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- glutaraldehyde alone, glutaraldehyde followed by post-fixation with osmium, or, most frequently, by fixation with osmium only. The material illustrated was fixed for 2 hours with percent osmium tetroxide in 0.5N Krebs solution and, unless indicated in the figure

legends, examined unstained, Strontium (10 mM) was also included in the osmium fixative in one embedding in an attempt to minimize the loss of Sr^{2+} during fixation (13) (Fig. 4 in this series). It was clearly ascer-tained that Sr^{2+} could be localized to the sarcoplasmic reticulum and the mitochondria of smooth muscle, regardless of the type of fixation used, and its localization was to the same sites (sarcoplasmic reticulum and mitochondria) whether it was added or absent from the fixative. The identification of sarcoplasmic reticulum of smooth muscle was unequivocal as the result of a large series of conventional electron micrographs, including the use of ferritin, horseradish peroxidase, and lanthanum as extracellular markers [(14);
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Stereoscopic Depth Movement: Two Eyes Less Sensitive than One

Abstract. Visual sensitivity to stimuli with sinusoidal movement was examined under a number of conditions of binocular stimulation. Sensitivity to stereoscopic movement in depth was reduced in comparison to that for monocular movement. The reduced sensitivity appeared to be due to the presence of stereoscopic depth movement, as opposed to stereoscopic stimulation, binocular movement, or fusion of the images.

The dynamic properties of human stereoscopic depth perception may be investigated by the use of moving stimuli viewed stereoscopically. Lit and other workers (1) have carried out a number of studies on the stereoacuity for physical stimuli that either move linearly or oscillate sinusoidally in a frontal plane. However, because the stimuli contained both types of movement, these studies do not provide information on the relative effects of cues of monocular and stereoscopic movement in stereoacuity. Using stereoscopic random-dot stimuli of correlated stereograms, Julesz and Payne (2) studied stereoscopic apparent movement. Two types of stimulus presentation were studied: stimuli that could be seen as moving both monocularly and stereoscopically, and stimuli that could be perceived as moving only in the stereoscopic mode of presentation with all monocular movement cues eliminated. (In none of these studies was movement in depth produced; frontal plane movement of stimuli perceived in depth was the mode of movement investigated.) Julesz and Pavne measured the alternation frequency of the two apparent positions for each type of stimulus at which the apparent movement percept disappeared and the stimuli appeared simultaneous. The critical frequency for simultaneity was significantly higher for the monocular apparent movement than for the stereoscopic apparent movement, although Julesz and Payne do not comment on this fact. This observation corresponds to a reduction in sensitivity to apparent movement with a stimulus providing only stereoscopic cues for movement as compared with one providing stereoscopic and monocular cues. I could find no other experiments in the literature that compared monocular and stereoscopic movement thresholds.

To investigate the problem of movement perception in stereoscopic vision and to extend the findings of Julesz and Payne, I used real movement that oscillated sinusoidally in depth at a range of oscillation frequencies. The display stimuli consisted of thin, bright vertical lines, subtending 1 degree in height and 2 minutes in width, seen against a dark background. The stimuli were produced on the face of a fastphosphor Dumont oscilloscope by a sawtooth signal at 30 khz with a luminance of 3.4 cd/m^2 and were viewed with a natural pupil, because there was no overall change in stimulus luminance. The stimuli were displaced sinusoidally (that is, in simple harmonic motion) in a horizontal plane with an amplitude that could be varied by the subject. The stimulus configuration observed by the subject, produced by conventional orthogonal polarizers, consisted of a stationary line and an oscillating line seen with each eye at an average separation of 20 minutes. The moving lines could be oscillated in phase, which corresponded to a real movement version of the movement used by Julesz and Payne, or in antiphase. When the subject stereoscopically fused the stimuli to his two eyes to obtain the Cyclopean view, he perceived a stationary line and a moving line suspended in space in the dark. If the moving lines to each eye oscillated in phase he would perceive the line moving from side to side (binocular frontal movement). When the oscillations were in antiphase, the movement appeared toward and away from him (stereoscopic depth movement).

The visual sensitivity to monocular and stereoscopic depth movement was compared. The subject set the amplitude of the movement until it appeared just not visibly moving. The peak-topeak amplitude of the movement at this threshold setting was measured. The monocular movement amplitude was taken as the measure in the case of the stereoscopic movement, in order to make a comparison of monocular movement information required for monocular as compared to stereoscopic movement threshold.

For both subjects the sensitivity to depth movement in stereoscopically viewed stimuli varies as a function of frequency in a manner similar to sensitivity to frontal-plane movement viewed monocularly, but a general reduction in sensitivity occurs over the whole frequency range in the case of stereoscopic depth movement (Fig. 1). There is little possibility that these results are contaminated by differences in eye movements with the two types of stimuli, because the system for eye movement is unable to track a moving stimulus above about 2 hz (3), and the results are qualitatively similar above and below 2 hz. Furthermore, because the moving stimulus was accompanied by a fixed reference, vergent tracking of the moving stimulus would produce retinal movement of the reference stimulus, and hence would not reduce movement sensitivity. The fixed angular size of the stimulus (1 degree) might be expected to counteract the stereoscopic cue of depth movement. In fact the two cues were fully reconciled in the



Fig. 1. Movement sensitivity (reciprocal of threshold angle of movement) as a function of oscillation frequency of sinusoidal movement [log-log coordinates (9)]. Filled circles, monocularly viewed movement. Open circles, stereoscopic depth movement. Upper graph for subject C.W.T. Lower graph for subject J.T. (10). Each data point is mean of three readings. The vertical bars show one standard deviation from the mean (11). The readings were taken in alternation of ascending and descending series, together with alternation of monocular and stereoscopic conditions.

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strong and immutable perception that the line increased in size as it moved away, and vice versa. The size cue may be eliminated by masking the two moving stimulus lines with oblique masks oriented so that the length of the stimulus lines actually increases as the stereoscopically perceived line approaches the subject. The apparent length of the perceived line then remains constant, but I found that the depth movement sensitivity was reduced to the same extent as before.

The data therefore lead to the surprising conclusion that the visual system is considerably less sensitive to moving stimuli presented to both eyes, in such a way as to cause fusion and a depth movement percept, than to the monocular component of the same stimulus. The effect may be observed directly by setting the depth movement to just below threshold when viewing stereoscopically, and then closing one eye. Movement is then perceived and will disappear again on opening the eye and fusing the stimuli. The effect is equally evident on fixating the stimulus to the left or right of the moving stimulus and is thus not limited to stimuli astride the midline in which only input from one eye goes to each hemisphere.

This reduction in stereoscopic movement sensitivity as compared with monocular movement sensitivity contrasts with the evidence that for static stimuli, stereoacuity is at least as good as monocular vernier acuity (4). However, Richards (5) has recently reported that static and movement stereoscopic abilities are independent because the mechanism for either may be absent in a given individual with the other intact. Furthermore, Richards (6) has also found that sensitivity to movement as measured by the spiral aftereffect is approximately twice as great as sensitivity to depth movement generated by the same monocular stimulus.

The factors that are involved in stereoscopic movement beyond monocular movement are: binocular rather than monocular vision, binocular rather than monocular movement, stereoscopic fusion to produce a depth percept, and antiphase movement in the two eyes. To determine which aspect of the process of stereopsis produces the reduction in movement sensitivity, six conditions were isolated and investigated in subject C.W.T.

The conditions selected were as follows: (i) Monocular stimulus with no binocular information. (All the following conditions are binocular.) (ii) Monocular movement (stereoscopically fused), examines the effect of monocular as opposed to binocular movement in a stereoscopic presentation. (iii) Binocular frontal plane movement (fused), produced by in-phase movement in the two eyes, examines the effect of the plane in which movement occurs. (iv) Stereoscopic depth movement (fused) is effected by antiphase movement to the two eyes and is identical with the depth movement stimulus of the first experiment. (v) As for (iii) but with unfused stimuli (see below) to examine the effect of fusion on in-phase movement sensitivity. (vi) As for (iv) but unfused, to examine the effect of fusion on antiphase movement sensitivity. The stimuli presented to each eye and a plan view of the stimuli as perceived by the subject for each condition are shown in Fig. 2. For the unfused conditions, a moving spot was presented to one eye and a moving line to the other. The subject reported no tendency to fuse these disparate stimuli, and in fact found it difficult to keep them superimposed. Hence, four separate stimuli were perceived when binocular rivalry did not occlude them. No impression of location or movement except in the depth plane of the physical stimulus was ever observed. Threshold sensitivity in these conditions was examined at two frequencies (0.5)and 5 hz) with nine readings for each condition. One reading was made under



Fig. 2. Six conditions of observation of movement stimuli. Upper box of each pair is stimulus impinging on each retina. Lower box of each pair is stimulus as perceived by subject.



Fig. 3. Movement sensitivity for the six conditions of Fig. 2 at two frequencies. Bar height is the average of nine readings. (The absolute bar height shown has no significance, as the ordinate is a log axis and has no zero, but is shown to relate to the panel below describing viewing conditions.) Dashed lines represent one standard deviation on each side of mean. M, monocular. Left histogram, 0.5 hz. Right histogram, 5 hz. Subject C.W.T. (12).

each of the total of 12 conditions, followed by a second under each condition, and so on for nine readings. The order was randomized within each set of 12 conditions.

The conditions may be grouped into three pairs, which may be described as the conditions of (fused) lateral movement (i and iii), the conditions of (fused) depth movement (ii and iv) and the unfused conditions (v and vi). In no case at either frequency was there a significant difference between the members of any pair (Fig. 3). On the other hand, movement sensitivity in the depth movement conditions was significantly lower than in the lateral movement conditions at both frequencies, and significantly lower than the unfused conditions at 5 hz. Correspondingly, while the sensitivities in the unfused conditions are insignificantly different from the lateral movement sensitivities at 5 hz, they occupy a middle position between the lateral and depth movement sensitivities at the frequency of 0.5 hz. In detail, (vi) differs from (i) and (iii), whereas (v) differs from (iv) but not from (ii).

Therefore, movement sensitivity as measured by retinal subtense is significantly reduced in conditions where stereoscopic depth movement predominates (ii and iv). The reduction in sensitivity from condition (i) to condition (iv), which is close to a factor of 2 at both frequencies, is somewhat less than that found in the first experiment. This is probably due to the diversity of experimental conditions used in this second experiment, which produce different adapting conditions.

The reduction in depth movement sensitivity at 5 hz is not due solely to the presence of opposite movement in each eye (by comparison with the unfused conditions) nor is the presence of a binocular fused image sufficient to produce a reduction in sensitivity. Similar results hold at 0.5 hz except that the unfused sensitivities are depressed relative to the sensitivities for



Fig. 4. Possible model of movement detection system. First stage, optical and retinal processing in each eye. Second stage, postchiasm disparity detectors D_n , only two shown for simplicity. Third stage, interaction of outputs of disparity detectors (excitation, solid lines; inhibition, dashed lines). The properties of the mutual inhibition as a function of retinal distance of the disparate stimuli will not be included in this basic model for reasons of simplicity. Fourth stage, movement detection. lateral movement. The subject had difficulty in holding a steady fixation in the absence of fusion, and the resulting instability in the field probably acted as a confusing factor at the lower frequency in the unfused conditions.

The reduction in stereoscopic movement sensitivity appears to be essentially restricted to conditions in which stereoscopic depth movement is present [conditions (ii) and (iv)]. Condition (ii) also involves a lateral component in the Cyclopean perception of the stimulus. However, the geometry of the presentation was such that the lateral component of the Cyclopean movement subtended an angle of half that subtended by the monocular moving stimulus required in the stereoscopic display. This means that condition (ii) can show a reduction of sensitivity to stereoscopic movement by a factor of 2 before being confounded by the presence of lateral movement in the stimulus. Because the observed reduction is somewhat less than a factor of 2, a reduction in sensitivity to depth movement is demonstrated, but no information is available as to the effects on lateral movement sensitivity. Condition (iii), in which no reduction is evident, demonstrates that in the absence of depth movement a fused binocular image produces a similar sensitivity to the monocular case.

One hypothesis for the physiological basis for such a system is suggested by the data of Barlow, Pettigrew, and coworkers (7) on the stereoscopic response of single neurons in the visual cortex of the cat. They found that, whereas a single cortical neuron would respond to a frontal plane stimulus movement, stimuli moving at different depths stimulated different "disparitydetecting" neurons. Furthermore, they have demonstrated a binocular occlusion of the single unit response (relative to the monocular response) when the disparity of moving stimuli to each eye was misaligned from the optimum disparity for that unit. Other authors have failed to find such occlusion (8). The psychophysical findings reported herein require two further neural connections to exist. The perceptions of depth movement would require the existence neurons which detected relative of changes in the outputs of different sets of disparity-detecting neurons. The reduction of depth movement sensitivity would require some sort of inhibitory process whereby the output of a neuron responding to movement in one direction in one eye is reduced by the presence of movement in the opposite direction (condition iv), or by the presence of a "no movement" signal (condition ii), in the corresponding region of the retina of the other eye. Because both conditions involve differential disparity information over time, the binocular occlusion found by Pettigrew and coworkers might well be brought into play by a stimulus with stereoscopic depth movement, such as was used in my experiment.

The information for retinal position from the two eyes is processed into disparity information for elements of similar form on the two retinas (see model in Fig. 4). After this disparity stage, there is an interaction stage in which mutual inhibition between signals of different disparities occurs. The final stage in the model is a comparator responding to spatiotemporal differences in disparity, such as to detect depth movement.

A number of features in the model are implied by the present data. The frequency response of the inhibitory interactions must be approximately constant as a function of frequency in the frequency range examined in Fig. 1, otherwise the monocular and stereoscopic curves would have dissimilar forms. The model assumes that monocular as well as stereoscopic movement information is processed in a unitary pathway. If separate pathways were involved, separate mechanisms would be required for suppression of the monocular information in the stereoscopic stimulus and reduction of the stereoscopic sensitivity. A unitary model is therefore more parsimonious. In order to accommodate monocular movement sensitivity it must be assumed that the binocularly driven cells will fire with only monocular input, which is supported in the data of the above neurophysiological investigations, and that the disparity remains spatially coded up to the movement detection stage, so that lateral movements at a constant disparity can stimulate the movement detector.

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- The standard deviation was computed for the logarithmically transformed deviations from each individual mean averaged over all conditions for each subject. A one-way analysis of variance was computed
- for the data at both 0.5 hz and 5 hz. A log transformation of the data was found necessary in order to assume homogeneity of the variance under all conditions. A significance level of P = .01 was used.
- 13. My thanks to T. Corwin for his suggestions. Supported by Foundations Fund for Research in Psychiatry grant 70-481.
- 15 April 1971; revised 24 June 1971

Growth Inhibition by Mechanical Stress

The report by Neel and Harris (1) on the motion-induced inhibition of growth in Liquidambar bears a close resemblance to our observations that Cucurbita melopepo plants subjected to daily measurements of petiole length and leaf area were smaller than undisturbed plants of the same age. A similar growth inhibition was reported for Bryonia (2) and collectively the results demonstrate a need for caution in the design and interpretation of experiments that involve any form of mechanical manipulation of growing plants.

We have now measured the effect of subjecting greenhouse-grown C. melopepo plants to daily handling during the month of August. Eighteen 10-dayold plants were selected and nine were chosen to be handled briefly at noon each day. The handling involved gently shaking the petioles, individually, for 30 seconds and lightly stroking the leaf blades with the fingers once across the upper surface. New leaves were similarly treated as they unfolded during the experimental period. Petioles were numbered 1 to 4 consecutively from the primary petiole. The remaining plants, as controls, were left undisturbed.

After 20 days of treatment the experiment was stopped and the petioles, shoots, leaf blades, hypocotyls, and roots of control and handled plants were compared. The lengths and fresh weights of the stems and petioles of the handled plants were significantly less than in controls (Table 1) but the handled petioles showed a significant increase in volume per unit length as measured by water displacement (Fig. 1) which indicates an increase in radial growth. The fresh weights of the leaf blades, roots, and hypocotyls were unchanged by treatment as were the leaf blade areas and hypocotyl lengths.



Fig. 1. Effect of handling on the ratio of length to volume of petioles of Cucurbita melopepo. Data for petioles 1 to 4 have been combined.