computer equipment was on loan from the Brain and Perception Laboratory (Bristol) and the Bristol Eye Hospital. The author would like to thank Michael Erb for acting as subject, and Manfred Fahle for helpful discussions.

REFERENCES

Barlow H. B. and Reeves B. C. (1979) The versatility and absolute efficiency of detecting mirror symmetry in random dot displays. *Vision Res.* **19**, 783–793.

Braddick O. J. (1974) A short-range process in apparent motion. *Vision Res.* **14**, 519–527.

Cavanagh P., Boeglin J. and Favreau O. E. (1985) Perception of motion in equiluminous kinematograms. *Perception* **14**, 151–162.

Cavanagh P., Tyler C. W. and Favreau O. E. (1984) Perceived velocity of moving chromatic gratings. *J. opt. Soc. Am.* **A1**, 893–899.

de Weert C. M. M. and Sadza K. J. (1983) New data concerning the contribution of colour differences to stereopsis. In *Colour Vision* (Edited by Mollon J. D. and Sharpe L. T.), pp. 553–562. Academic Press, New York.

Gregory R. L. (1977) Vision with isoluminant colour contrast: 1. A projection technique and observations. *Perception* **6**, 113–119.

Grinberg D. L. and Williams D. R. (1985) Stereopsis with chromatic signals from the blue-sensitive mechanism. *Vision Res.* **25**, 531–537.

Lu C. and Fender D. H. (1972) The interaction of colour and luminance in stereoscopic vision. *Invest. Ophthal.* **2**, 482–489.

Moreland J. D. (1980) Spectral sensitivity measured by motion photometry. In *Colour Deficiencies V* (Edited by Verriest G.), Vol. 5, pp. 299–305. Adam Hilger, Bristol.

Mullen K. T. (1985) The contrast sensitivity of human colour vision to red-green and blue-yellow chromatic gratings. *J. Physiol., Lond.* **359**, 381–400.

Mullen K. T. and Baker C. L. (1985) A motion aftereffect from an isoluminant stimulus. *Vision Res.* **25**, 685–688.

Ramachandran V. S. and Gregory R. L. (1978) Does colour provide an input to human motion perception? *Nature, Lond.* **275**, 55–56.

Srinivasan M. V. (1985) Shouldn't movement detection necessarily be "colour-blind"? *Vision Res.* **25**, 997–1000.

Troscianko T. (1984) Random-dot symmetry perception, and coding of phase, in achromatic and isoluminant displays. *Perception* **13**, A17.

Troscianko T. (1985) Colour and symmetry perception: hemispheric differences. *Perception* **14**, A24–A25.

Troscianko T. and Gregory R. L. (1985) How perception is coloured. In *Mondial Couleur 85, Proc. 5th AIC Congr.*, Vol. 2, Chap. 2. Centre Francais de la Couleur, Paris.

Troscianko T. and Low I. (1985) A technique for presenting isoluminant stimuli using a microcomputer. *Spatial Vision* **1**, 197–202.

Wyszecki G. and Stiles W. S. (1967) *Color Science*, p. 212. Wiley, New York.

Zeki S. M. (1978) Uniformity and diversity of structure and function in rhesus monkey prestriate visual cortex. *J. Physiol., Lond.* **277**, 273–290.