Different loci suggested to mediate tilt and spiral motion aftereffects

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Interocular transfer of two figural aftereffects was examined in orthotropes and strabismic subjects. Within both groups there were persons with an appreciable degree of stereoacuity and others who had little or none. Experimental evidence from a variety of sources has suggested that stereopsis depends upon binocularity of units in the geniculostriate system. For the tilt aftereffect, interocular transfer correlated with stereoacuity among both orthotropes and strabismics. For the spiral motion aftereffect, interocular transfer did not correlate with stereoacuity; it was present among orthotropes and absent among strabismic individuals. The correlation of stereoacuity with interocular transfer of the tilt aftereffect agrees with previous observations and is consistent with the interpretation that this effect is mediated at a cortical level. The lack of a correlation between stereoacuity and interocular transfer of the spiral motion aftereffect suggests that this effect is mediated by units other than those responsible for stereopsis. Richards and Smith,[9] on the basis of certain phenomenal differences between the spiral motion aftereffect and other figural aftereffects, have suggested that the former is mediated at a midbrain level. If strabismic persons lack binocular units in midbrain, the present results are consistent with their hypothesis.

Key words: strabismus, intraocular transfer, tilt aftereffect, spiral motion aftereffect

A series of studies in cat, monkey, and man have suggested that stereopsis is mediated by neurons in the geniculostriate system that respond selectively to congruent input to the two eyes. The well-documented reduction in stereoacuity associated with visual anomalies such as strabismus, anisometropia, and aniseikonia has been interpreted as resulting from a deficiency in the number of such units and, by extension, in the total complement of binocularly responsive cortical cells.[6, 7, 12, 14] Binocular units in visual cortex have also been suggested as mediators of interocular transfer of certain figural aftereffects.[6, 7, 14] Consistent with this suggestion are reports of a highly significant positive correlation between stereoacuity and interocular transfer of both the tilt aftereffect[6] and the rotary motion aftereffect.[7] Another motion aftereffect, the spiral motion aftereffect, has also been generally regarded as mediated at a cortical level. Ware and Mitchell[14] interpreted the failure of the spiral motion aftereffect to transfer interocularly in strabismic subjects with minimal stereoacuity as consistent with a reduction in the number of binocular cortical units in these individuals. However, Richards and Smith[9] have viewed the relation between an accommodation stimulus (vergence micropsia) and spatial extent of the spiral motion aftereffect as suggesting mediation at a subcortical locus. Under this hypothesis,

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the failure of strabismic subjects to transfer this motion aftereffect interocularly would be interpreted as resulting from a deficiency in the number of binocular units in midbrain.

As a means of determining at what level of the visual system the spiral motion aftereffect is mediated, I evaluated the relation between interocular transfer of this aftereffect and degree of stereoacuity. If transfer of the spiral motion aftereffect is mediated by binocular units in the geniculostriate system, the magnitude of transfer would be expected to correlate with stereoacuity. On the other hand, such a relation might be absent if the spiral motion aftereffect is mediated by neurons distinct from those that mediate stereoacuity.

Subjects who participated in this study included persons with no vergence error (orthotropes) and strabismic individuals with uncorrected errors of vergence. Within both groups were persons who displayed an appreciable degree of stereoacuity and persons who did not. For each subject, degree of stereoacuity was compared with interocular transfer of each of two aftereffects, the spiral motion aftereffect and the tilt aftereffect. I included the tilt aftereffect to observe whether the relation Mitchell and Ware[6] had found between interocular transfer of this effect and degree of stereoacuity held for the present population of subjects.

Methods

Subjects. Sixteen strabismic individuals, eight orthotropes with normal binocular vision, and four orthotropes with monocular amblyopia participated. Strabismic individuals and amblyopic orthotropes were referred through the pediatric clinic of the New England College of Optometry and by optometrists in the Boston area.

Strabismic individuals included eight esotropes and eight exotropes; in each group half the subjects were amblyopes and half, alternating suppressors. In all strabismic subjects a horizontal error of vergence of at least 5 degrees had been noted prior to one year of age and was not intermittent. None of the strabismic subjects displayed abnormal retinal correspondence in a standard test employing retinal afterimages. Two of the strabismic subjects displayed appreciable stereoacuity, and 14 displayed none. The four orthotropes with monocular amblyopia included three persons with marked monocular astigmatism and one with anisekonia. Each of these persons constantly suppressed vision in the nondominant eye and displayed no appreciable stereoacuity.

Evaluation of visual status. When available, clinical records provided preliminary information concerning visual acuity, stereoacuity, eye dominance, vergence error, and pattern of use of the eyes. This information was supplemented and confirmed by tests of visual functioning conducted at the beginning of the first experimental session.

Visual acuity was evaluated with a Snellen Chart located 6.1 m from the subject. Stereoacuity was determined with a test using Julesz random-dot stereograms which varied in degree of disparity.[8] Following a convention used by Mitchell and Ware,[6] stereoacuity was defined as the reciprocal of the stereothreshold. Following standard clinical practice, the dominant eye was defined as the eye used to direct the preferred hand toward a visual target with both eyes open. Subjects were classified as strabismic or orthotropic by a standard clinical cover test reported sensitive to vergence errors of 4.00 D. The difference in position of the images of a distant light source reflected on the two corneas confirmed the results of the cover test.

Tilt aftereffect

Apparatus. An apparatus described in Mann et al.[4] was used both to induce and measure tilt aftereffects. A transilluminated disc, inscribed with a square wave grating at four cycles per degree of visual angle is housed within an opaque cylinder. The disc is 37.5 cm from the end of the cylinder through which the subject looks. The subject can easily change the orientation of the grating by rotating the cylinder by hand; a pointer mounted on the outside of the cylinder permitted the experimenter to note the orientation of the grating with respect to a fixed protractor. The grating was suprathreshold for all subjects.

Induction. To induce the aftereffect, the subject was asked to scan the grating with the stripes tilted 10 degrees clockwise. Prolonged scanning of this stimulus display has been shown to cause a vertical grating of the same frequency to appear rotated counterclockwise.[6] The aftereffect can be measured as a clockwise postexposure shift in settings of the apparent vertical.

Procedure. If the subject normally wore corrective lenses, the lenses were removed. The entire session was conducted in a darkened room. The experimenter adjusted the orientation of the grating to a nonvertical position. The orientation to which the grating was set was either clockwise or counterclockwise from vertical, according to a fixed pseudorandom sequence, and ranged within 80 degrees. The subject could not see the disc while this adjustment was being made. Then the disc was transilluminated for 2 sec while the subject set the grating to apparent vertical by rotating the cylinder. Four practice trials were given with the subject permitted binocular of the qrating. Monocular test trials followed, during which a soft eyepatch was worn over the eye not beinq used. The two eyes were used on alternate trials during testing, with each eye mediating eight settings of the vertical.

Upon completion of pre-exposure testing, the subject was exposed to the inducing display. Monocular view of the transilluminated disc was provided with the grating set at 10 degrees clockwise. The subject was instructed to move his eye right and left over the tilted grating. After 3 min the light illuminating the grating was extinguished, and the stripes were set by the experimenter to a nonvertical orientation. The grating was then transilluminated for 2 sec while the subject set it to apparent vertical. This concluded one postexposure trial. Next the grating was returned to the inducing orientation (10 degrees clockwise) and illuminated for another 40 sec exposure period, during which the subject again scanned the pattern using the same eye. At the end of this exposure period, the grating was again extinguished, set to a nonvertical position, and reilluminated for 2 sec, during which the subject used the eye which had not been exposed to the inducing display to mediate a single setting of the vertical. The cycle of exposure and test was repeated until both exposed and nonexposed eye had each mediated eight settings.

Four to 7 days later, a second session was provided in which the fellow eye was exposed to the inducing display. Order of the sessions in which the dominant and nondominant eyes were exposed was counterbalanced within each subject group.

Spiral motion aftereffect

Apparatus. A spiral motion aftereffect was induced and measured with an apparatus described by Richards and Smith.[9] This pattern consists of a seven-throw clockwise logarithmic spiral with a three-throw counterclockwise logarithmic spiral at its center and is depicted in Fig. 1. It was attached to a disc which rotated at 30 rpm; at the viewing distance of 3 feet the pattern subtended 16 degrees of visual arc and was suprathreshold for all subjects. The extent of aftereffect was measured with a test field which consisted of a random array of black and white squares. At the viewing distance of 3 feet, each square subtended 0.2 degrees of visual arc; the entire test field subtended 20 degrees of arc.

Fig. 1. Spiral used to generate a motion aftereffect of central expansion with peripheral contraction.

Induction. To induce the aftereffect, the subject was asked to view the pattern rotating at 30 rpm clockwise. Prolonged view induces an illusion of central expansion with peripheral contraction.

Procedure. Each session began with a sequence of monocular exposure followed by monocular report of the aftereffect. One eye of a subject was occluded while he used the other eye to view the spiral pattern as it rotated clockwise. After 3 min, the disc was held stationary, and the subject viewed the aftereffect against the test field, verbally reporting when the apparent expansion/contraction ceased. A second 3 min exposure period followed, with the same eye exposed. At the end of this, the subject then reported the duration of aftereffect, using the previously nonexposed eye to view the test field. A 30 min period intervened, and the entire procedure was repeated with the same eye exposed to view of the moving spiral. The session was repeated 1 week later for exposure of the contralateral eye; order of the sessions in which the dominant and nondominant eyes were exposed was counterbalanced within each subject group.

Results

Tilt aftereffect. To assess the extent and interocular transfer of tilt aftereffect, I computed a mean and variance value for pre-

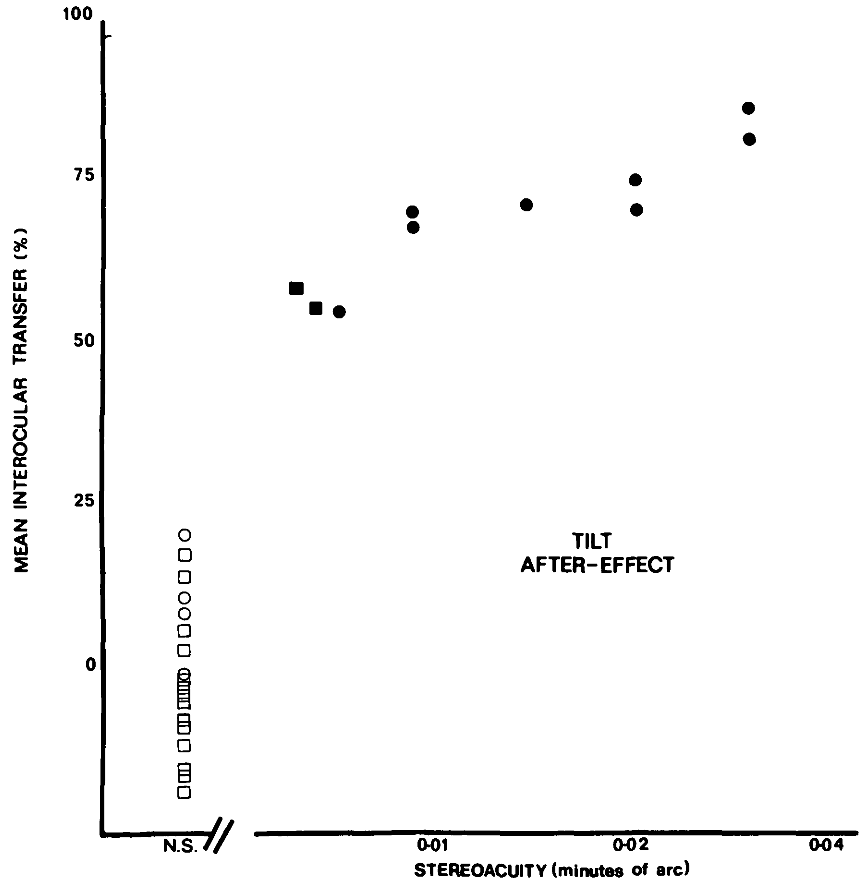

Fig. 2A. Relation between degree of stereoacuity (in minutes of arc) and interocular transfer of the tilt aftereffect. Filled circles, orthotropes with appreciable stereoacuity; open circles, orthotropes with no appreciable degree of stereoacuity; filled squares, strabismic subjects with an appreciable degree of stereoacuity; open squares, strabismic subjects with no appreciable stereoacuity.

exposure and postexposure settings of the vertical mediated by each eye during each session. For each eye, differences between the means of pre-exposure and postexposure settings were calculated for each session and evaluated with t tests. A positive value was assigned to shifts in the clockwise direction.

For all subjects tested, differences between pre-exposure and postexposure settings mediated by the eye exposed to the inducing display were significant at the 0.001 level, regardless of whether the eye was dominant or nondominant. These differences ranged from +2.5 degrees to +5.0 degrees, with a mean value of +3.1 degrees for normal orthotropes, +3.0 degrees for orthotropes with monocular amblyopia, and +3.3 degrees for strabismic subjects. All normal orthotropes also showed significant postexposure shifts in settings mediated by the nonexposed eye. In addition, two strabismic subjects who displayed appreciable stereoacuity also transferred the aftereffect to the nonexposed eye. The 14 strabismic subjects and the four amblyopic orthotropes, all of whom displayed no appreciable stereoacuity, showed no significant interocular transfer of the aftereffect. For these subjects, postexposure settings mediated by the unexposed eye did not significantly differ from pre-exposure settings (for d.f. = 14; criterion for rejecting the Null hypothesis: $1.76 > t > + 1.76$; $p < 0.05$).

The mean value of aftereffect for the nonexposed eye was divided by the mean value of aftereffect for the exposed eye to obtain a

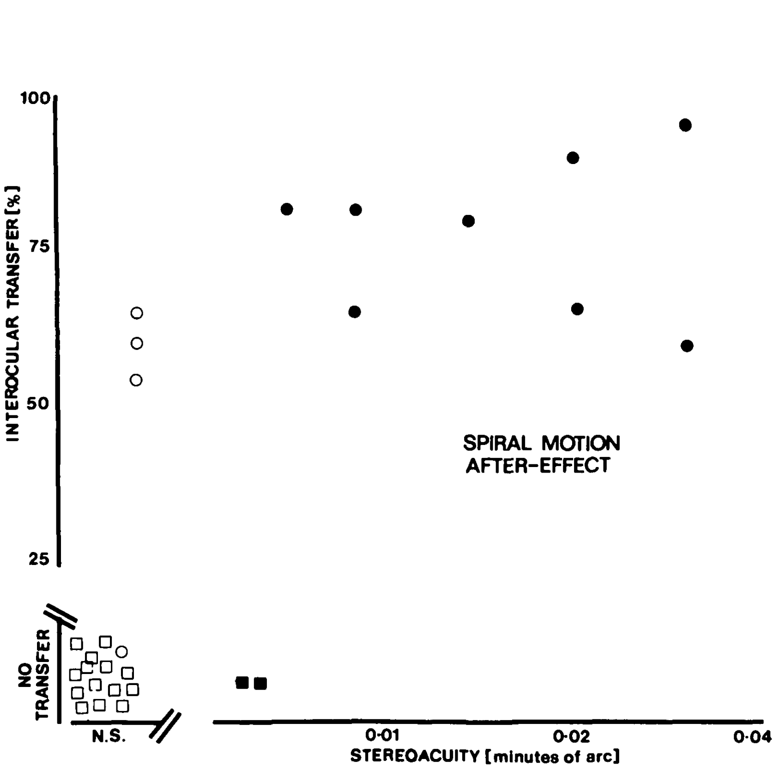

Fig. 2B. Relation between degree of stereoacuity and interocular transfer of the spiral motion aftereffect. For explanation of symbols see legend to Fig. 2A.

measure of interocular transfer. These values are expressed as percentages and plotted against stereoacuity in Fig. 2A. A Spearman rank correlation coefficient between these values and measures of stereoacuity was significant ($r = +0.91$; $p < 0.001$).

Spiral motion aftereffect. All subjects reported a spiral motion aftereffect when tested with the exposed eye, whether it was dominant or nondominant. Duration of the effect in the exposed eye ranged from 15 to 45 sec, with mean value of 27 sec for normal orthotropes, 22 sec for amblyopic orthotropes, and 24 sec for strabismic subjects. All normal orthotropes and three out of the four orthotropic amblyopes (the three anisometropes) also reported an aftereffect when tested with the nonexposed eye. Transfer occurred regardless of whether the dominant or nondominant eye had been exposed. In contrast, none of the 16 strabismic subjects reported appreciable transfer of the aftereffect to the nonexposed eye.

The mean duration of aftereffect in the nonexposed eye was divided by the mean duration of aftereffect in the exposed eye to obtain a measure of interocular transfer. These values are expressed as percentages and plotted against degree of stereoacuity in Fig. 2B. For subjects with appreciable stereoacuity, a Spearman rank correlation coefficient between interocular transfer and measures of stereoacuity was not significant ($r = 0.32$; $p > 0.5$).

Discussion

Two figural aftereffects were studied, the tilt aftereffect and the spiral motion aftereffect. Each effect could be induced in the dominant and nondominant eye of all subjects. However, the subject groups differed with respect to interocular transfer of these aftereffects. In orthotropes with stereoacuity within the normal range, both aftereffects transferred from the exposed eye to the nonexposed eye. In amblyopic orthotropes in whom stereoacuity is reduced, there was appreciable interocular transfer of the spiral motion aftereffect but no transfer of the tilt aftereffect. Among strabismic subjects, there was no interocular transfer of the spiral motion aftereffect, and only those two strabismic subjects with appreciable stereoacuity displayed appreciable transfer of the tilt aftereffect.

The observations of a strong positive correlation between stereoacuity and magnitude of transfer of the tilt aftereffect is consistent with previous reports.[6, 14] In contrast, among orthotropes and strabismic subjects in the present population, interocular transfer of the spiral motion aftereffect does not correlate with stereoacuity. Orthotropes with reduced stereoacuity reported transfer of this effect, whereas strabismic individuals who displayed appreciable stereoacuity did not. This suggests that the spiral motion aftereffect may be mediated by neurons distinct from those geniculostriate units presumed to mediate both stereoacuity and the tilt aftereffect. This possibility is consistent with the opinion of Richards and Smith[9] that the spiral motion aftereffect is mediated at a midbrain level.

It is known that cells in the midbrain of monkey are responsive to stimulus motion and may be driven by input to either eye.[1, 5, 13] Although the majority of collicular units are not selectively responsive to direction of motion in the frontal plane, Updyke[13] has described a population of deep layer neurons which respond selectively to an approaching stimulus. These cells appear to be triggered by an optically expanding pattern; fatigue of such units by exposure to an optically expanding stimulus might underlie the illusion created by prolonged view of a rotating spiral. Cells in the deep layer of monkey superior colliculus are also reported to habituate to moving stimuli[5] and to maintain habituation across changes in stimulus shape, velocity, and wavelength. The tendency of these cells to preserve habituation accords with the maintenance of the spiral motion aftereffect across changes in test field. This parallel is consistent with the view that the spiral motion aftereffect is mediated by collicular neurons.

Since the spiral motion aftereffect does not transfer interocularly among strabismic individuals, the implication is that these persons have a reduced complement of binocularly responsive units in midbrain. Studies of the superior colliculus of cats displaying vergence errors provide support for this suggestion. In normal cats, cells in the superior colliculus are selectively responsive to stimulus motion and may be driven by input to either eye.[2, 11] However, in cats with a naturally occuring vergence error (Siamese) the complement of binocularly driven midbrain units is reduced.[2] Cats reared with one eye sutured frequently develop vergence errors[10] and have also been shown to lack binocular units in superior colliculus.[11] Some reduction in the number of binocularly driven collicular units has also been observed in kittens reared with an artifically produced strabismus.[3]

The precise nature of the relation between midbrain binocularity and strabismus remains unknown—is strabismus an antecedent or a consequence of a reduction in midbrain binocularity? Some insight into this question might be provided by human subjects in whom an error of vergence was surgically corrected very early in life. Such persons would be expected to show interocular transfer of the spiral motion aftereffect if reduced midbrain binocularity is a consequence of vergence error. On the other hand, if reduced binocularity is the antecedent of disvergence, no interocular transfer would be expected. In this connection, assessment of interocular transfer of the spiral motion aftereffect in young children in whom no vergence error has been detected might reveal deficits in binocularity predictive of later strabismus. Such an outcome would support the view that a deficiency in the number of binocular units in midbrain antedates strabismus.

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