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The Training Of Human Voluntary Torsion: Tonic And Dynamic Cycloversion.

Richard Balliet
University of the Pacific

THE TRAINING OF HUMAN VOLUNTARY TORSION: TONIC AND DYNAMIC CYCLOVERSION

By

Richard Balliet

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This dissertation, written and submitted by

RICHARD BALLIET

is approved for recommendation to the Committee on Graduate Studies, University of the Pacific

Dean of the School or Department Chairman:

Bruce E Spivey

Dissertation Committee:

Ken Nakayama, Chairman

Paul Bailey

Brian Brown

Bruce E Spivey, Dean

Dated September 13, 1976

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Abstract of the Dissertation

Torsion is defined as any rotation around the visual axis of the eye. Since the middle of the 19th century some researchers have doubted that functional ocular torsions occur in man. Researchers who have reported torsional eye movements found that these movements were either controlled reflexively, as in the counter-rolling of the eyes during lateral head tilt, or visually induced, as in large field rotary-nystagamus. It has never been found that ocular torsion could be controlled voluntarily. It was my conviction that the human oculomotor system is more plastic than the existing torsional data suggests. I felt that by employing optimal stimulus-response conditions voluntary torsion could be trained.

Using a visual biofeedback technique 3 subjects (2 normals, 1 unilateral intermittant exotrope) were trained to make accurate voluntary tonic cycloversions up to 26.5 degrees in magnitude. Tonic cycloversions were defined as cycloversions which could be sustained for a 5 second duration.

Two subjects (1 normal, 1 unilateral intermittant exotrope) were further trained to make dynamic cycloversions up to 30 degrees in magnitude. Similar to voluntary horizontal versions the voluntary cycloversional slow pursuit of a (rotating) object increased with the amount of visual feedback. Subjects' abilities to perform voluntary cyclotorsional saccadic tracking of rotating stimuli further demonstrated dynamic cycloversions. Cyclotorsional saccadic magnitude vs. peak velocity relationships corresponded to those of horizontal saccades.

Towards the end of training subjects were able to make voluntary cycloversions in the absence of any visual stimulus. In all tests where rotating visual stimuli were used voluntary cycloversions were not found to be significantly visually induced. All voluntary cycloversions were shown to be pure cycloversions around the visual axes.

In summary, these results suggest that existing slow pursuit and saccadic systems control trained voluntary cycloversions. I propose that in making voluntary cycloversions, the visuomotor system, theoretically, utilizes primitive slow phase and fast flicks from the phylogenetically old vestibulo-ocular motor reflex apparatus in a manner similar to the way the voluntary horizontal and vertical slow pursuit versional eye movement system utilizes this control apparatus. It is possible that this type of visuomotor reorganization may not be limited to just the new voluntary cycloversional eye movements reported in this thesis.

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ABSTRACT

Torsion is defined as any rotation around the visual axis of the eye. Researchers who have reported torsional eye movements found that these movements were controlled reflexively, as in the counter-rolling of the eyes during lateral head tilt, or were basically visually induced, as in large field rotary-nystagmus. Ocular torsion completely under voluntary control has never been reported.

During preliminary research I found some individuals who consistently demonstrated large torsional response variability. These subjects felt that they may have had sporadic voluntary control of their torsion. In addition, I have believed for some time that the human oculomotor system is more plastic than the existing literature suggests. I hypothesized that if adequate stimulus-response conditions were employed voluntary torsion could be trained.

Three subjects (2 normals, 1 unilateral intermittent exotrope) were trained to make accurate voluntary tonic cyclotorsions up to a range of 26.5 degrees using a visual feedback technique. Tonic cyclotorsions were defined as cyclotorsions which could be sustained for a five second duration.

Two subjects (1 normal, 1 unilateral intermittent exotrope) were further trained to make voluntary dynamic

cyclotorsions up to a range of 30 degrees. The amount of voluntary cyclotorsional slow pursuit of a (rotating) object increased with the amount of visual feedback, similar to voluntary horizontal slow pursuit of an object. In the extreme feedback condition where there was an absence of any visual stimulus, subjects demonstrated a series of torsional saccadic movements with virtually no slow components. These results are similar to the horizontal saccades often found during attempted pursuit in the absence of a horizontally moving stimulus.

Subjects were also able to perform voluntary cyclotorsional saccadic tracking of rotating stimuli. Cyclotorsional saccadic magnitude vs. peak velocity relationships corresponded to those of horizontal saccades.

Voluntary cyclotorsions were found not to have significant visually induced components in control studies where subjects were required to relax and observe the rotating visual stimuli used in the aforementioned pursuit and tracking tests.

All voluntary cyclotorsions reported here were shown to be pure cycloversions occurring around the visual axes, even though only monocular visual stimuli (when occurring at all) were used.

These results suggest that existing slow pursuit and saccadic systems control trained voluntary cycloversions. I propose that in making voluntary cycloversions, the visuomotor system utilizes the primitive slow phase and fast flicks from the phylogenetically old vestibulo-ocular motor reflex apparatus in a manner similar to the way the voluntary horizontal and vertical slow pursuit versional eye movement systems utilize this control apparatus.

SECTION I. TONIC CYCLOVERSION

Introduction

In vision research eye movements are usually defined by their horizontal and vertical components. Under certain stimulus conditions researchers have reported a third component, cyclorotations (cyclotorsions) around the visual axis of the eye.

Involuntary cyclotorsions have been stated to occur during vergence (Hering, 1868; Donders, 1876; Landolt, 1876; Allen, 1954; Allen and Carter, 1967), and during lateral head tilt (Davies and Merton, 1957; Miller, 1962; Colenbrander, 1963; Belcher, 1964; Petrov and Zenkin, 1973). Cyclotorsional movements have also been reported to be basically visually induced by large field stimuli (25-50 degs.). These movements include optokinetic cyclotorsion (Brecher, 1934; Kertesz, 1969; Crone, 1975), fusional cyclovergence (Crone and Eberhard-Halm, 1975), and tonic cycloversions (Crone, 1975).

Torsional eye movements have never been reported to be completely under voluntary control. In agreement are vision research texts by such authors as Ogle (1964), Howard and Templeton (1966) and Adler (1975) which state that voluntary torsional control does not occur.

In our laboratory using subjective afterimage/ real-line matching techniques, we have found that during version movements "normal" subjects are usually in substantial agreement with Listing's Law (Nakayama and Balliet, (1976)*). We have found, however, large torsional deviations from Listing's Law in strabismus patients, and to a lesser extent in a few normal observers (Nakayama, 1975). Some of these individuals demonstrated consistently large torsional response variability ranging up to 2-3 degrees only in specific versional gaze positions. These results are not consistent with Listing's Law and our other data where torsional variability was less than 0.7 degrees. Upon questioning, some subjects said they felt that for certain gaze positions they may have been sporadically controlling their torsion by some unknown voluntary

* In simplified form, Listing's Law quantitatively specifies that for every versional gaze position there exists only one orientation of the globe in the head.

mechanism. In light of the aforementioned research this statement did not make sense. However, I have felt for a long time that the plasticity of the human oculomotor system has not been adequately explored. I hypothesized that if adequate stimulus-response conditions were employed voluntarily controlled cyclotorsional eye movements could be trained. If successful I would be substantiating a new eye movement of major significance in the study of human cyclotorsion and oculomotor plasticity.

Method

Subjects

Subject M.N. (age 31) was a unilateral intermittent exotrope (left eye - 30 degrees). Normally, he allowed his exotropia to be manifest. He had, otherwise, normal stereopsis, eye movements, and corrected acuity. M.N. was selected because of his extremely high motivation and his repeated demonstration of large torsional response variability (about 3.0 degrees) when tested for Listing's Law (see Introduction). As my first subject, he was separately trained and tested over a period of 13 months for five hours per week. Working closely with M.N. I used various training techniques in order to find adequate stimuli which would allow him to make voluntary cyclotorsional responses.

When M.N. had reached a level of performance which appeared asymptotic, two normal subjects, R.B. (author; age 30) and C.H. (age 26) were chosen because they were highly motivated. These two subjects had normal stereopsis, eye movements, and normal or corrected normal acuity. Contact lenses were worn by C.H. Both subjects were trained and tested over a period of two months using the procedures evolved during the training of M.N. Before training, C.H. and R.B. could make only uncontrolled sporadic cyclotorsions of ± 0.7 degree. This figure is the noise of our subjective measurements.

Training and Testing Procedure

Many different training procedures were used with M.N. I will report only upon the final visual feedback method used most successfully with M.N. and exclusively with subjects C.H. and R.B. In general the following procedures were conducted during both training and testing.

During visual feedback training the subject was seated in a dark room with one eye occluded. Head movement was fixed to within 6 min. arc. by a full mouth impression bite plate (see Ditchburn, 1973, regarding the accuracy of this technique), so that the fixating eye was looking at a fixation point and/or line stimulus in approximately primary position. (For subject M.N. his exotropic eye was occluded while he fixated with his non-strabismic eye). The subject was required to give to his fixating eye a single 11 degree by 15 min. vertical afterimage inducing flash (3 degree x 15 min. and 26 degree x 15 min. stimuli were also used for M.N.). The afterimage was generated by a partially occluded Honeywell Strobar flash unit; flash duration ≅ 1.0 msec. at 30 cm. distance. The afterimage represented to the subject his eye position. By horizontally sliding the bite plate mechanism, the subject then imaged this afterimage parallel to a vertical luminous real-line of equal visual angle which was viewed at 100 cm distance in primary position (Fig. 1; #1). The real-line was a partially occluded "white" 110 volt G.E. luminescent panel. It was bisected by a 15 min. circular black fixation point. To prevent visual suppression of the lines by one another a Variac was used so that the subject could control the real-line's intensity over a range of 0 - 2.0 ft. lamb. He also controlled a servo-motor system which allowed adjustment of the real-line's lateral angle of tilt. This angle of tilt could be observed by the subject directly and/or by a digital voltmeter (D.V.M.) readout. The D.V.M. had an accuracy of ± 1 min. The subject was instructed to keep his afterimage matched parallel <u>only</u> by cyclorotating his eye(s) to the real-line which he progressively rotated more and more (left or right) from the vertical (Figs. 1; #2, #3). Usually 20 min. arc. increments were used. No instructions were given as to what type of eye movement was to be used to get to this position, e.g. slow pursuit, saccades, nystagmus, etc. Such matches which could be subjectively held for a minimum duration of five seconds were defined as subjectively measured tonic cyclotorsions. All training and testing measures of subjective tonic torsion were relative to a plumbed vertical afterimage/real-line match. Subjects were encouraged to train equally in both incyclo and excyclo torsional directions. Subjects trained usually at the rate of one hour per day.

Subjective Testing Measurement

As during training, afterimage/real-line matches which could be subjectively held for 5 seconds were defined as subjectively measured tonic cyclotorsions.

Objective Testing Measurement

Objective measures of tonic torsion were obtained from photographs taken with a 35 mm Nikon F-2 motor drive camera with lenses and bellows attachments equivalent to a lens with a focal length of 400 mm. Two Vivitar 292 strobe flash units provided illumination. Photos were taken at 100 cm distance by means of a first surface mirror mounted at 30 cm distance in front of the subject at a 45 degree angle, so positioned to be 5.0 degrees off the subject's primary visual axis. Subject:image ratio was 1:1. The camera was actuated by the subject while he simultaneously held subjectively determined tonic cyclotorsional matches. Present in all photographs was a vertical stationary reference marker which could be read to 0.03 mm (10 min. arc.). The marker was mounted next to the eye in the camera's focal plane and was placed in exact position by an XYZ microscope stage and bubble leveling system. During photographic analysis slides were magnified 12 times in size by a Kodak Auto-Focus Carousel projector. The image was rear projected onto a horizontal table screen made of translucent "white" Mylar. Landmarks used in measurement were two limbal-scleral blood vessel junctions which bordered the diameter of the iris and approximately bisected the pupil. The orientation of a line formed between these two points relative to the stationary vertical marker was used in determining objective cyclotorsion. Fig. 2 illustrates an example of this technique showing a 20 degree voluntary cyclotorsional difference between the two photographs. All photographic cyclotorsional measurements were defined relative to the average eye position at a vertical subjective afterimage/real-line match (0 degrees). Torsional measurements were repeatable to within ±4 min. arc. Horizontal-vertical eye movements were obtained by comparing the center of the pupil to small corneal reflex marks, assuming an average corneal radius of 12 mm. These measurements were repeatable to within ± 10 min. arc.

Results

Experiment 1(a): The Training of Voluntary Tonic Cyclotorsion

Fig. 3 shows the training of voluntary tonic torsion for subjects C.H. and R.B. Hours of training at 1 hr/day vs. the total range of subjectively measured torsion for the right eye are plotted using small symbols. These are maximum tonic torsional ranges (mean of 8 measures) which can be held for a 5-second duration. The three large squares and the one large circle show simultaneous objective measurements (each is the mean of 8 measures).

Subject C.H. produced up to 26.5 degrees (12.0 degrees incyclo, 14.5 degrees excyclo) of tonic torsion in approximately 30 hours. Subject R.B. produced about 20 degrees of tonic torsion (9.0 degrees incyclo, 11.0 degrees excyclo) in approximately 25 hours. Both subjects showed about an 0.8 degree/hour training rate. Good agreement between subjective and objective torsion testing results can be seen. Not shown, subject M.N. had a final objectively measured tonic torsional range of approximately 20 degrees (10.0 degrees incyclo, 10.0 degrees excyclo). His training results are not shown because of differing procedures used in his training over a period of 13 months (as described in Subjects section).

The torsional ranges reported should not be considered maximal. With further experimentation of about 10 hours of voluntary dynamic torsion (not reported here) the objectively measured ranges of C.H. and M.N. increased to 27 and 30 degrees, respectively. Even at this point the subjects felt that these figures were conservative and that they were not near their peak voluntary torsional capabilities.

Experiment 1(b): The Accuracy of Subjective Tonic Torsion

Howard and Evans (1963) and Howard and Templeton (1966) stated that the method of using subjective afterimages to measure torsion required much practice and that such methods had not been adequately validated against objective measures of torsion. They estimated that subjective afterimage matches were unlikely to be accurate to more than one degree. Recently, Flurr (1975), in a study which compared the subjective and objective recording of ocular counter-rolling as a result of head tilt, found objective measures varied over a range of 0-3.0 degrees, whereas subjective error was 3.0 to 10.0 degrees. Crone and Eberhard-Halm (1975), on the other hand, found close correspondence when they objectified their subjective measures of fusional cyclovergence. Typically, a standard deviation of 0.2 degree was found for their objective measures which was even a little greater than their subjectively measured torsion. Because the careful analysis of photographs is a slow, arduous process, all the visual feedback training (as described in Training Procedures) used subjective afterimage/real-line matches in order to immediately monitor cyclotorsion. I was, therefore, concerned about my subjective measures, particularly in light of the fact that making voluntary cyclotorsions can be a very difficult task (to be described later). It could be predicted that subjective torsional responses might overestimate actual objectively measured torsion. As it turned out, my concern was not unfounded, but happily it was determined not to be of major consequence.

In order to make an assessment of the accuracy of the subjects' subjective tonic voluntary torsional response measures, a series of photographs was taken at the termination of testing for all subjects. Agreement between objective measures of eye rotation and subjective tonic torsional matches was usually quite good. In Figs. 4, 5 and 6 subjective vs. objective torsion is plotted for different testing times and conditions for the fixating eyes (right) of subjects R.B., C.H. and M.N. respectively. Each data point is the mean of 4-10 trials; the error bars represent standard deviations. The diagonal lines that are drawn in represent perfect subjective-objective torsion matches.

Subject R.B. was tested only after 35 hours of training. Fig. 4 shows near perfect agreement between his subjective matches and objective measures. He subjectively overestimated his torsional matches by an average of 5 percent.

Subject C.H. was tested at the end of 16, 25 and 35 hours of training (Fig. 5). She generally showed good agreement between her subjective and objective measurements, but tended to have relatively smaller amounts of objectively measured torsion compared to subjectively measured torsion in the incyclotorsional direction. It should be noted that for all subjects this direction was the most difficult throughout training and testing. No reason could be determined for this finding. This problem led to far greater subjective overestimations in this direction. Her average matching error for the end of 16, 25 and 35 hours of training was equal to subjective overestimations of 19.6, 1.1 and 4.9 percent, respectively.

Crone and Eberhard-Halm (1975) have found that field size is an important factor in the visual induction of cyclotorsion. They reported that fusional cyclovergence occurred when field sizes were 25 degrees in visual angle. They also reported, as have Kertesz and Jones (1970), that field sizes of less than 10 degrees visually induced little or no fusional cyclovergence. I wished to determine if different sized stimulus lines had differential visual induction effects on voluntary tonic cyclotorsion.

Subject M.N. was trained and tested after 13 months of variable training (see Subjects) with three different stimulus line sizes of 3 degrees, 11 degrees and 26 degrees (x 15 min. arc.). Fig. 6 shows these test values. For clarity the 3 and 26 degree stimulus line data have been displaced up and down, respectively, on the ordinate by 10 degrees. It can be seen that all test line sizes produced similar results. No visual induction effects are apparent. The larger angle tonic torsional positions in the incyclotorsion direction had, as with C.H., the worse accuracy. Total mean matching errors for 3, 11 and 26 degree test lines were equal to subjective overestimations of 8.5, 13.3 and 10.3 percent, respectively.

Experiment 2: The Apparent Difficulty of Tonic Torsion

During final testing, observers subjectively overestimated their afterimage matches by an average of 6.9 percent. This bias was probably due to the fact that there is an effort factor in making voluntary tonic cyclotorsions. For example, difficulty can be defined to be inversely related to the duration which voluntary tonic torsion can be held. Shown in Fig. 7 for R.B. is an average plot of his estimate of difficulty compared to his subjectively measured voluntary tonic cyclotorsional range during three different phases of training. Similar relationsships exist for the other two subjects. Cyclotorsion was defined as a total range, not as separate ranges of excyclo and incyclo torsion. Throughout training the ranges of voluntary tonic torsion in these two directions were approximately equivalent. Sixty seconds was found to be the average duration that R.B. could maintain a vertical afterimage/ real-line match without discomfort. This 10 percent level of difficulty was considered the minimum amount of difficulty achieved with practice in order to fixate the afterimage adjacent to the real-line. Zero percent was equal to the subject's eyes being closed. One hundred percent was the maximum tonic torsion that could be held for 5 seconds. In pain and effort this is analogous to any muscular task which can be done for only 5 seconds.

Curve (a.) represents the estimated magnitude of difficulty at the end of the initial days of training at 5 hours. The subject's range of torsion was 4.0 degrees; but within this limited range the amount of effort increased sharply from about 0.7 degree (the variability of subjective measurements at fixation), so that virtually all voluntary tonic torsional angles required large amounts of effort. Curve (b.) shows that after a total of 35 hours of training to extend his voluntary cyclotorsional range the subject could cyclorotate his eye over a range of 20 degrees. His overall amount of difficulty with the task decreased tremendously. For example, at 4.0 degrees he then experienced only about 18 percent difficulty compared to 100 percent in curve (a.). This same effect occurred even more when he further practiced within this same 20 degree range for an arbitrarily determined time of 10 more hours (curve c.)). It should be noted that during this time he was not allowed to extend the limits of this cyclotorsional range. It can be seen that all torsional angles were easier and that he gained access of up to 6 degrees of virtually effortless cyclotorsion which he could hold for as long as he could fixate. The dashed line in (c.) indicates that the subject's torsional range was extended to about 21 degrees.

The point I wish to stress is that given enough time one can, through training, gain access to a large amount of "effortless" voluntary tonic cyclotorsion. I believe that the range of effortless voluntary torsion could become far in excess of the 6 degrees at which I arbitrarily stopped.

Experiment 3: Test for Voluntary Cycloversion

As previously stated, all training and testing was conducted monocularly. The left eye was always occluded in darkness while the voluntary tonic cyclotorsion of the fixating right eye was measured. Of obvious concern was how much torsion was occurring in the occluded eye in the absence of its own visual stimulus. Subjects felt muscle tension in both eyes, indicating that both eyes were probably moving together. During the training of our three subjects we photographed their left and right eyes independently on the same day. The left eye was in the dark with no visual stimulus while the right eye was fixating on the matching stimuli. Fig. 8 shows objectively measured voluntary tonic torsion of the right eye for a specific subjective tonic torsion afterimage/real-line match. The ordinate shows the objectively measured cyclotorsion of the left eye, photographed while the right (fixating) eye was holding an equivalent subjective match. The diagonal line (slope equal to 1.0) represents perfect conjugacy. For all three subjects it can be seen that the left eye, although occluded, was conjugate with the right fixating eye. (Not shown, the slope of a regression line fit to this data is equal to 0.96.) Therefore, the voluntary tonic torsions which I have trained monocularly are, in fact, voluntary tonic cycloversions.

Experiment 4: Test for Pure-Wheel Rotations During Voluntary Tonic Cycloversion

I found upon further analysis of the photographs that horizontal and vertical eye movements of both eyes during voluntary tonic cycloversions were usually within the variability of my measurement technique, which was ± 10 min. arc. Of 1500 photographs, less than 10 percent showed horizontal-vertical eye movements which were greater than this figure, with none of these greater than ± 30 min. These were not systematically related to torsional position and were usually diagonal in direction. This is what would be expected for the normal range for slow fixation drifts and flicks during the fixation of a spot (Ditchburn, 1973; Yarbus, 1967). Thus, at no time was there any indication of vertical movements or vergence during voluntary tonic cycloversion. These eye movements are, therefore, pure-wheel rotations, occurring around the visual axes of the eyes. These results are in opposition to arguments by Jampel (1975) who has stated that such movements are neurologically and structurally impossible.

Experiment 5: Control Test for Visual Induction of Tonic Cyclotorsion

As mentioned in the introduction, torsion may be visually induced simply by the static inclination of a large-field (25 degrees) multiple lined stimulus (Crone, 1975). I had previously found in Experiment 1(b) that for subject M.N. stimuli of 3, 11 and 26 degrees had no effect in either subjectively or objectively measured torsion (Fig. 6). I had also noted that throughout training and testing all voluntary torsions required an amount of willful muscular effort which was judged by all subjects as inversely related to the amount of voluntary torsion measured (Fig. 7). I was thus convinced that these measurements were of "voluntary" torsion. To find out just how much torsion the standard 11 degree x 15 min. arc. line stimulus did visually induce, I ran a special test of induction after all torsion training had been completed. Subjects

were instructed to relax and simply look for 30 seconds at only the real-line which was held at different fixed lateral angles in space. This was done both with and without the usual vertical afterimage line. At the end of the 30 seconds, photographs of the right (fixating) eye were taken in order to objectively measure any visually induced torsion. The time interval of 30 seconds was comparable to the longest time required to obtain a voluntary torsion afterimage/real-line match. The same results were found whether or not the subject had an afterimage. The results of these two conditions have been summarized (Fig. 9). The tilt of the real-line vs. objectively measured torsion is shown for all three subjects. For clarity, the curves for M.N. and C.H. have been displaced, respectively, up and down on the ordinate by 3 degrees. Means and standard deviations are plotted. Only R.B. shows a trend in the direction of visually induced torsion, i.e. (1) a clockwise rotation of the stimulus would visually induce excyclotorsion;
(2) a counterclockwise rotation of the stimulus would visually induce incyclotorsion. R.B. shows a magnitude of response which never exceeded 0.75 degree. This is a relatively insignificant 7-8 percent of the torsional response shown previously for R.B. in Fig. 4.

Discussion

I have been successful in showing that the human oculomotor system is sufficiently plastic that it may be trained to make, with good accuracy, voluntary tonic cyclotorsions up to a magnitude of 26.5 degrees. Using the methods described in this paper, training occurred at about 1 degree/hour. I have also demonstrated that these torsions are pure cycloversions which are uncontaminated by vertical or horizontal (vergence) movements. These voluntary torsions have no significant visually "induced" components. As discussed in the introduction, this new eye movement is in opposition to past reports that man cannot make voluntary cyclotorsions. One may ask -- Why has it taken so long to demonstrate that the human oculomotor system has the ability to make voluntarily controlled large-angle cycloversions?

In answer to this, I should like to mention that in the initial stages of this experimentation, while I was trying to find optimal training techniques with M.N., I was also trying to train voluntary cyclotorsion with two other normal subjects, until now not mentioned. During the several months of this experimentation, only M.N. was motivated to endure this preliminary work. After four months the other two subjects became despondent and gave up because they could not initiate objectively measured torsion greater than ± 1.0 degree. Without the perseverance of M.N. there is little doubt that I would not have continued this research. However, once a seemingly optimal stimulus response paradigm was reached with M.N. I was able to train without failure the other normal subjects reported upon here. I was happy to find that the normals could, in fact, do this task as well as the unilateral intermittent exotrope, M.N. With my current training techniques I can probably train anyone to make tonic voluntary cycloversions. The amount of voluntary tonic torsion is dependent only upon the individual's time and motivation.

It should be noted that the training of voluntary torsion requires a tolerance for extreme concentration and physical discomfort in addition to the muscle tension mentioned in Experiment 2. All subjects experienced at one time or another head-body rolling and counter-rolling, stomach nausea, headaches and/or very rapid body fatigue. In regard to concentration, subjects agreed that in order to make cyclotorsions nothing could enter their minds but the logic that their afterimage (eye) could be rotated without the rotation of their heads. Particularly during initial training subjects kept trying to rotate their afterimages to the real-line by turning their heads. It was found to be very difficult to inhibit this "reflex". For instance, the full mouth bite plate allows a maximum head rotation around the visual axis of 6 min. arc. (Ditchburn, 1973). Because of this and the fact that the plates were made of a hard, brittle compound, many were broken. For example, about 12 bite plates were made for R.B. One day the bite plate did not break; instead, R.B. cracked his lower rear molar. After R.B. finally conceded to himself that he could rotate his eye without rotating his head there were no further problems of this sort. On the other hand, once subjects acquire control over about 20 degrees of torsion the amount of effort within that 20 degrees is comparatively low (Fig. 7). At this point, with the exception of the sensation of head-body rotation, the above "symptoms" disappear and the voluntary cyclorotation of one's eyes can actually become uniquely enjoyable.

Near the time of completion of this study I translated the classic 1929 paper by Noji which has been referenced by Howard and Evans (1963) and Ogle (1964) as one of the first studies indicating the presence of the reflexive visual "induction" of eye torsion. Noji studied only one subject (himself). Noji's technique for the visual "induction" of eye torsion involved his very gradual tilt of an objective visual line 14 degrees in visual angle on which he projected an afterimage line of approximately equal size (subjective matching technique). He had to use a considerable amount of effort and practice. Only after a minimum of five continuous days of "exercise" was he able to make cycloversions over a total range of about 15 degrees. It is difficult to say whether the tilt of the objective line or the presence of the afterimage coupled with training was the crucial factor in producing Noji's eye torsion. From my work I hypothesize that Noji did not visually "induce" torsion, but probably trained himself to make the first voluntary cyclotorsional eye movements. If I am correct, the present research would be yet another example of a phenomenon in science not being discovered, but rather rediscovered.

SECTION II. DYNAMIC CYCLOVERSION

Introduction

In Section I of this thesis I have substantiated a new class of eye movements. Humans were trained to make non-visually induced voluntary tonic cycloversions (cyclotorsions) up to 26.5 degrees. During the experiment subjects' heads were held rigid by a full mouth bite plate. One eye was occluded. Using the other eye they were required to make a parallel match of a single 11 deg. x 15 min. vertical afterimage inducing flash to an equally sized vertical luminous real-line. The subject was instructed to keep his afterimage matched parallel to the real-line by cyclorotating his eye(s) to the real-line which he progressively tilted more and more (left or right) from the vertical. With practice, subjects could make a voluntary tonic cyclotorsional match at any point within their trained cyclotorsional range. Subjective matches were defined as tonic if they could be held for a five-second duration. Because of a certain amount of "effort" involved with the task, subjective matches were found to be overestimations by an average of 6.9 percent when compared to objective measurements. Of major importance is the fact that instructions were not given as to the type of dynamic cyclotorsional eye movements which were to be used to attain this tonic cyclotorsional control.

I was interested in what type of voluntary dynamic eye movements had become accessible during the training of these voluntary tonic cyclotorsions. With further training and testing I wished to determine if humans were capable of (1) cyclotorsional pursuit of objects and (2) cyclotorsional saccadic tracking of objects. Also of interest was the type of eye movements made during (3) dynamic cyclotorsion in the absence of any stimulus. If subjects could make these voluntary dynamic cyclotorsional eye movements it would be of interest to compare these responses to "normal" horizontal-vertical eye movements. The similarities and differences between these voluntary eye movements would further our understanding of the control mechanisms underlying the human potential to make voluntary cycloversions, a response which had previously been considered to be impossible (Ogle, 1964; Howard and Templeton, 1966; Adler, 1975).

Method

Subjects

Two subjects, M.N. and C.H., were tested. These subjects had previously been trained to make voluntary tonic cyclotorsions of 20 and 26. 5 degrees respectively. Subject C.H. had normal stereopsis, eye movements and corrected acuity. Subject M.N. had a left intermittent exotropia of 30 degrees; he otherwise had normal stereopsis, eye movements, and corrected acuity. Normally, he allowed his exotropia to be manifest. Because the objective photographic measurements required that the radial iris markings of the eye be used as landmarks, subjects were required to make all test determinations without optical aids. The uncorrected near acuity for the right eye of M.N. and C.H. was, respectively, equal to 20/45 and 20/100. Neither subject had appreciable astigmatism.

General Training and Testing Procedure

The subject was seated in an illuminated room with his head fixed to within ± 6 min. by a full mouth bite plate (Ditchburn, 1973). With the exception of test 3, all training and testing was done monocularly. The left eye was occluded. The right eye viewed a fixation point and/or other stimuli in approximately primary position.

The subject gave to his fixating eye 8 consecutive 11 deg. x 36 min. vertical inducing flashes in order to form a single afterimage of the same size. This number of flashes was necessary to insure that the afterimage persisted under the floodlight illumination required to take motion pictures. This afterimage was generated by a partially occluded Honeywell Strobar flash unit; flash duration $\cong$ 1.0 msec. at 30 cm distance. The afterimage represented to the subject his eye position. A horizontally sliding bite plate mechanism allowed the subject to then image this afterimage parallel to a vertical black real-line of equal visual angle which was viewed in space in primary position at 100 cm distance. A matte white 40 degree field of 100 ft. Lamb. surrounded all presented stimuli. The real-line's lateral angle of tilt was determined by a servomotor system which was controlled by a signal generator. A digital voltmeter gave a constant readout of the real-line's tilt to an accuracy of ±1.0 min. arc. During training and testing, the real-line was programmed with various wave forms of varying durations. Using a visual feedback technique the subject was instructed to constantly keep his afterimage matched parallel to the real-line by only cyclorotating his eye(s) regardless of the real-line's orientation.

The subject's ability to make saccadic tracking and slow pursuit could be evaluated by using step or ramp waveforms of differing amplitude and duration. In addition, if the subject was instructed to rotate only his afterimage without any real-line pursuit stimulus or to try to voluntarily cyclorotate his eye while only looking at a fixation point, we could examine the relative ability to make slow pursuit cyclotorsions given different amounts of visual pursuit feedback information.

The training of dynamic cyclotorsion was completed after about five sessions of two hours/day. On the first day stimulus parameters were determined. The following four sessions consisted of the training of appropriate responses. The subjects' assessments of their responses were made using afterimage/real-line matches as immediate feedback indicators to gauge control of voluntary dynamic cyclotorsion. Subjects agreed that this amount of time was sufficient to acquire the necessary responses.

Testing Analysis

Measures of dynamic torsion were made from photographs taken with a 16mm Bolex H16 reflexive movie camera running at either 64 frames/sec during saccadic tracking testing or 24 frames/sec during slow pursuit testing. A 150 mm P. Angeniet zoom lens and 30 mm of extension tubes were required to obtain a subject:image ratio of 1:1 for the right eye. Movies were taken at 30 cm distance by means of a first surface mirror in front of the subject at a 45 degree angle, placed 5.0 degrees off the subject's primary pupillary axis. Two Color Tran 650 watt flood lights at 100 cm distance provided the constant illumination required. All photographs included a stationary vertical reference marker which could be read to 0.03 mm (10 min. arc.). The marker was mounted next to subject's right eye in the focal plane and was placed in position by a bubble level and XYZ microscope stage.

During photographic analysis each frame was individually measured for cyclotorsion as well as horizontal and vertical movements. Over 10,000 frames of film were analyzed. A 16 mm L.W. single frame motion picture projector magnified each frame 10 times in size. Using a system of first surface mirrors this image was rear projected onto a horizontal table screen made of translucent "white" Mylar. Torsional movements of the eye were measured using the termination points (near the limbus) of the two radial iris markings which were approximately adjacent to the center of the pupil. The orientation of a line formed between these two points relative to the stationary vertical marker was used in determining objective cyclotorsion. All photographic cyclotorsional measurements were defined relative to the average eye position at a vertical tonic subjective afterimage/real-line match (0 degrees). Torsional measurements were repeatable to within ± 6 min. arc. Horizontal-vertical movements were obtained by comparing the center of the pupil to two small corneal reflex marks assuming an average corneal radius of 12 mm. These measurements were repeatable to within ± 10 min. arc. Attention was not given to recording accurate latencies because of apparent anticipatory responses.

Results

Experiment 1(a): Voluntary Cyclotorsional Slow Pursuit: Complete Visual Feedback

It was determined from the subjective pretest measurements of M.N. and C.H. that if the real-line was programmed to rotate with a ramp function of 1.6 degs./sec. for 10 seconds (16 degrees) (Fig. 10) it could be pursued with the subject's afterimage. Higher and lower velocity targets were more difficulty to follow. The excyclotorsional real-line stimulus for subject M.N. (right eye) rotated clockwise from -8 degrees through vertical to +8 degrees. Incyclotorsional real-line stimulus rotation (right eye) was used by subject C.H. Subjects M.N. and C.H.'s test results are shown in Figs. 11 and 12. Time vs. relative torsional magnitude are plotted. The relative pursuit ramp stimulus is drawn in for comparison. Traces are numbered in the order taken. It can be seen that both subjects demonstrated slow voluntary cyclotorsional pursuit movements. For M.N. traces #3 and #4 and for C.H. trace #2 are particularly accurate. Intermixed with these were small corrective saccades. Close approximations to the actual target velocity were usually maintained. These pursuit responses appear to be similar to those found for the normal pursuit of horizontally or vertically slowly moving objects (Ditchburn, 1973; Steinman, et. al., 1969, Yarbus, 1967). During the torsional saccadic components both subjects sometimes demonstrated what appear to be long, slow drifts of glissadic overshoots as well as some small dynamic overshoots (see Bahill, Clark, Stark, 1975a).

Experiment 1(b): Voluntary Cyclotorsional Slow Pursuit: Partial Visual Feedback

Subjects M.N. and C.H. were then asked to attempt the same slow pursuit movements as in Experiment 1(a) (e.g. 16 degrees at 1.6 degs./sec.), but without the visual feedback of the real-line. Subjects were only allowed an afterimage and a black 36 min. fixation point on a 40 degree white surround. The subject was directed to voluntarily cyclorotate the center of his afterimage around the fixation point while trying to imagine the real-line. Figs. 13 and 14 show the test results for subjects M.N. and C.H. Time versus relative torsional magnitude are plotted. Subjects demonstrated less slow smooth movements with more saccades. Some dynamic and slow saccadic overshoots can be seen. Subjects also tended to make torsional movements which were far greater than 16 degrees. Maximum dynamic voluntary torsional magnitude of this type of pursuit stimulus was 25 degrees for C.H. and 30 degrees for M.N. It is notable that C.H. was able to make some long slow pursuit movements while imagining the real-line and using only the afterimage as her feedback.

Trace #5 shows a velocity of 1.6 degrees/sec! Her other traces #6 and#7 have a velocity of about 3 degs./sec. Subject M.N. also shows some slow pursuit of about 3 degs./sec. in his trace #7. These results correspond to reports that it is possible to slowly pursue one's own horizontally moving afterimage (Mach and Bachart, 1969; Heywood and Churcher, 1971).

Experiment 1(c): Voluntary Cyclotorsional Slow Pursuit: No Visual Feedback

Subjects were finally asked to try to make approximately the same slow cyclorotary pursuit movements as in Experiment 1(a) (e.g. 16 degrees at 1.6 degs./sec.), but with no visual stimulus other than a single 36 min. fixation point on a 40 degree white surround. Subjects were instructed to attempt these movements using any available sensory feedback. In Figs. 15 and 16 time vs. relative torsional magnitude are plotted for this experiment. As would be expected for normal horizontal or vertical eye movements, subjects demonstrated little ability to make cyclotorsional slow pursuit (Yarbus, 1967; See Steinbach (1976) for exceptions to this usually found result.). Movements were a series of step-like torsional saccades with virtually no slow components. C.H. showed a few dynamic overshoots of less than 0.25 degree. Subject M.N. in this test demonstrated numerous glissadic and a few apparent dynamic overshoots of 1.5 degrees. The maximum dynamic cyclotorsional magnitudes during these tests were 27 degrees for C.H. and 24 degrees for M.N. These tests show that the voluntary torsions that I have trained are not visually induced torsions. Subjects need no stimulus at all to voluntarily cyclorotate their eyes.

Summary of Voluntary Cyclotorsional Slow Pursuit:
Experiments 1(a), (b) and (c)

It has been demonstrated that humans can, in fact, make reasonably accurate dynamic cyclotorsional pursuit movements which are dependent upon the amount of retinal feedback.* A summary of tests 1(a), (b) and (c) is shown in Fig. 17. This bar graph shows the percentage of time during which subjects made slow pursuit movements during the three different pursuit feedback test conditions. Correct pursuit movements were conservatively defined as those which were in the correct real or imaginary stimulus direction with a velocity between 0.5 and 15.0 degs./sec., and a minimum duration of 500 msec. As would be expected during normal horizontal slow pursuit (Heywood and Churcher, 1971), subjects made the most voluntarily controlled cyclotorsional slow pursuit move-

* Models of servomechanical feedback control relationships between target and retinal motion and resulting pursuit of saccadic movements are included in papers by Young and Stark (1973), and Robinson (1968) among others.

ments in the pursuit test situation where the most complete visual feedback was given (Fig. 17 (a)). A lower occurrence of torsional slow pursuit resulted when subjects had only their afterimages as visual feedback (Fig. 17(b)). Under the conditions where the subjects were required to make torsional pursuit without any stimulus at all (Fig. 17(c)), slow voluntary torsions occurred infrequently.

Experiment 2: Voluntary Cyclotorsional Saccadic Tracking

A test similar to that used in Experiment 1(a) was designed to allow subjects to make voluntary torsional saccades. Subjects were instructed to track the real-line with their afterimage. The real-line was moved by a step function (10 msec. duration) of either 4, 8 or 16 degrees; M.N. used a clockwise rotation from vertical to +4 or +8 degrees, or from -8 to +8 degrees (excyclotorsional stimulus for right eye). C.H. used an opposite stimulus, from vertical to -4 or -8 degrees, or from +8 to -8 degrees (incyclotorsional stimulus for right eye). This procedure is exemplified in Fig. 18 for a 4 degree saccade.

Figs. 19-24 show the test results. Time vs. relative torsional magnitude are plotted. The correct stimulus step magnitude is indicated by the arrows. These figures show that voluntary cyclotorsional saccades can be made which appear very similar to voluntary horizontal or vertical saccades. Voluntary torsional saccades may be single, sequential, or overlapping. The saccadic tracking of M.N.

often showed eye movements which looked like large dynamic overshoots (Figs. 21 and 23) including many of 2.0 degrees. C.H. demonstrated dynamic overshoots, but these were within the norm as to magnitude and rate of occurrence when compared to normal horizontal saccades (Bahill, Clark and Stark, 1975a). I have no clear explanation for the large apparent dynamic cyclotorsional saccadic overshoots found in some of the traces of M.N. Although he is a unilateral intermittent exotrope, it should be remembered that these traces are of his non-strabismic eye. Also, I found no unusual horizontal eye movements for either of his eyes when measured with an infrared iris sceleral border photoelectrode technique, accurate to 30 min. There is one possible explanation. In these tests the mental concentration needed to perform the task under the conditions required for photography was very fatiguing. Bahill and Stark (1975) have found that the occurrence and magnitude of dynamic overshoots increases with fatigue. M.N. reported that he had been feeling tired for several days prior to and through his testing day. In addition, both subjects reported large amounts of saccadic suppression. Afterimages seemingly completely disappeared during and somewhat after voluntary saccades greater than about 4-5 degrees. These two factors could possibly have caused unusual ocular motor control.

During the 4-deg. voluntary torsional saccadic tests (Figs. 19, 20) subjects either overshot the correct stimulus position by as much as 100 percent, or, in the case of M.N., the appropriate eye positions were achieved by making small fixation drifts and/or small saccades. Both subjects reported that an accurate 4 degree saccade was virtually impossible to make and had to be coaxed to even attempt them. The 8 and 16 degree saccades were judged far easier tasks. These results suggest a possible inability to make voluntary cyclotorsional saccadic trackings of less than 4 degrees.

Summary of Voluntary Cyclotorsional Saccadic Tracking: Magnitude vs. Peak Velocity

If all of the saccades shown in Figs. 19-24 are analyzed for their peak velocity vs. magnitude, it is found that this data reasonably fits the magnitude vs. peak-velocity relationship for normal horizontal saccades. Figs. 25 and 26 show Bahill, Clark and Stark's (1975b) data for comparison. The regression line with the error range bars is derived from their data. The data of other researchers (Westheimer, 1954; Yarbus, 1967) show similar relationships. My data points are fitted with the other regression line.

Subject M.N. has an approximately parallel fit, whereas, the data fit for C.H. is not quite parallel. This is probably because I had only 13 saccades to compare for C.H., many of which were overlapping and, thus, difficult to define. With M.N. I had 27 saccades, few of which were overlapping. The regression lines for the data are displaced downwards in velocity by an average of 32 percent for M.N. and an average of 28 percent for C.H. This underestimation of velocity is expected since the photographic analysis of 64 frames/sec. does not have the frequency response to give instantaneous velocity measures. This is analogous to a low-pass filter with a band width of approximately 32 Hz. This would, therefore, lower the measured peak velocities by about 30-40 percent (Bahill, Clark and Stark, 1975a; Fig. 5). It is concluded that voluntary saccadic cyclotorsions are controlled by the same neural mechanisms which determine ordinary horizontal saccades. In addition it is probable that the total active muscle velocities and passive globe viscosities which are involved during the voluntary cyclorotations of the eye are close to those for ordinary horizontal saccades.

Experiment 3: Tests for Pure Wheel Cycloversion During Voluntary Dynamic Cyclotorsion

In section I., I have reported objective measures of voluntary tonic cycloversion. In the present tests for dynamic cyclotorsion I only measured the fixating eye (right). The other eye was occluded by an eye patch in order to make the afterimage/real-line cyclotorsional matching task as simple as possible for the subject, so that no binocular fusion would be required. The real-line stimulus could also be occluded from the left eye of the subject by a partition placed 30 cm from the eye. Using this method I could observe both eyes simultaneously in order to determine if dynamic cycloversions occurred during the monocular stimulation of the fixating eye or under conditions of no visual stimulation. Binocular visual inspection of the subjects' eyes was made during all of the voluntary dynamic cyclotorsional tests reported here. During all of these tests subjects were observed to be performing conjugate cyclotorsions; i.e. cycloversions.

In addition, no vertical or horizontal vergence movements appeared to occur during these voluntary dynamic cycloversions. Movies of the fixating eye demonstrated similar results. Horizontal and vertical eye movements were within the variability of my measurement technique (± 10 min. arc.) in about 95 percent of the frames. Movements in the remaining 5 percent did not vary systematically and usually consisted of diagonal saccades less than 30 min. This is within the range of simple fixation variability that one would expect for a point stimulus (Ditchburn, 1973). It, therefore, can be concluded that all of the voluntary dynamic cyclotorsions which I have trained are conjugate pure wheel cycloversions occurring around the visual axes of the eyes. These results are in opposition to arguments by Jampel (1975) who has stated that such movements are neurologically and structurally impossible.

Experiment 4: Control Tests for Visual Induction of Dynamic Cyclotorsion

It has been previously reported that rotating stimuli can visually induce cyclotorsion (Brecher, 1934; Kertesz, 1970 and Crone, 1975). I wished to know the amount of this visually induced cyclotorsion which may have been a possible torsional component in dynamic voluntary torsion Experiments 1(a) and 2. To accomplish this I exactly replicated these experiments except for one difference. Subjects were instructed to simply relax and observe the slow pursuit ramp stimulus moving at 1.6 degs./sec. (Experiment 1(a)) or the saccadic step stimulus of either 4, 8, or 16 degrees (Experiment 2). The subjects did these experiments both with and without the usual monocular vertical afterimage line. Similar results were found for both subjects under both slow pursuit and saccadic tracking stimulus conditions. Representative results of both subjects for the slow pursuit stimulus are shown in Fig. 27. Time (sec.) is plotted relative to the amount of cyclotorsion. An upwards direction on the ordinate indicates that the eye was rotating in the same direction in which the stimulus was rotated. It can be seen that within the noise of our torsional measurements (± 6 min.) these test conditions did not visually induce systematic cyclotorsion. Of 17 traces, 10 showed no cyclotorsional movements (strip #1), five traces showed torsional fixation drifts of 0.2-1.0 deg./sec. with magnitudes less than

1.0 degree (strips #2 and #3), and two traces showed single saccades less than 1.0 degree (strips #4 and #5). The movements were not systematic in their direction. These results are greater in magnitude than those found by Fender (1955). He reported torsional fixation motions of the eye which were flicks 2 min. arc. and slow, irregular drifts 5 min. arc. The larger magnitude of my results (when found) may be because my subjects have acquired voluntary neural access to their cyclotorsional movements, thus adding a greater amount of torsional "noise" to their oculomotor cyclotorsional control systems. This hypothesis is strengthened by subjects' reports that only after training did they have difficulty maintaining a vertical (0 degree) afterimage/real-line match. The main significance of these results is that the stimulus configurations used in our experiments do not visually induce cyclotorsion. Therefore, it can be concluded that the results reported in this paper have no visually-induced components.

Discussion

Slow Pursuit and Saccadic Tracking Data

The data presented here demonstrates that humans can be trained to make voluntary dynamic cyclotorsions around the visual axis up to 30 degrees in magnitude. It has been shown that these movements have no visually-induced components.

After training, subjects displayed the ability to make reasonably accurate voluntary cyclotorsional slow pursuit and saccadic tracking of rotating stimuli.

In the case of voluntary cyclotorsional slow pursuit of rotating stimuli, cyclorotations looked similar to voluntary horizontal slow pursuit eye movements. The amount of voluntary cyclotorsional slow pursuit of a (rotating) object increased with the amount of visual feedback. In the extreme test situation, where no stimulus was present, the subject was instructed to try to imagine the slow pursuit of a rotating stimulus. As would be expected for normal horizontal pursuit under these conditions, a series of step-like cyclotorsional saccades occurred which had virtually no slow pursuit components.

Voluntary dynamic cyclotorsional saccadic tracking of a rotating stimulus was demonstrated to be reasonably accurate for 8 and 16 degree stimulus steps. During these movements glissadic and dynamic cyclotorsional saccadic overshoots occurred. These look similar to those reported for horizontal saccadic overshoots (Bahill, Clark, Stark, 1975a), except in some of the traces of M.N. where apparent dynamic overshoots were sometimes as large as 2.0 degrees in magnitude (see Section II, Experiment 2(a) for possible explanation of this effect). Curiously, subjects were unable to make voluntary cyclotorsional saccadic trackings of stimuli steps of 4 degrees. When they would even attempt the task, they either made slow cyclotorsional fixation drifts or overshot the correct stimulus position by as much as 100 percent. The most important finding of this saccadic data is that when magnitude vs. peak velocity is examined it is found that voluntary cyclotorsional saccades have similar curves to those of normal horizontal saccades (Bahill, Clark and Stark, 1956). It is likely that both types of saccades have the same neural origin.

Theoretical Implications of Slow Pursuit and Saccadic Tracking Data

Voluntary cyclotorsional slow pursuit and saccadic tracking of rotating stimuli are very similar to the slow pursuit and saccadic tracking of horizontally moving stimuli. These results suggest that existing slow pursuit and saccadic mechanisms control trained voluntary cyclotorsions. In addition, it is important to remember that voluntary cyclotorsions are versions occurring around the visual axes even though the visual stimuli (when existing at all) are presented monocularly. I propose that these components originate from the phylogenetically old vestibulo-ocular reflex motor apparatus used for stabilizing the retinal image slip. These primitive slow phase and fast flicks may have been utilized by the visuomotor system in making voluntary cycloversions, in much the same way as they have been hypothesized to be used in the production of voluntary horizontal and vertical slow pursuit and saccadic versional eye movements (Robinson, 1972). Clinical evidence (Fox and Holmes, 1926; Dix et al., 1971; Henriksson, 1973) supports this hypothesis by indicating that all types of slow eye movements, including vestibular slow phase, optokinetic slow phase, and pursuit eye movements, originate from the same slow phase system. The finding that voluntary saccades, the fast phase of vestibular and of optic nystagmus all share the same fast-saccadic system (Ron et al., 1972; Henriksson and Nilsson, 1975) further supports this hypothesis.

Visuomotor Plasticity

If voluntary dynamic cycloversions are but an apparent conditioned process of visuomotor reorganization from existing old phylogenetic components, it may be assumed that such reorganizations may not be limited to the creation of voluntary cycloversions. Other visuomotor initiated oculomotor organizations could be formed, as well. Henriksson and Nilsson (1975) recently reviewed the plasticity and the dynamic properties of the vestibulo-ocular reflex arc. They concluded that this motor system has tremendous potential for modification from specific types of long term visual stimulation. One such example, recently reported by Melville Jones and Gonshor (1975), demonstrated that not only can the vestibulo-ocular reflex be temporarily excited or suppressed by appropriate retinal stimuli, but that retinal influence can be so versatile that upon the optical reversal of vision (by wearing dove prisms for 14 days) a complete reversal of the vestibulo-ocular reflex occurs in man. The constraints of such a visuomotor reorganization are probably determined by exact stimulus parameters, training techniques, and in some cases subject motivation. (See Henriksson and Nilsson (1975) concerning attention effects on the vestibulo-ocular reflex arc.)

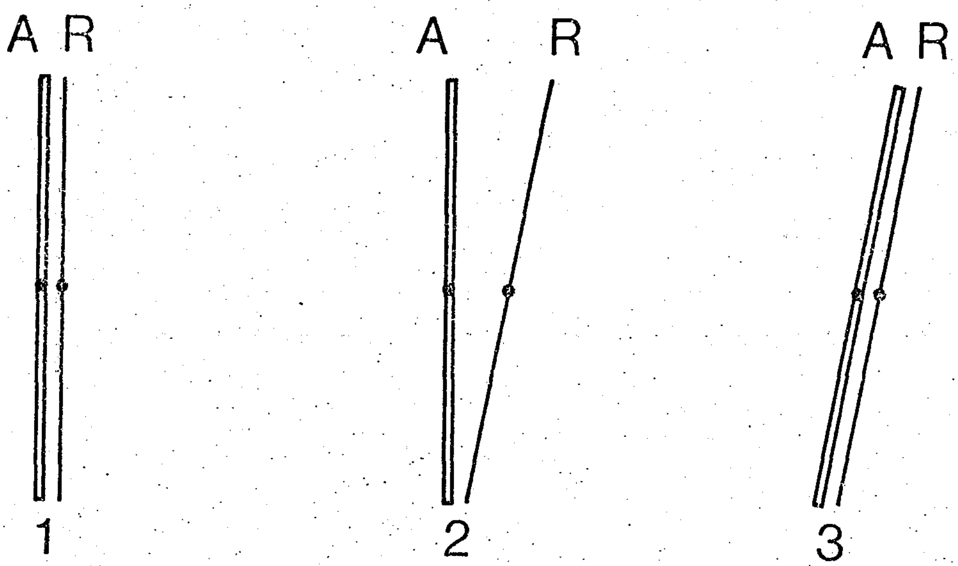
Limits of Voluntary Dynamic Cycloversions

During the training of dynamic cycloversions I held C.H. and M.N. to about a 30 degree limit. At the time I did not have a clear indication as to what the muscular or optic nerve constraints of this system were. However, during and after the training of dynamic cycloversions I found that both subjects were rapidly acquiring a great amount of voluntary cycloversional control (see Section I, Exp. 1(b) concerning changes in effort and performance during training). After all experimentation had ended they became insistent that they had the potential to make torsions far in excess of 30 degrees. At this point I learned that they were practicing and demonstrating their "novel skill" of making cycloversions at home, at parties and to people on the street (of course, without any visual stimulus with the exception of some environmental fixation point). I told them that if they had to make unsupervised cycloversions, to be sure not to "push themselves".

What is the limit of voluntary cycloversions? In 1963, Colenbrander reported the largest reflexive cycloversions up to that time. He found that lateral head tilts of ± 60 degrees in a centrifuge at 2 g. produced a range of static counter-cycloversions up to 30 degrees (± 15 degrees). In 1973 Petrov and Zenkin found during slow dynamic lateral head tilts of 10 deg./sec. the largest reflexive counter-cycloversional magnitudes (monocularly measured) thus far reported. They reported average counter-cyclotorsions of 31 degrees during average head tilts of 41 degrees (relative to vertical). One cyclotorsion of 37 degrees was made during a 49 degree head tilt (relative to vertical). These results indicate an average reflexive cyclotorsional range of at least 62 degrees. It can be concluded that the human reflexive cyclotorsional system can make eye rotations which are at minimum twice the magnitude of the voluntary cycloversions which I have reported here (30 degrees). It is possible that with extended training a similar voluntary cycloversional range could be acquired.

FIGURES

Fig. 1 Representation of the monocular stimulus situation used in the training of voluntary tonic cyclotorsion. (1) Subject matches a vertical afterimage with an equally sized real-line 11 degs. x 15 min. at 100 cm distance; (2) he then rotates the real-line from vertical, usually in 20 min. arc. movements; (3) he then must try to make a parallel match to this slightly inclined real-line with his afterimage which represents his eye position.



A R
1
A R
2
A R
3

Fig. 2 These two photographs show a tonic voluntary cyclotorsional eye movement of 20 degrees.

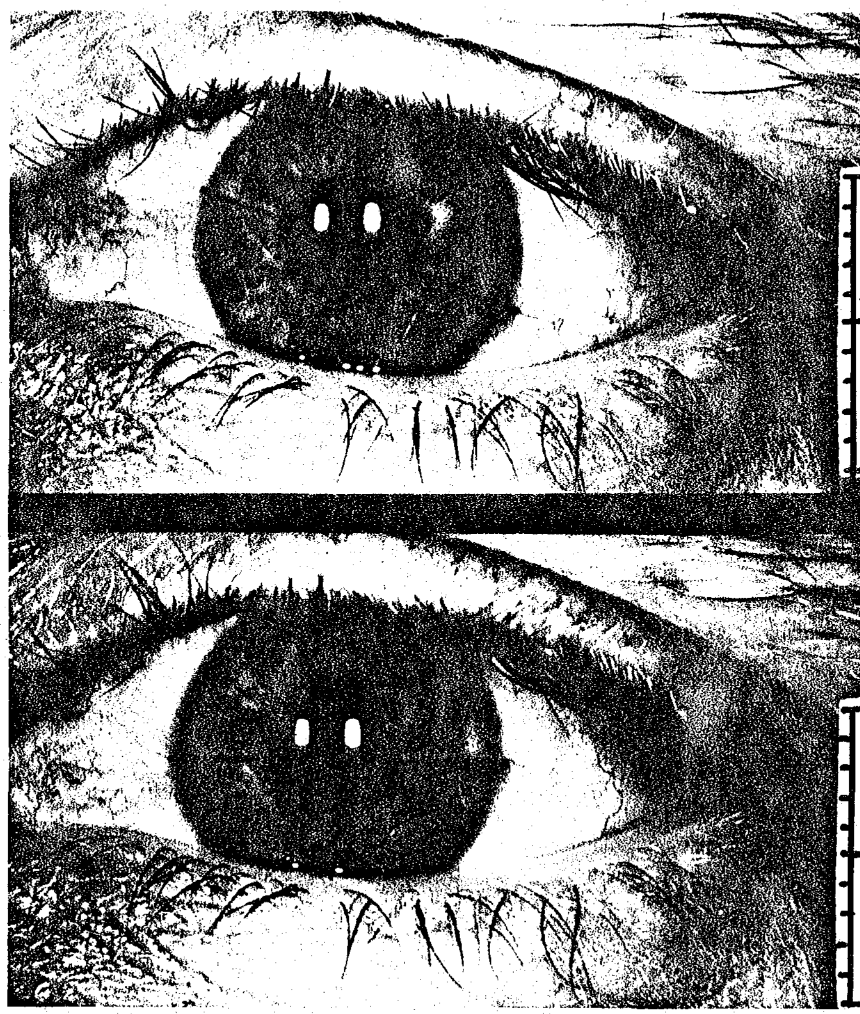


Fig. 3 The training of voluntary tonic cyclotorsion for subjects C.H. and R.B. Hours of training at 1 hr./day vs. the total range (degrees) of subjectively measured torsion are plotted by the small symbols. These are maximum tonic ranges which can be held for a 5 second duration. The three large squares and the one large circle are simultaneous objective measures.

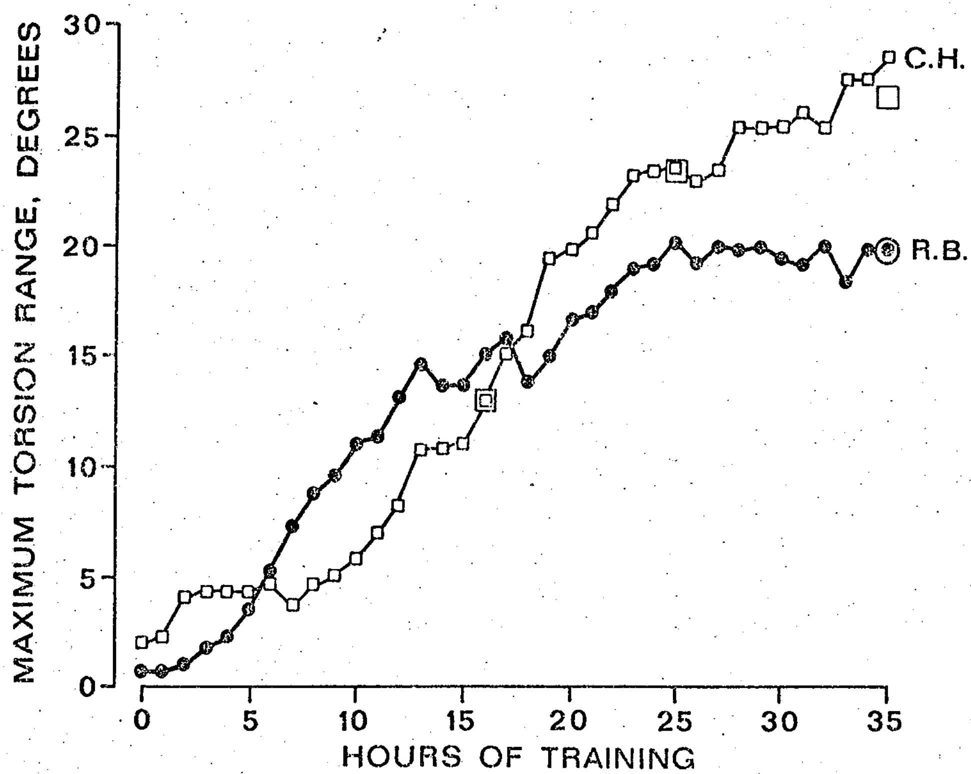

MAXIMUM TORSION RANGE, DEGREES
0
5
10
15
20
25
30
HOURS OF TRAINING
0
5
10
15
20
25
30
35
C.H.
R.B.

Fig. 4 The accuracy of subjective matches compared to objective measures of voluntary tonic cyclotorsion for R.B. at 35 hours of training. Means and standard deviations are shown. The diagonal line represents a perfect match.

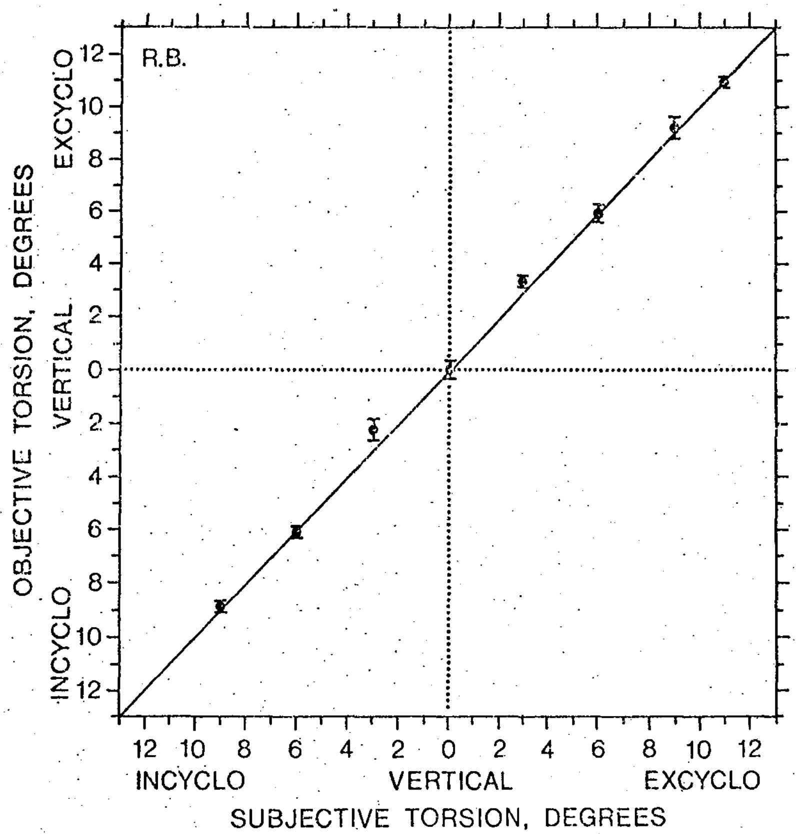
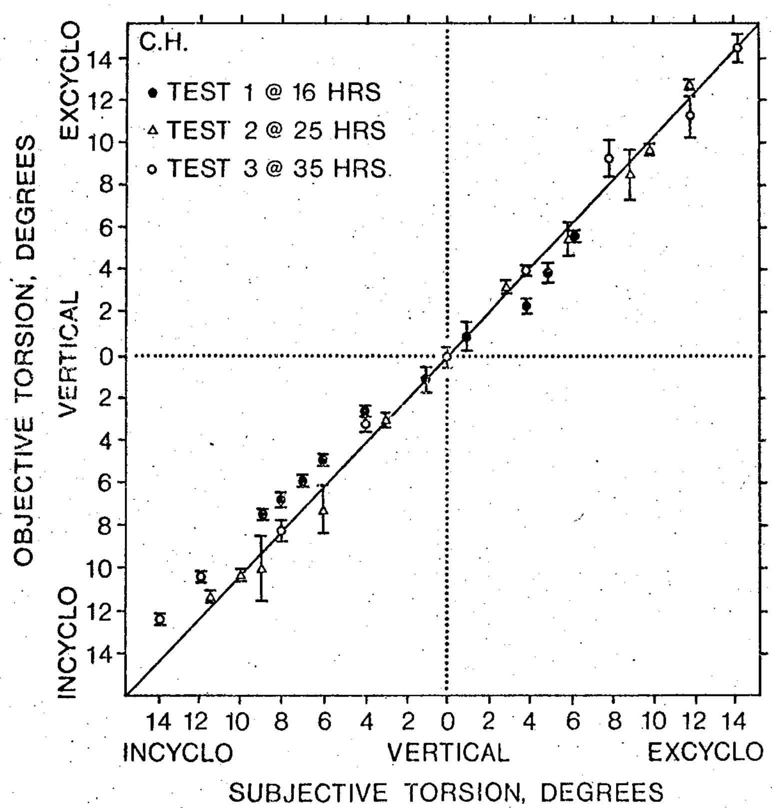

R.B.
OBJECTIVE TORSION, DEGREES
EXCYCLO
VERTICAL
INCYCLO
12 10 8 6 4 2 0 2 4 6 8 10 12
12 10 8 6 4 2 0 2 4 6 8 10 12
INCYCLO
VERTICAL
EXCYCLO
SUBJECTIVE TORSION, DEGREES

Fig. 5 The accuracy of subjective matches compared to objective measures of voluntary tonic cyclotorsions for subject C.H. at 16, 25 and 35 hours of training. Means and standard deviations are shown. The diagonal line represents a perfect match.



C.H.
• TEST 1 @ 16 HRS
▵ TEST 2 @ 25 HRS
○ TEST 3 @ 35 HRS
OBJECTIVE TORSION, DEGREES
EXCYCLO
VERTICAL
INCYCLO
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
14 12 10 8 6 4 2 0 2 4 6 8 10 12 14
INCYCLO
VERTICAL
EXCYCLO
SUBJECTIVE TORSION, DEGREES

Fig. 6 The accuracy of subjective matches compared to objective measures of voluntary tonic cyclotorsion for subject M.N. These are final test results after 13 months of variable training (see subjects). Data for three different stimulus line sizes are represented. For clarity the 3 and 26 degree stimulus data have been displaced up and down, respectively, on the ordinate by 10 degrees. Means and standard deviations are shown. The diagonal line represents a perfect match.

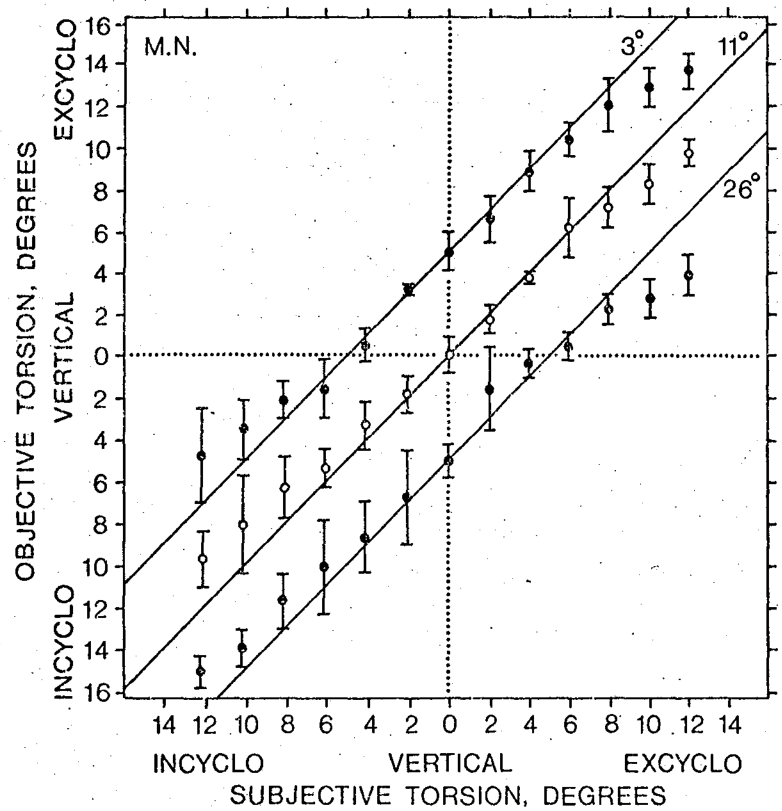
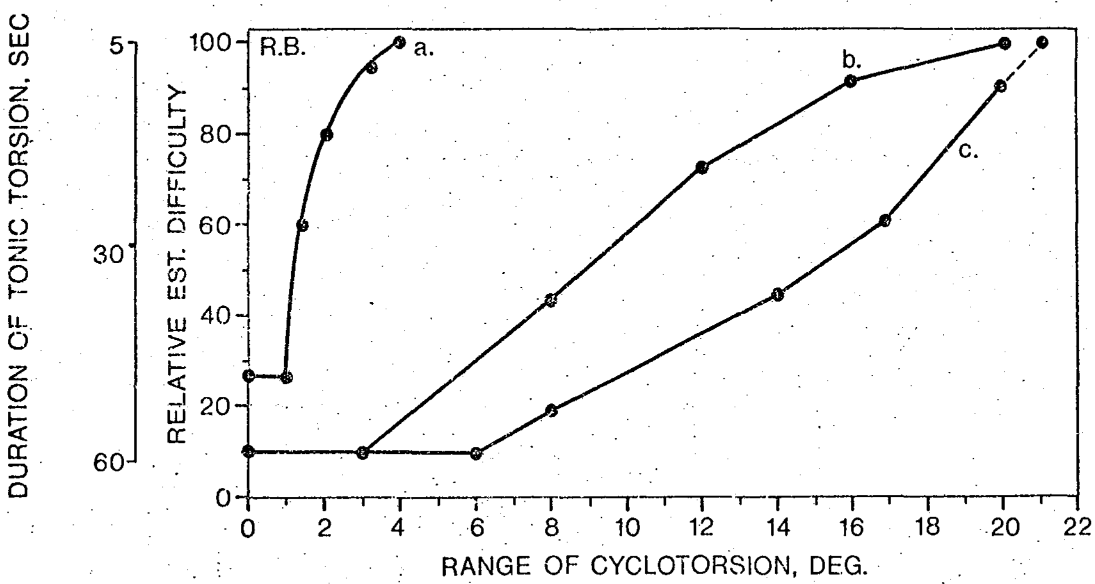
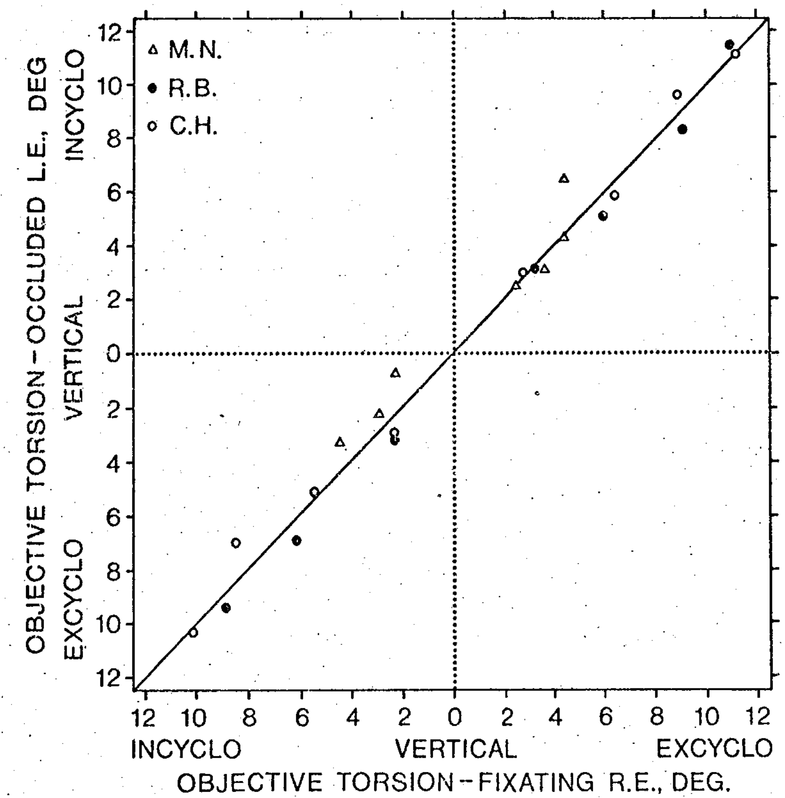

M.N.
3°
11°
26°
OBJECTIVE TORSION, DEGREES
EXCYCLO
VERTICAL
INCYCLO
16
14
12
10
8
6
4
2
0
2
4
6
8
10
12
14
16
14 12 10 8 6 4 2 0 2 4 6 8 10 12 14
INCYCLO
VERTICAL
EXCYCLO
SUBJECTIVE TORSION, DEGREES

Fig. 7 The subjective difficulty of voluntary tonic torsion over time. Estimated difficulty is defined to be inversely related to the duration which voluntary tonic torsion can be held. 5.0 seconds is equal to 100 percent effort. This is compared to the amounts of subjectively measured voluntary torsion during three different phases of training; (a) and (b) represent estimated difficulty at respectively 5 and 35 hours of training; (c) represents further training of 10 more hours (45 hrs.) without trying to further extend the cyclo-torsional range achieved in curve (b). See text for further definitions.



R.B.
a.
b.
c.
DURATION OF TONIC TORSION, SEC
5
30
60
RELATIVE EST. DIFFICULTY
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
18
20
22
RANGE OF CYCLOTORSION, DEG.

Fig. 8 Objectively measured test for cycloversion during monocular visual stimulation. Data is the combined results for subjects M.N., R.B. and C.H., each of whom was tested at different times during training. The diagonal line (slope equal to 1.0) represents perfect conjugacy. Not shown, the slope of a regression line fit to this data is equal to 0.96.



M.N.
R.B.
C.H.
OBJECTIVE TORSION-OCCLUDED L.E., DEG
INCYCLO
VERTICAL
EXCYCLO
12
10
8
6
4
2
0
2
4
6
8
10
12
12 10 8 6 4 2 0 2 4 6 8 10 12
INCYCLO
VERTICAL
EXCYCLO
OBJECTIVE TORSION-FIXATING R.E., DEG.

Fig. 9 Control test data for visual induction of cyclotorsion. Subjects M.N., R.B., and C.H. are shown. For clarity the curves for M.N. and C.H. have been displaced, respectively, up and down on the ordinate by 3 degrees. Means and standard deviations are shown. Subjects were instructed to relax and simply look for 30 seconds at only the real-line which was held at different fixed positions in space. Only R.B. shows any indication of visual induction. His magnitude of response is a relatively insignificant 7-8 percent of his previously shown torsional response in Fig. 4.

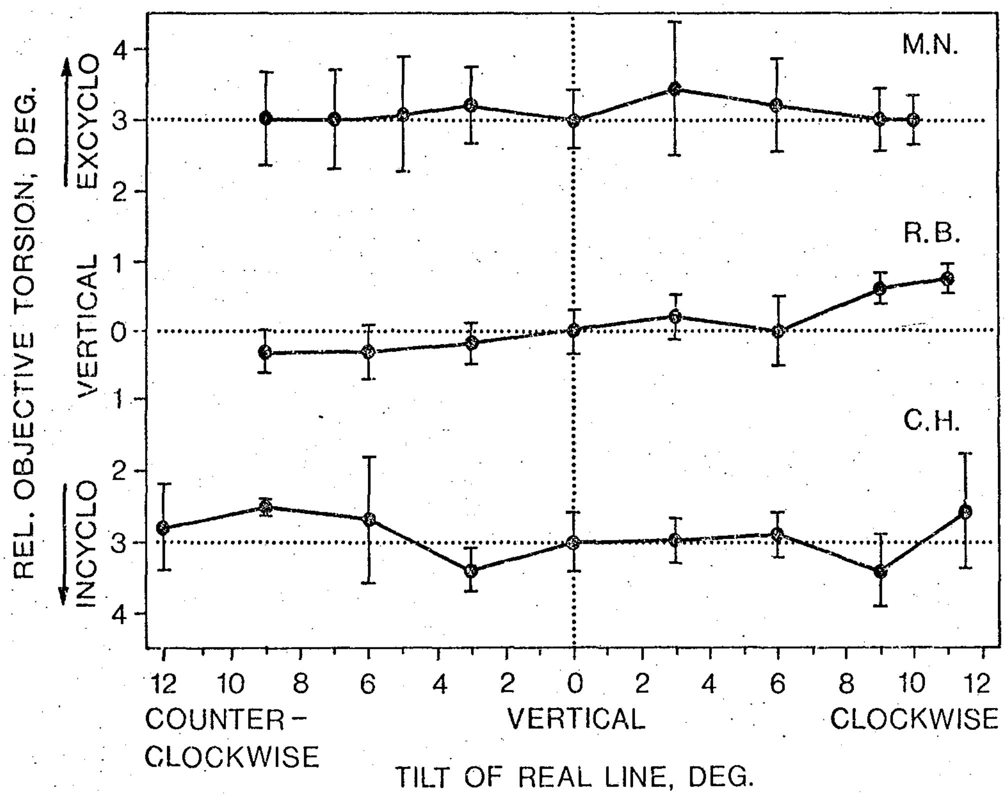

M.N.
R.B.
C.H.
REL. OBJECTIVE TORSION, DEG.
EXCYCLO
VERTICAL
INCYCLO
4
3
2
1
0
1
2
3
4
12 10 8 6 4 2 0 2 4 6 8 10 12
COUNTER-CLOCKWISE
VERTICAL
CLOCKWISE
TILT OF REAL LINE, DEG.

Fig. 10 Representation of the monocular stimulus situation used in the training and testing of voluntary cyclotorsional slow pursuit. The subject tonicly matched a previously vertical afterimage line to a real-line stimulus at, for example, -8 degrees. The real line was then programmed to rotate clockwise with a ramp function of 1.6 degrees/second for 10 seconds until it reached +8 degrees (a total of 16 degrees). The subject's task was to pursue this stimulus by the rotation of his afterimage (his eye).

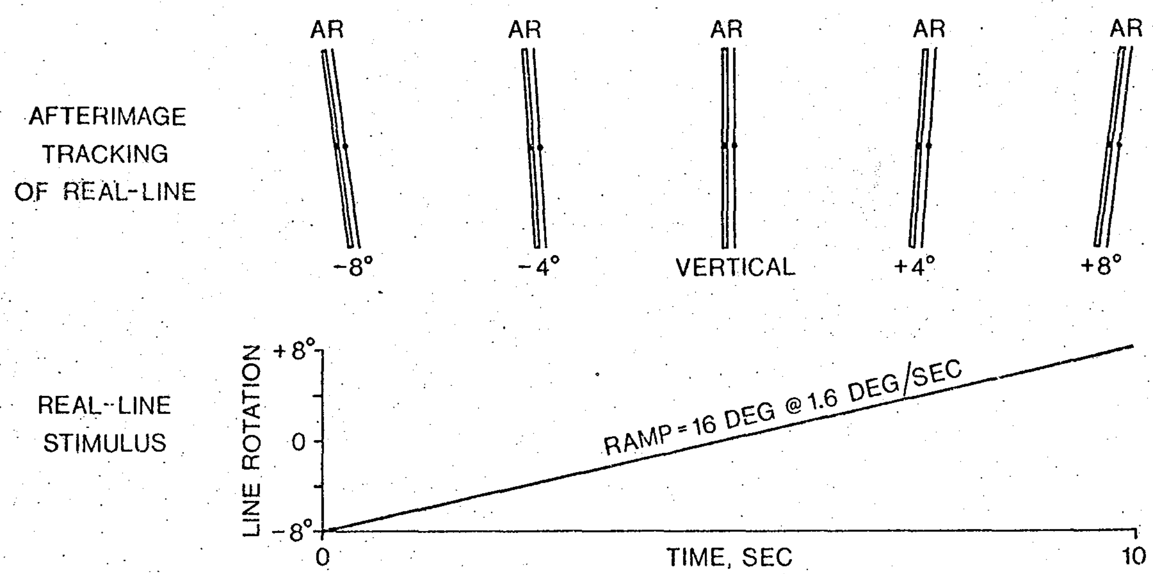

AFTERIMAGE
TRACKING
OF REAL-LINE
AR
AR
AR
AR
AR
-8°
-4°
VERTICAL
+4°
+8°
REAL-LINE
STIMULUS
LINE ROTATION
+8°
0
-8°
RAMP = 16 DEG @ 1.6 DEG/SEC
0
TIME, SEC
10

Fig. 11 Test results of voluntary cyclotorsional slow pursuit: Complete visual feedback, subject M.N. Lines have been drawn in representing a stimulus velocity of 1.6 degrees/second. Good pursuit can be seen in traces #3 and #4.

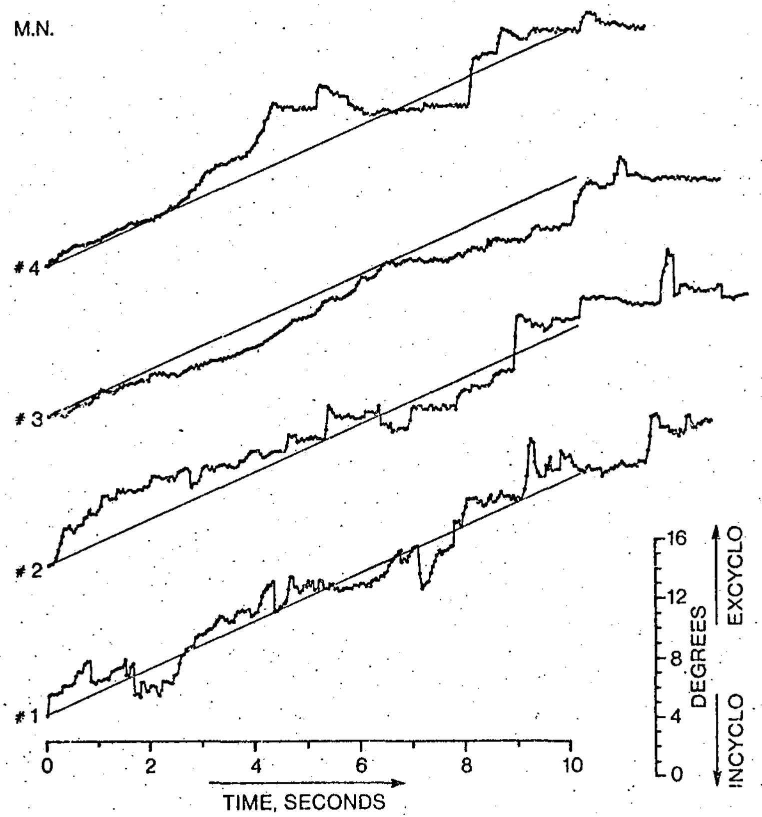

M.N.
4
3
2
1
0
2
4
6
8
10
TIME, SECONDS
16
12
8
4
0
DEGREES
EXCYCLO
INCYCLO

Fig. 12 Test results of voluntary cyclotorsional slow pursuit: Complete visual feedback, subject C.H. Lines have been drawn in representing a stimulus velocity of 1.6 degrees/second. Particularly good pursuit is seen in trace #2.

C.H.

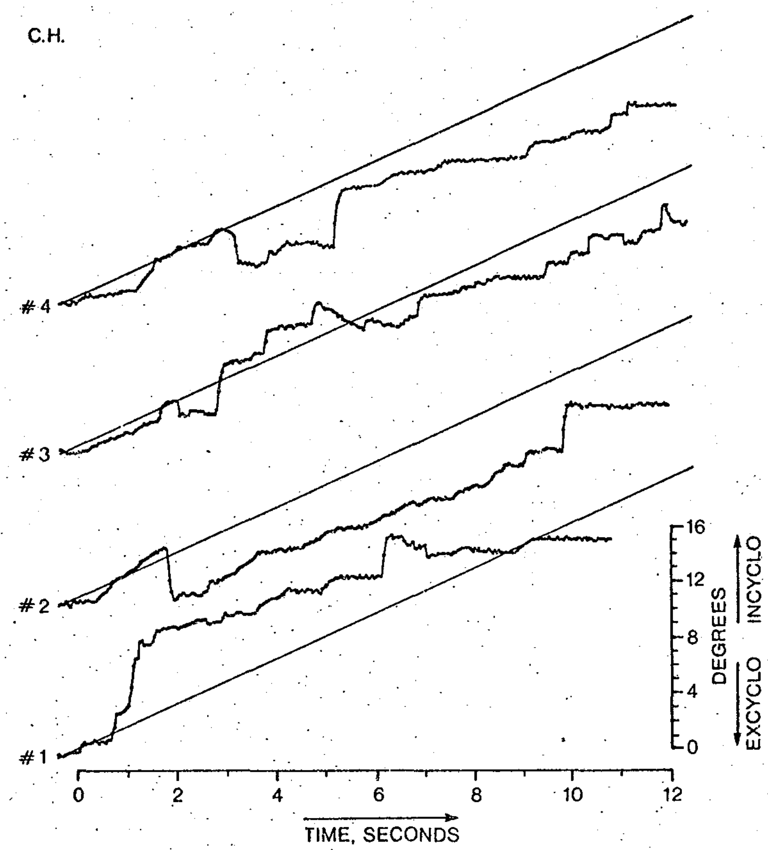
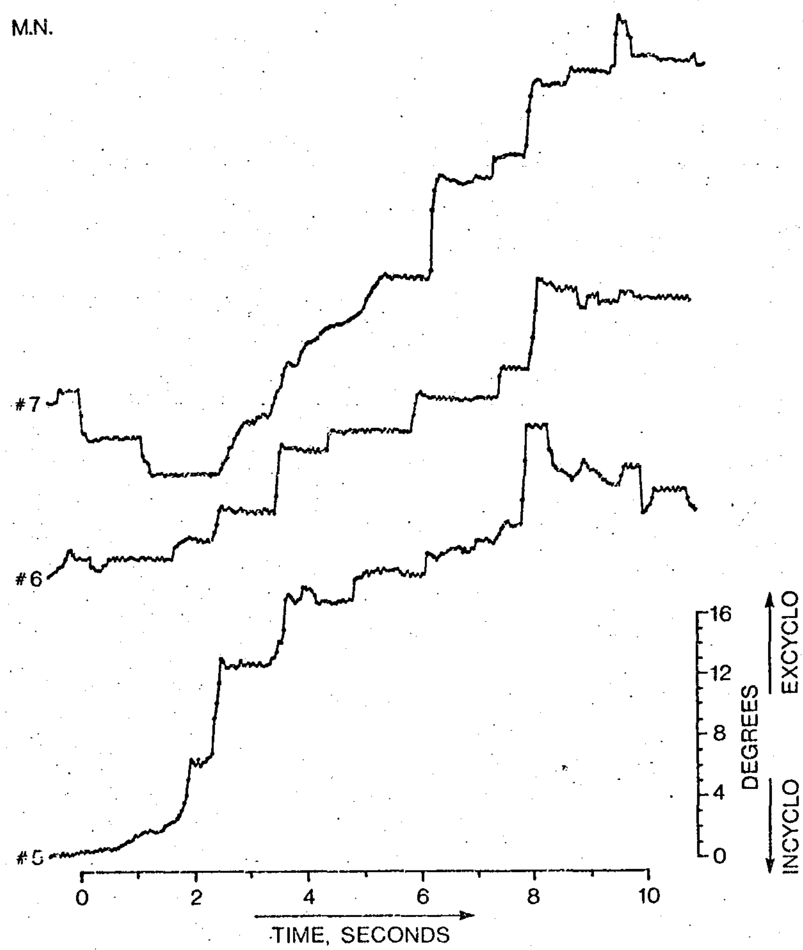

#4
#3
#2
#1
0
2
4
6
8
10
12
TIME, SECONDS
16
12
8
4
0
DEGREES
INCYCLO
EXCYCLO

Fig. 13 Test results of voluntary cyclotorsional slow pursuit: Partial visual feedback, subject M.N. Some slow pursuit and cyclorotations up to 30 degrees can be seen in trace #7.



M.N.
#7
#6
#5
0
2
4
6
8
10
TIME, SECONDS
16
12
8
4
0
DEGREES
EXCYCLO
INCYCLO

Fig. 14 Test results for voluntary cyclotorsional slow pursuit: Partial visual feedback, subject C.H. Despite the partial feedback condition, slow pursuit can be seen. Trace #5 shows a velocity of almost 1.6 degs./sec. This is the same stimulus ramp velocity at which C.H. was trained and tested during cyclotorsional slow pursuit with complete visual feedback (see Fig. 12).

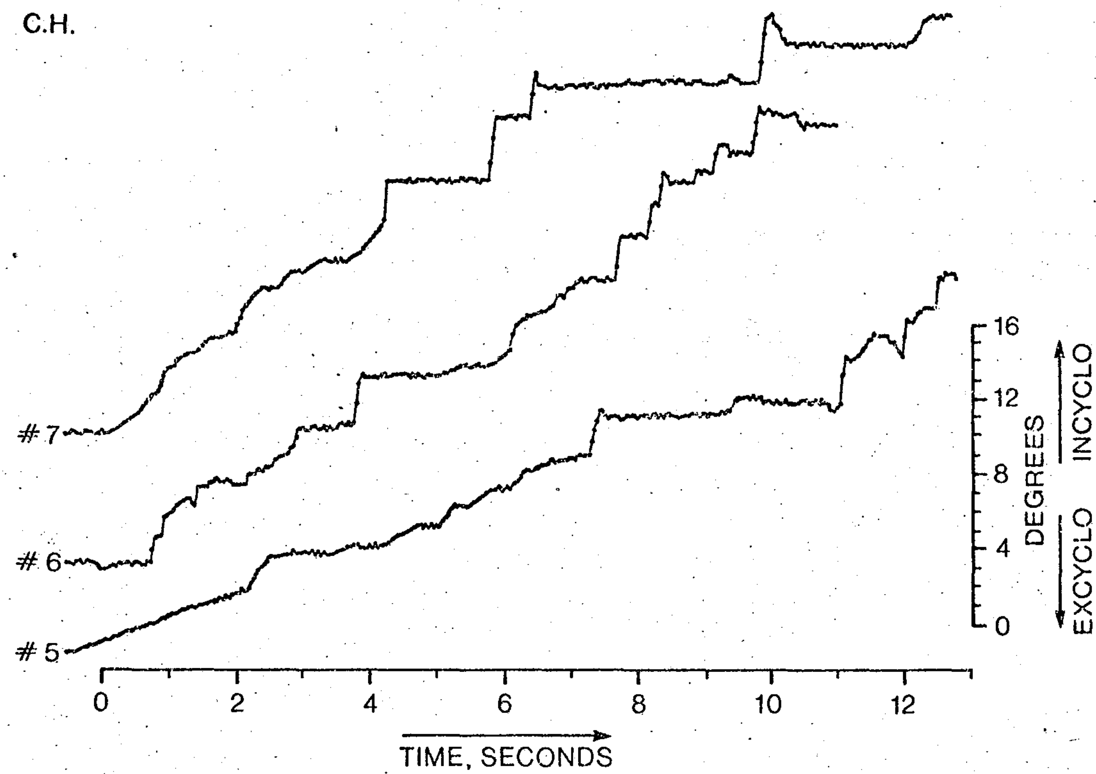
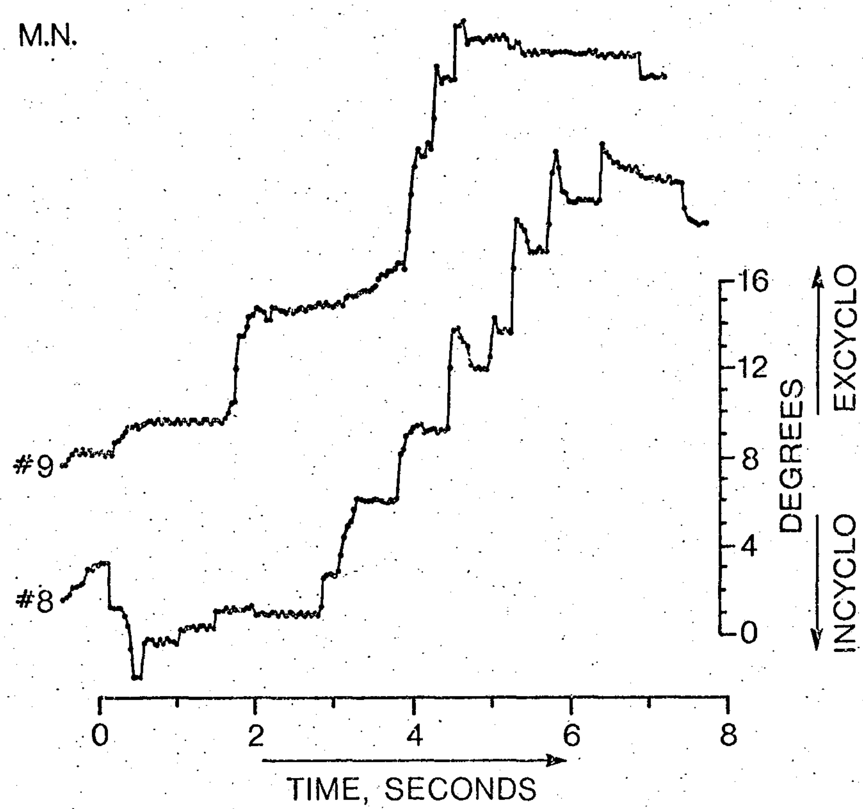

C.H.
#7
#6
#5
0
2
4
6
8
10
12
TIME, SECONDS
16
12
8
4
0
DEGREES
INCYCLO
EXCYCLO

Fig. 15 Test results for voluntary cyclotorsional slow pursuit: No visual feedback, subject M.N. Virtually no pursuit movements can be seen.



M.N.
#9
#8
16
12
8
4
0
DEGREES
EXCYCLO
INCYCLO
0
2
4
6
8
TIME, SECONDS

Fig. 16 Test results for voluntary cyclotorsional slow pursuit: No visual feedback, subject C.H. Virtually no pursuit movements can be seen.

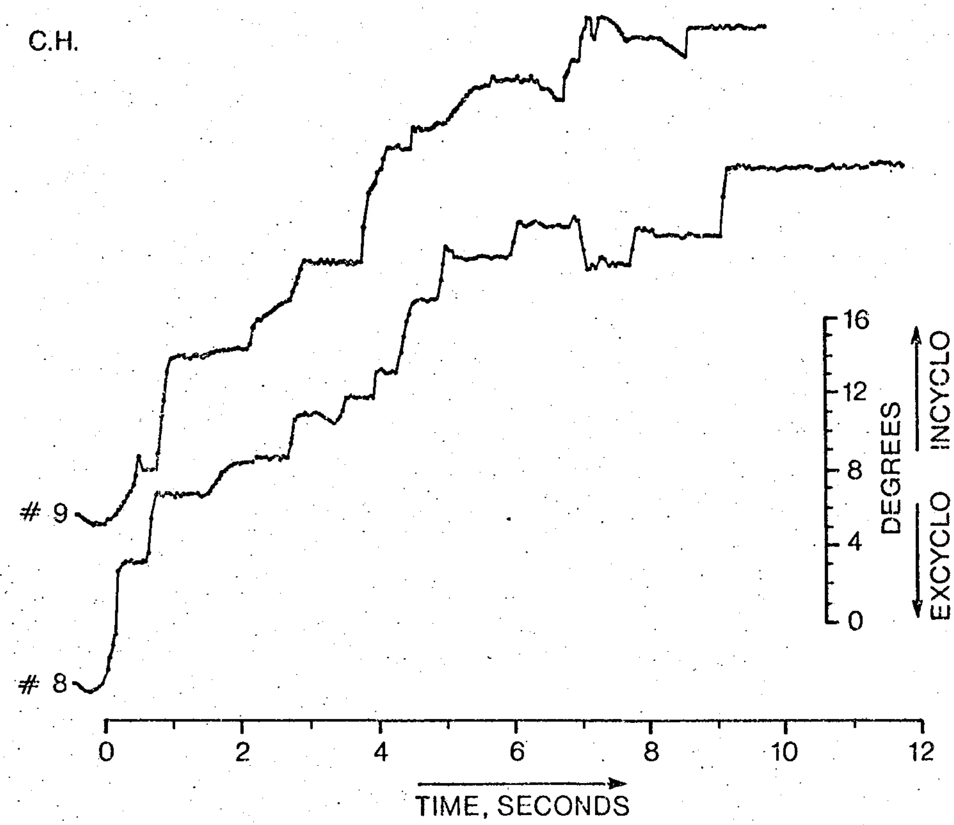

C.H.
9
8
16
12
8
4
0
DEGREES
INCYCLO
EXCYCLO
0
2
4
6
8
10
12
TIME, SECONDS

Fig. 17 Bar graph showing the percentage of time during which subjects made voluntary cyclotorsional slow pursuit movements during the three pursuit feedback test conditions. Correct pursuit movements were defined as those which were in the correct real or imaginary stimulus direction with a velocity between 0.5 and 15.0 degs./sec., and a minimum duration of 500 msec.

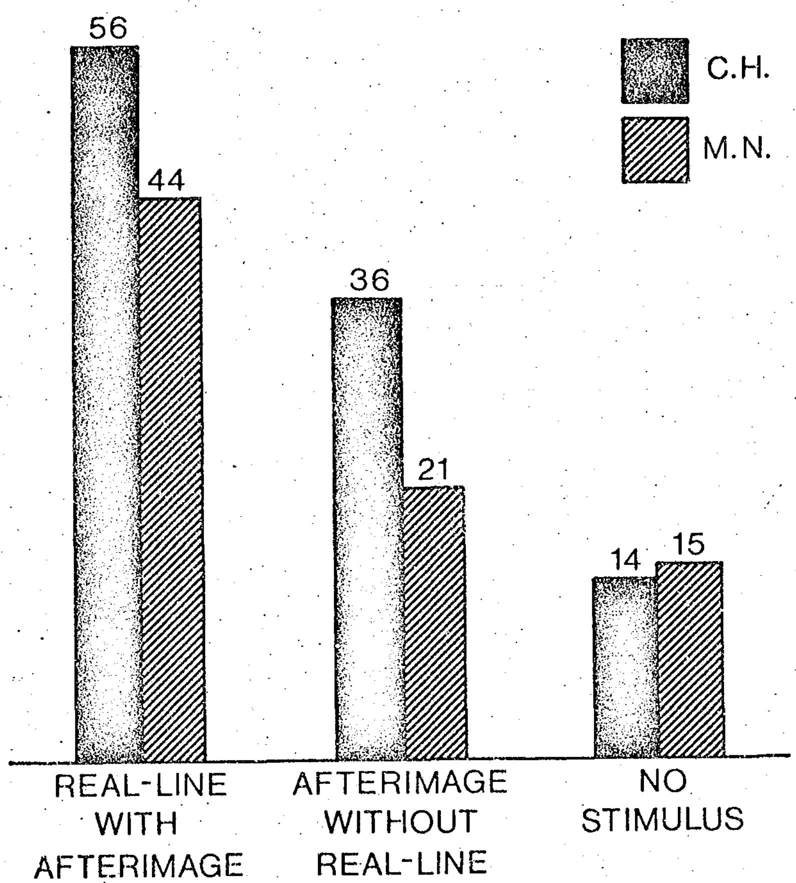

56
44
36
21
14
15
C.H.
M.N.
REAL-LINE WITH AFTERIMAGE
AFTERIMAGE WITHOUT REAL-LINE
NO STIMULUS

Fig. 18 Representation of the monocular stimulus situation used in the training and testing of voluntary cyclotorsional saccadic tracking. A 4 degree saccadic stimulus is exemplified. The subject tonicly matched a vertical afterimage line to a real-line stimulus at 0 degrees (vertical). The real-line was then programmed to rotate clockwise with a step function of 4 degrees. The subject's task was to track this stimulus as fast as he could by the rotation of his afterimage (eye). Similar procedures were used for 8 and 16 degree cyclotorsional saccadic tracking.

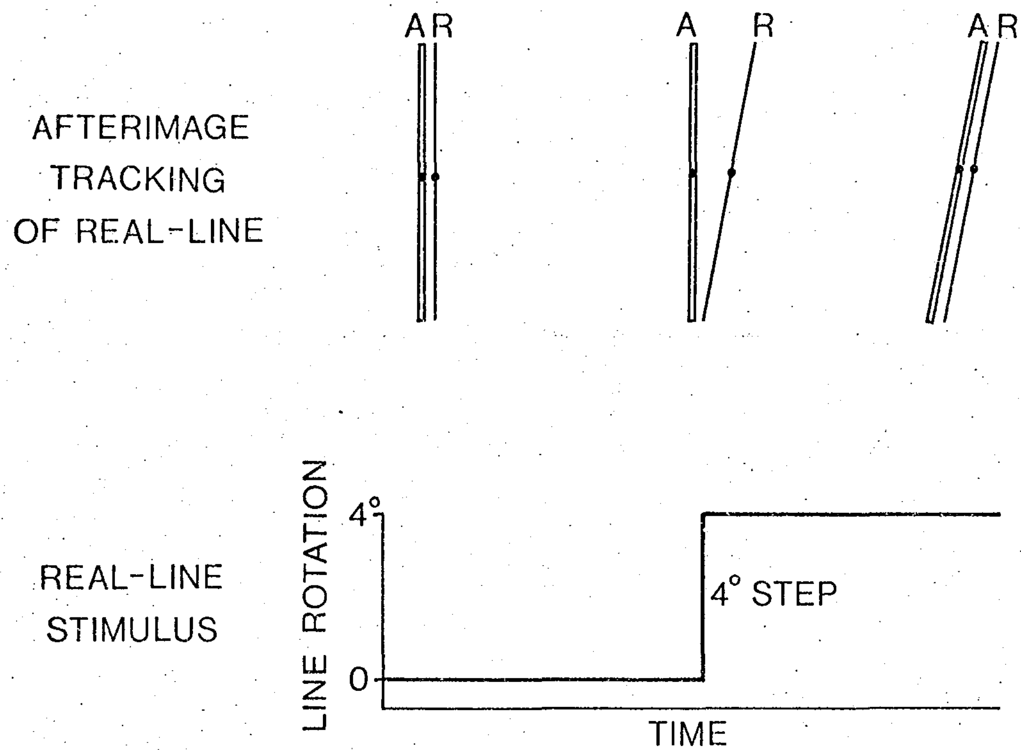
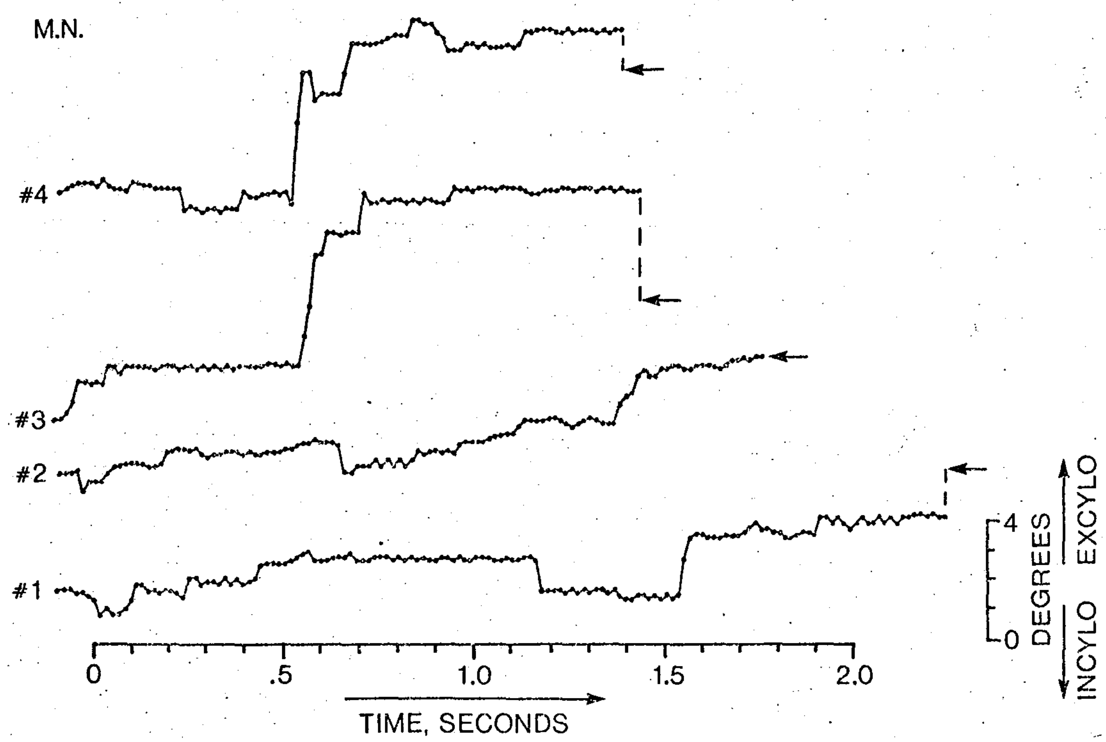

AFTERIMAGE
TRACKING
OF REAL-LINE
A R
A
R
A R
REAL-LINE
STIMULUS
LINE ROTATION
4°
0
4° STEP
TIME

Fig. 19 Test results of voluntary cyclotorsional saccadic tracking: 4 degree step stimulus, subject M.N. The correct stimulus step magnitude is indicated by the arrows. Accuracy is only attained by the production of slow fixation drifts. Saccadic movements overshoot by as much as 100 percent.



M.N.
#4
#3
#2
#1
0
.5
1.0
1.5
2.0
TIME, SECONDS
4
0
DEGREES
EXCYLO
INCYLO

Fig. 20 Test results of voluntary cyclotorsional saccadic tracking: 4 degree step stimulus, subject C.H. The correct stimulus step magnitude is indicated by the arrows. Normal cyclotorsional saccades are made. They, however, overshoot the correct stimulus step magnitude by as much as 100 percent.

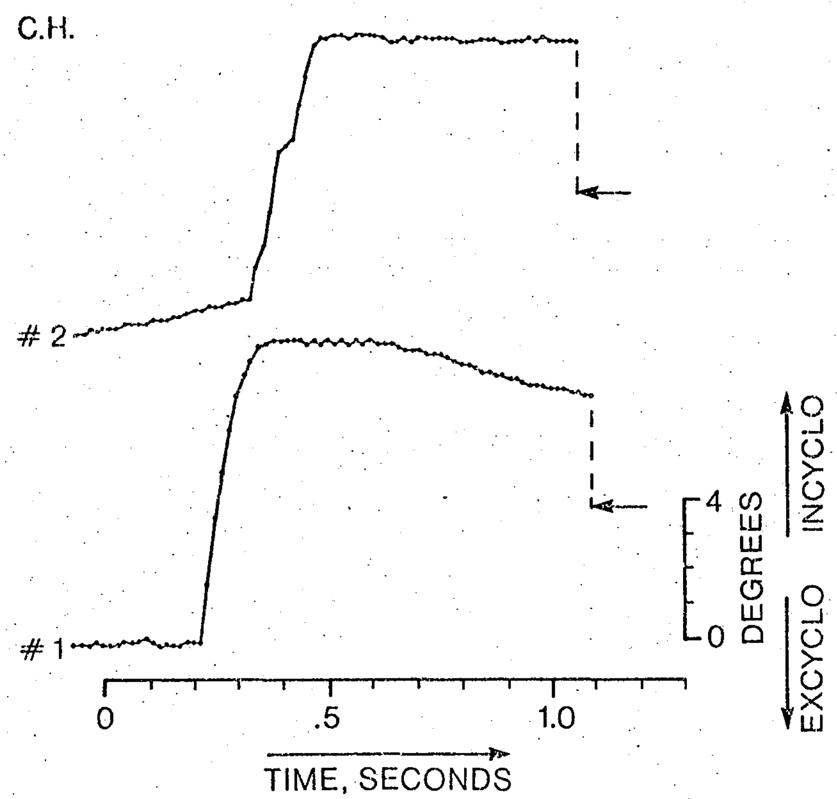

C.H.
2
1
0
.5
1.0
TIME, SECONDS
4
0
DEGREES
INCYCLO
EXCYCLO

Fig. 21 Test results of voluntary cyclotorsional saccadic tracking: 8 degree step stimulus, subject M.N. The correct stimulus magnitude is indicated by the arrows. Overlapping saccades, as well as dynamic and glissadic overshoots up to 2 degrees can be seen. Final saccadic accuracy is seen to be good.

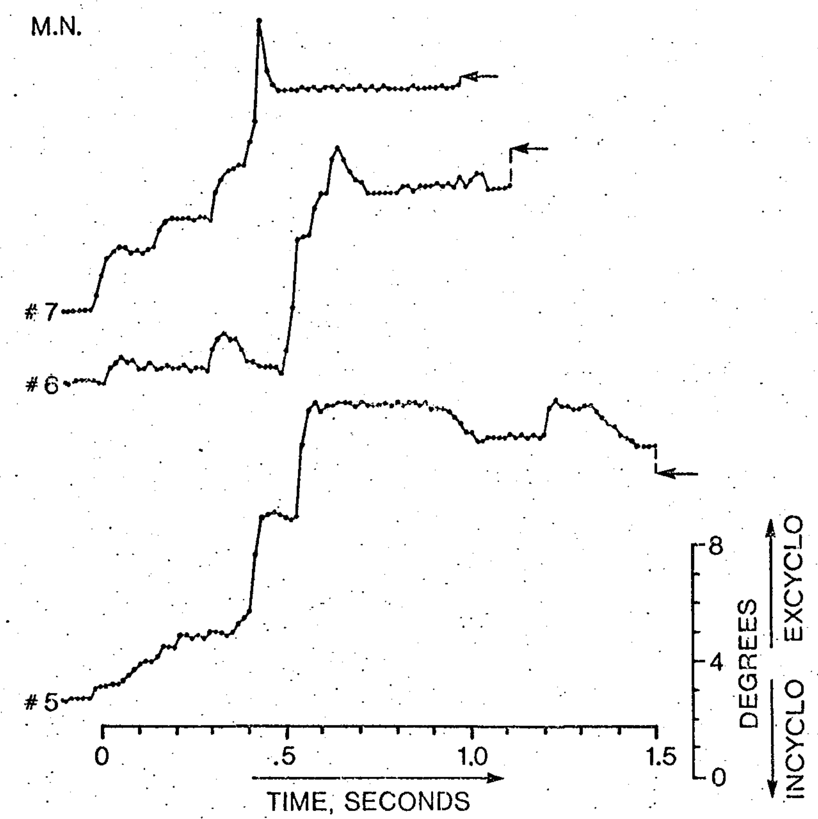

M.N.
7
6
5
0
.5
1.0
1.5
TIME, SECONDS
8
4
0
DEGREES
EXCYCLO
INCYCLO

Fig. 22 Test results of voluntary cyclotorsional saccadic tracking: 8 degree step stimulus, subject C.H. The correct stimulus magnitude is indicated by the arrows. Normal single and overlapping saccades can be seen. Saccadic accuracy is fair.

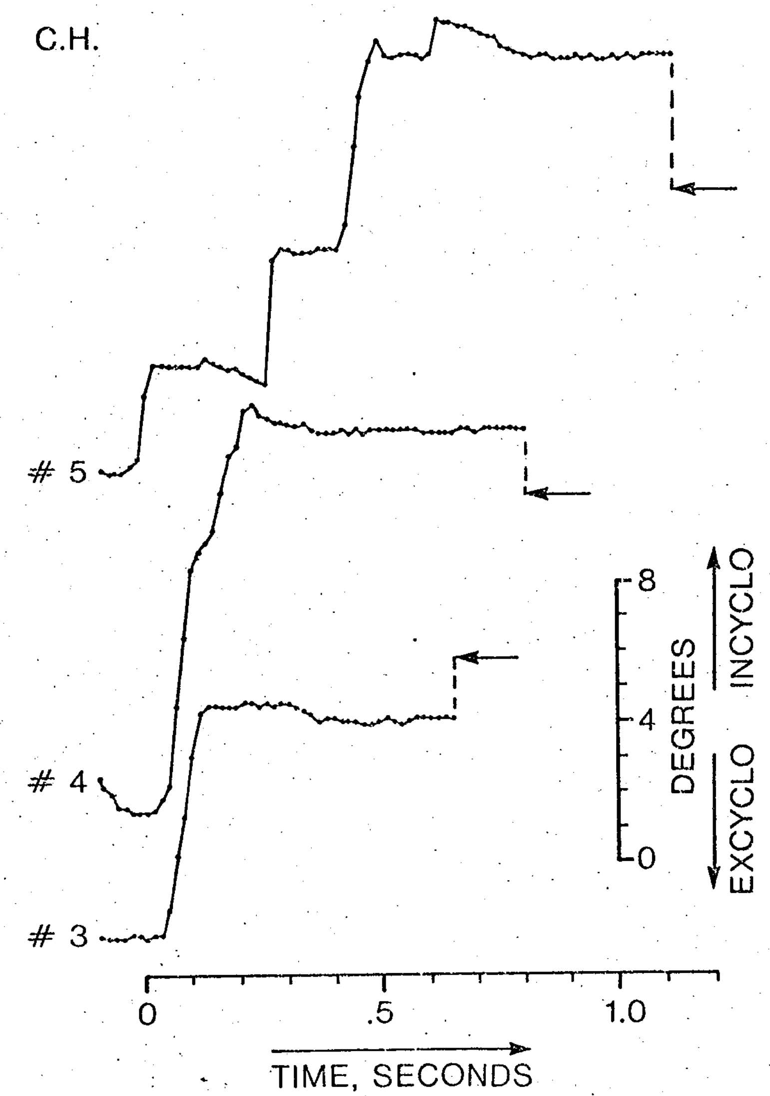

C.H.
5
4
3
8
4
0
DEGREES
INCYCLO
EXCYCLO
0
.5
1.0
TIME, SECONDS

Fig. 23 Test results of voluntary cyclotorsional saccadic tracking: 16 degree step stimulus, subject M.N. The correct stimulus magnitude is indicated by the arrows. Traces #8 and #10 show good final saccadic accuracy; however, these saccades have large apparent dynamic overshoots of up to 2 degrees.

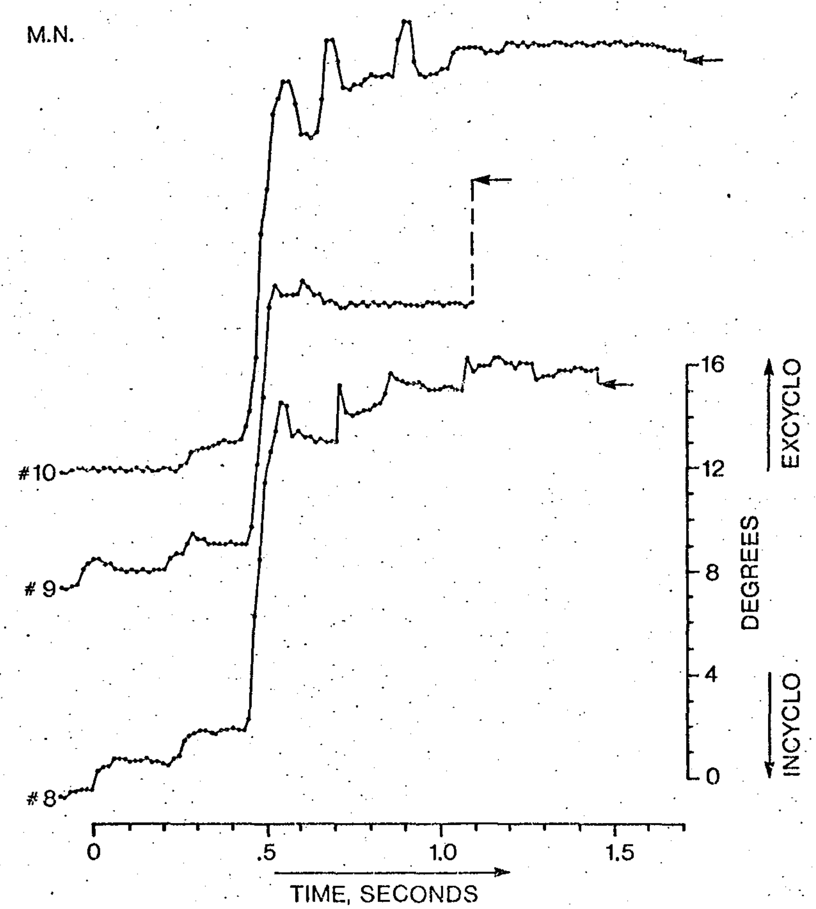
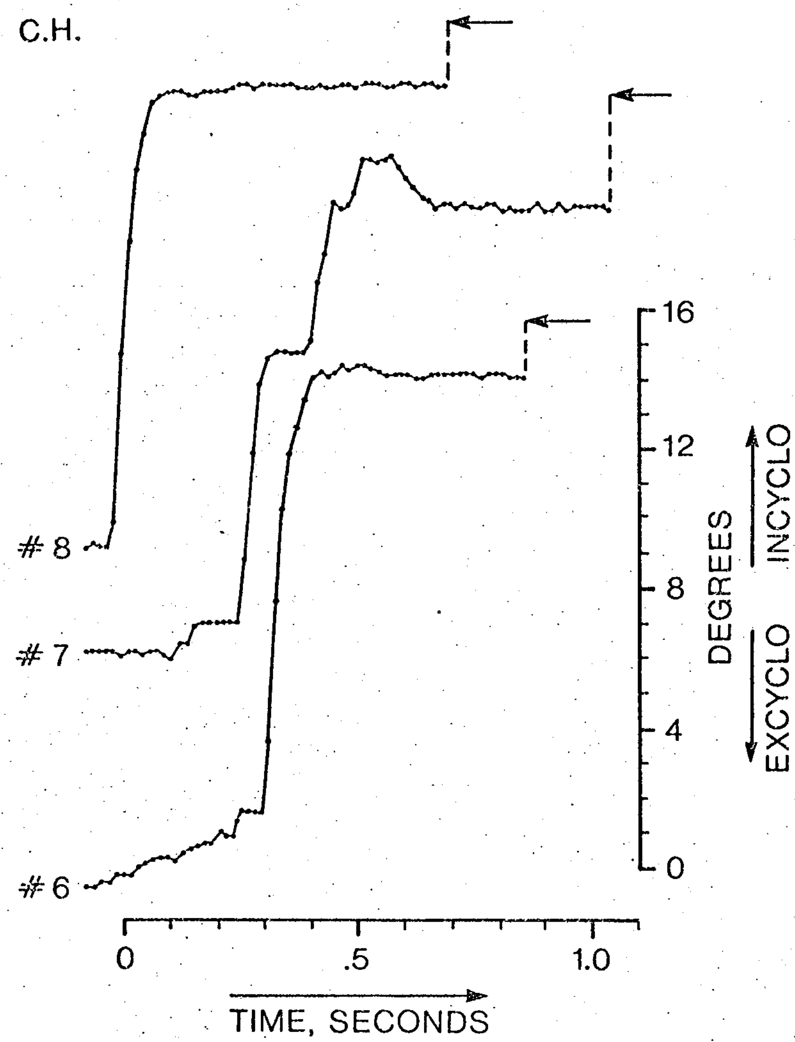
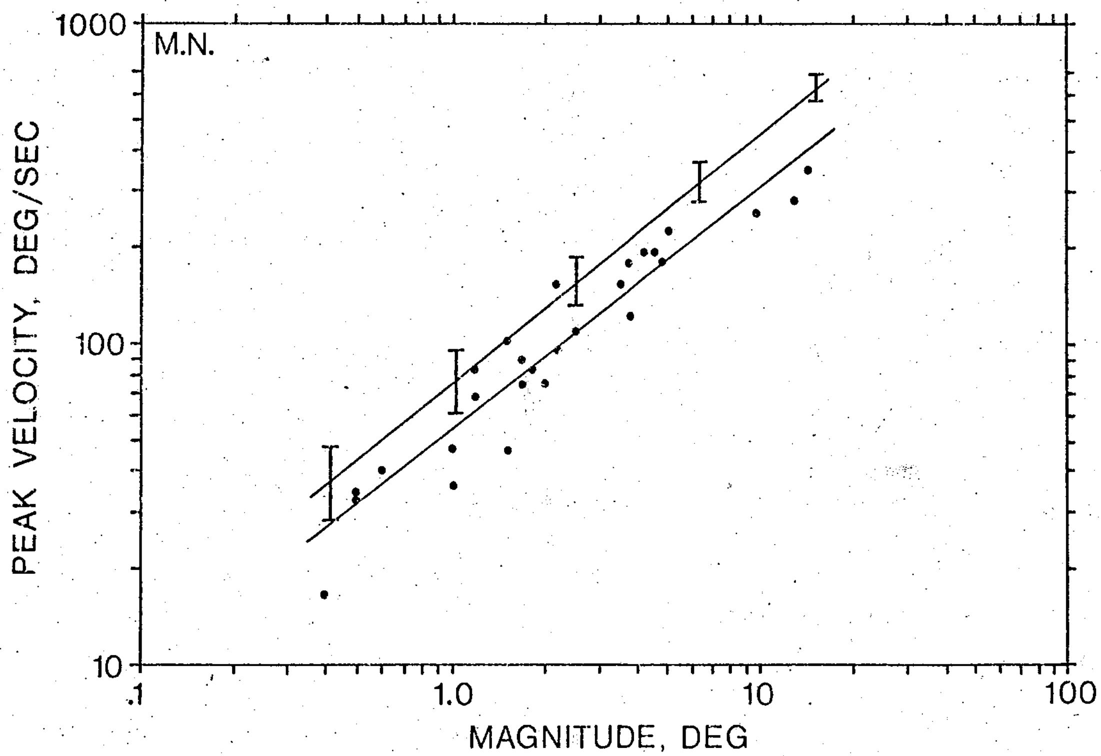

M.N.
#10
#9
#8
16
12
8
4
0
DEGREES
EXCYCLO
INCYCLO
0
.5
1.0
1.5
TIME, SECONDS

Fig. 24 Test results of voluntary cyclotorsional saccadic tracking; 16 degree step stimulus, subject C.H. The correct stimulus magnitude is indicated by the arrows. Good saccadic accuracy and normal looking saccades are demonstrated.



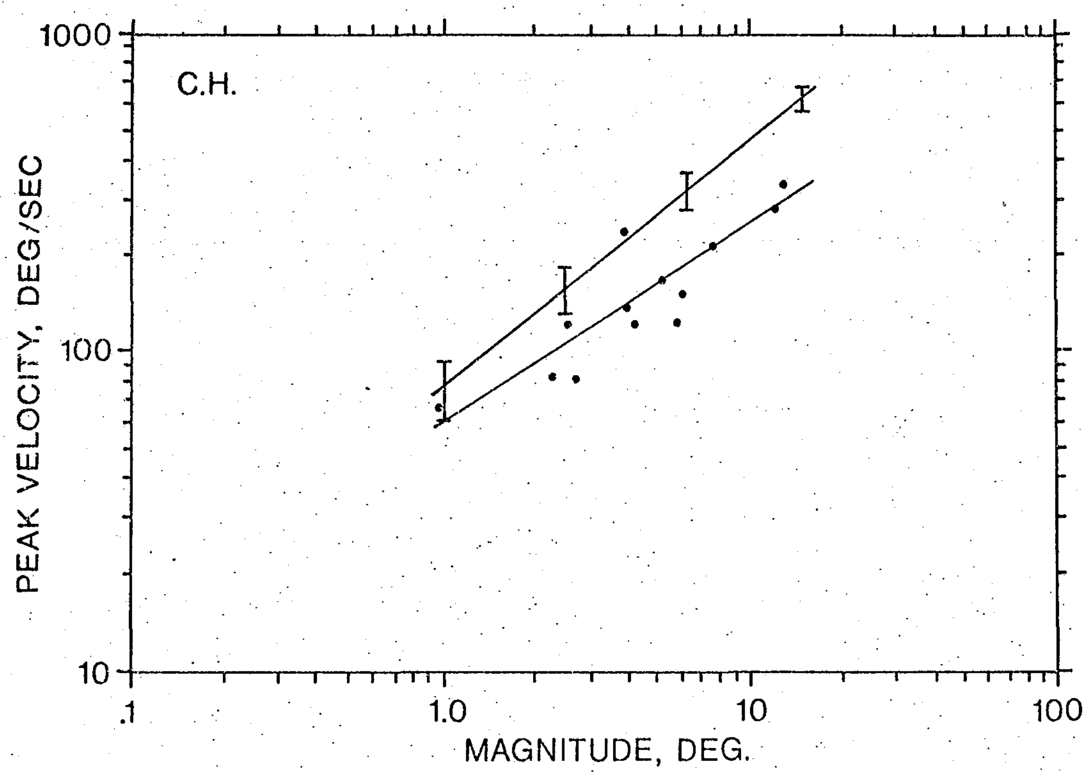
C.H.
8
7
6
16
12
8
4
0
DEGREES
INCYCLO
EXCYCLO
0
.5
1.0
TIME, SECONDS

Fig. 25 Voluntary cyclotorsional saccadic tracking: Magnitude vs. peak velocity results for subject M.N. The voluntary cyclotorsional saccades shown in Figs. 19, 21 and 23 have been analyzed for their peak velocity vs. voluntary cyclotorsional magnitude. The data points represent this analysis. They have been fitted with the lower regression line. Bahill, Clark and stark's (1975b) data for normal horizontal saccades is represented by the upper regression line; the bars show the range of their data.



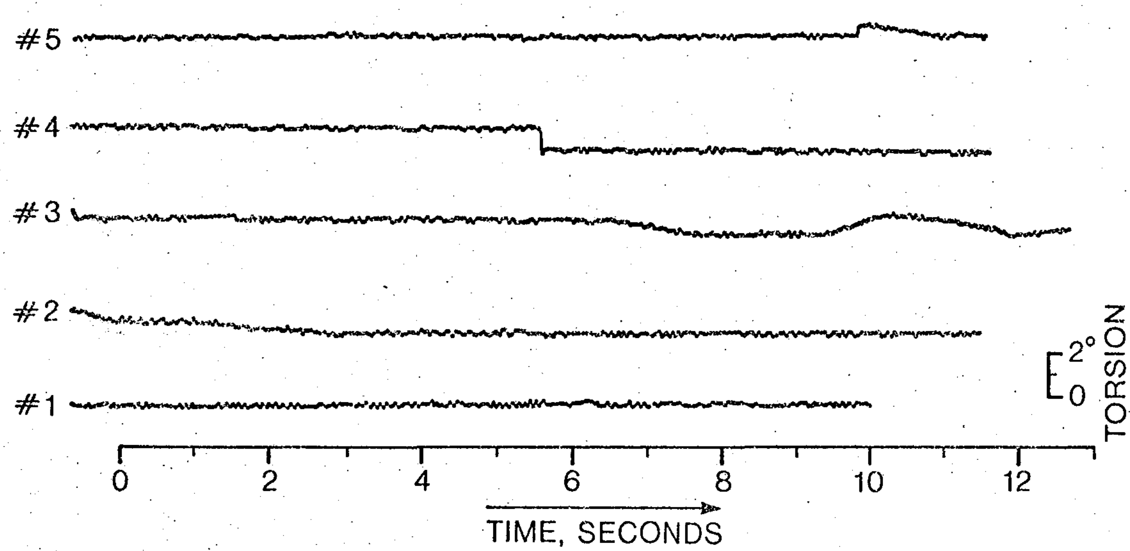
M.N.
PEAK VELOCITY, DEG/SEC
1000
100
10
.1
1.0
10
100
MAGNITUDE, DEG

Fig. 26 Voluntary cyclotorsional saccadic tracking: Magnitude vs. peak velocity results for subject C.H. The voluntary cyclotorsional saccades shown in Figs. 20, 22 and 24 have been analyzed for their peak velocity vs. voluntary cyclotorsional magnitude. The data points represent this analysis. They have been fitted with the lower regression line. Bahill, Clark and Stark's (1975b) data for normal horizontal saccades is represented by the upper regression line; the bars show the range of their data.



C.H.
1000
100
10
PEAK VELOCITY, DEG/SEC
.1
1.0
10
100
MAGNITUDE, DEG.

Fig. 27 Control test for visual induction of dynamic cyclotorsion. Subjects were instructed to simply relax and observe the slow pursuit ramp stimulus moving at 1.6 degs./sec. (Experiment 1(a)) or the saccadic step stimulus of either 4, 8 or 16 degrees (Experiment 2). Objective torsional measures over time are shown only for the slow pursuit ramp stimulus. These results are representative of all experiments and both subjects. An upwards direction on the ordinate indicates that the eye rotated in the same direction in which the stimulus was rotated. No significant visual induction effects are seen.



#5
#4
#3
#2
#1
2°
0
TORSION
0
2
4
6
8
10
12
TIME, SECONDS

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