

Investigative Ophthalmology & Visual Science

A Journal of Clinical and Basic Research

Articles

Training of voluntary torsion

Richard Balliet and Ken Nakayama

By means of a visual feedback technique, human subjects were trained to make large conjugate cyclorotary eye movements at will. The range of movement increased with training at a rate of approximately 0.8° per hour of practice, reaching 30° at the end of training. Photographs recorded the ability to make voluntary cyclofixations at any amplitude within the subject's range. Cyclotorsional pursuit was also trained, with ability increasing with greater amounts of visual feedback. In addition, torsional saccadic tracking was trained, showing a magnitude vs. peak velocity relationship similar to that seen for normal saccades. Control experiments indicate that all of these movements were voluntary, with no significant visual induction. With extended practice, large torsional movements could be made without any visual stimulation. The emergence of voluntary torsion through training demonstrates that the oculomotor system has more plasticity than has generally been assumed, reopening the issue as to whether other movements could also be trained to alleviate the symptoms of strabismus.

Key words: eye movements, torsion, saccades, slow pursuit, fixation, orthoptics, oculomotor plasticity

Cyclorotations are defined as rotations about the visual axis of the eye. These rotations are considered to be reflexive, with no indication of voluntary control. For example,

From the Smith-Kettlewell Institute of Visual Science, Department of Visual Sciences, University of the Pacific, San Francisco, Calif.

This paper is based on a Ph.D. dissertation submitted by the first author to the Department of Visual Sciences, University of the Pacific, San Francisco, Calif. 94115. The work was supported in part by NEI Grant EY01582 and the Smith-Kettlewell Eye Research Foundation.

Submitted for publication July 6, 1977.

Reprint requests: Dr. Richard Balliet, Smith-Kettlewell Institute, 2232 Webster St., San Francisco, Calif. 94115.

the eye can undergo a cyclorotation as it moves from one tertiary position of gaze to another, but the amount of this cyclorotation is fixed, being dictated by Listing's law.¹¹ In addition, involuntary cyclovergence has been reported to occur during convergence,¹ and reflexive cycloversions have been demonstrated to occur during lateral head tilt.^{14, 18} Cycloversional movements can also be induced visually by large field stimuli (25° to 50°). These movements include optokinetic cyclovergence,^{7, 8, 13} fusional cyclovergence,⁹ and tonic cycloversions.⁸ All of these previously reported cyclorotary eye movements occur either as a necessary consequence of other movements or as part of a sensorimotor

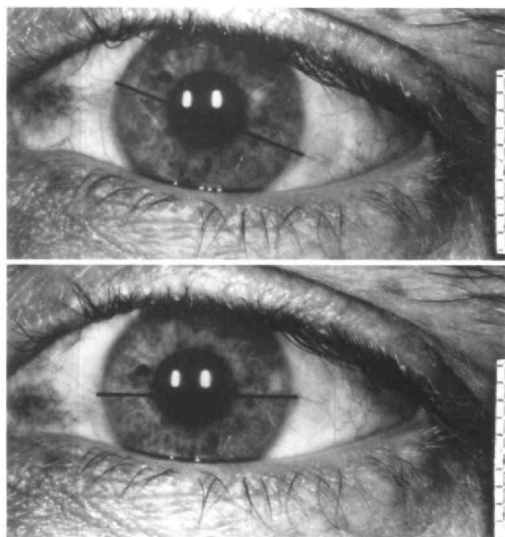


Fig. 1. Photographs showing a tonic voluntary cyclotorsion of 20° . Bars drawn in across the irises are similar to those used for photographic analysis. Vertical reference marker (present in all photographs) is seen at right.

reflex. There are no instances where one sees purposeful cyclofixations, or smooth and saccadic torsional tracking, phenomena which are common to voluntary horizontal or vertical eye rotations.

In this paper we will demonstrate that if an adequate sensory feedback loop is created, providing subjects with a very sensitive indicator of their own eye position, voluntary cyclotorsional eye movements can be trained. Methodology and results will be presented which will substantiate that once this relationship is established, large voluntary cyclorotations can be learned and brought under relatively fine control.

Tonic cycloverision

Methods

Subjects. We report the successful training of three subjects. Our first subject, M. N. (age 31) had unilateral intermittent exotropia, his left eye deviating 30° . Normally he allowed this exotropia to be manifest. Otherwise, he had normal stereopsis, eye movements, and corrected acuity. Initially both eyes were tested for possible deviations from Listing's law. They showed no systematic deviation, with the mean torsion in each eye being predictable by the direction of gaze.¹⁶ We did see,

however, a larger than average torsional response variability in all positions of gaze (S.D. = 0.75°). We reasoned that although small, M. N.'s torsional variability was clearly perceptible and perhaps sufficient to extend further by exploratory training procedures. As our first and pilot subject we worked closely with him, up to 5 hr/week over a period of 13 months, testing many methods to develop an apparently optimal approach. Then, having found successful procedures for M. N. (see later), we trained two normal individuals who showed no oculomotor abnormalities.

Subjects R. B. (one of the authors, age 30) and C. H. (age 26) were chosen because of their high motivation. These subjects had normal stereopsis and 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 2 months.

Training and testing procedure. Many different training procedures were used with M. N. We report only upon the final method used most successfully with him and exclusively with 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 the left eye always occluded. Torsional head movement was fixed to within $6'$ of arc by a full-mouth impression bite plate (see Ditchburn¹⁰). Fixating a target with the right eye, the subject activated a brief vertical electronic flash ($11 \times \frac{1}{4}^\circ$), leading to the formation of a clear vertical afterimage. By horizontally sliding the base of the bite plate mechanism, the subject then imaged the afterimage parallel to a vertical luminous real-line of equal visual angle which was viewed at 100 cm distance in primary position. The real-line was a partially occluded "white" 110 volt luminescent panel. It was bisected by a $15'$ circular black fixation point. The subject controlled the luminance of the real-line over a range of 0.2 to 1.0 log foot-lamberts to prevent visual suppression of the afterimage line by the target line (or vice versa). He also controlled a This rotation angle could be observed by the subject directly and/or by a digital voltmeter readout. The meter had an accuracy of $\pm 4'$.

The subject was instructed to keep his afterimage matched parallel *only* by cyclorotating his eye to the real-line which he progressively rotated more and more (left or right) from the vertical as training progressed. Usually $20'$ of arc increments were used. No instructions were given as to what type of eye movement was to be used to arrive at

this position, e.g., slow pursuit, saccades, nystagmus. Such matches which could be subjectively held for a minimum duration of 5 sec were defined as "cyclofixations." Subjects were encouraged to train equally in both incyclotorsional and excyclotorsional directions, training usually at the rate of 1 hr/day.

Photographic measurement of eye torsion. Objective measures of cyclofixations were obtained from over 1,500 photographs taken with a 35 mm Nikon F-2 motor-driven 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. High-resolution color photographs on Kodachrome II film were taken at 100 cm distance with a first-surface mirror mounted at 30 cm distance in front of the subject at a 45° angle, so positioned to be 5.0° off the subject's primary visual axis. At this angle systematic inaccuracies due to perspective distortion are minimal, not exceeding 3%. (See Appendix of Nakayama and Balliet¹⁶.)

The camera was activated by a button which could be pressed by the subject while he simultaneously held a subjectively determined cyclofixational match. Fixed to the bite bar was a vertical photographic reference marker positioned near the outer canthus. Thus each photograph contained all the information necessary to determine eye torsion, eliminating errors due to possible camera or film misalignment. During photographic analysis slides were magnified 12 times in size by a Kodak Carousel projector. The image was rear-projected onto a horizontal table screen made of translucent "white" Mylar. Landmarks used in measurement were two identifiable limbal-scleral blood vessel junctions which bordered a 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. 1 illustrates an example of this technique, showing a 20° voluntary cyclotorsional difference between the two photographs; the bar represents the line joining the two landmarks. All photographic cyclotorsional measurements were defined relative to average eye position when the observer was relaxed and not making voluntary eye torsions. Torsional measurements from the same photograph were repeatable to within $\pm 5'$ of arc.

Results

Training of cyclofixation. The training of cyclorotary eye movements requires a com-

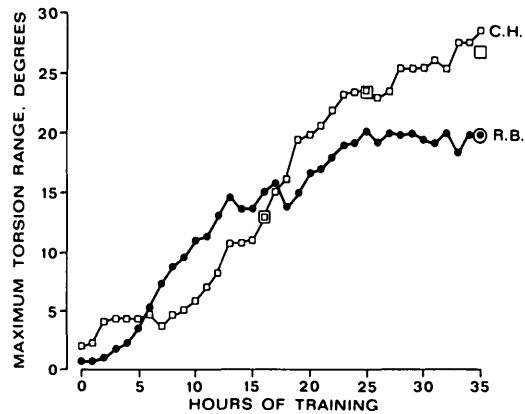


Fig. 2. Training of voluntary tonic cyclovergence for subjects C. H. and R. B. Hours of training at 1 hr/day vs. the total range (degrees) of psychophysically measured torsion is plotted by the small symbols. These are maximum tonic ranges which can be held for a 5 sec duration. The three large squares and the one large circle are simultaneous measures obtained photographically.

bination of optimal stimulus arrangements as well as physical and mental effort. Very small differences in the brightness of the afterimage and the real line led to the inhibition of the dimmer by the brighter, necessitating fine control of the intensity of the real-line to ensure the visibility of both. Attentive concentration was necessary to refrain from moving the afterimage with an attempted head movement. For example, during initial training, two subjects broke bite plates, attempting unsuccessfully to rotate the afterimage by making lateral head movements.

Slowly, however, the subjects succeeded in the task, learning to increase their range of torsional eye movements with greater and greater facility. Fig. 2 shows the remarkably steady increase of voluntary torsion as a function of hours of practice. Small symbols represent the maximum range of torsional difference measured psychophysically. The large symbols (square and circle) show the torsional ranges derived from photographic measurements; standard errors are small, within the size of the symbols. At the end of training, subjects had the ability to make cyclofixations at any cyclotorsional amplitude within the ranges specified.

Subject C. H. acquired a cyclofixation

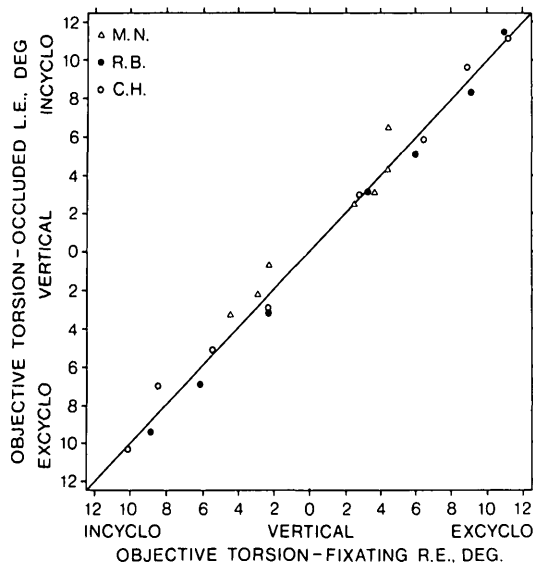


Fig. 3. Conjugacy of trained torsional eye movements. Comparison of the torsion in each eye (measured photographically) as the subject is matching the afterimage tilt to designated angles of the comparison line. Viewing is monocular through the right eye. Solid line represents perfect conjugacy.

range of 26.5° (12.0° incyclo, 14.5° excyclo) in approximately 30 hr. Subject R. B. acquired a cyclofixation range of about 20° (9.0° incyclo, 11.0° excyclo) in approximately 25 hr. Both subjects showed about an $0.8^\circ/\text{hr}$ training rate. These torsional ranges should not be considered as the maximum possible; for example, C. H. is clearly not at an asymptotic level at the end of 35 hr of training. Subject M. N. had a final objectively measured cyclofixation range of approximately 20° (10.0° incyclo, 10.0° excyclo). His training results are not shown because of differing procedures used in training of 250 hr over a period of 13 months (as described in the Subjects section).

It should be emphasized that the effort required to make these torsional movements *decreased* dramatically over the training period. Near the end of training, for example, torsional fixations of up to 6° to 8° were "virtually effortless" and could be made with the same ease as with ordinary fixations. It also appears that the acquired capacity to make these movements is long-lasting. M.

N., for example, could return to previous positions after having been away for 2 months. Furthermore, after approximately 1 year without any intervening experience, both C. H. and R. B. still had the capacity to make torsional movements of about one-half their previous torsional range.

Trained cyclofixation is not visually induced. As mentioned earlier, very small amounts of tonic eye torsion can be induced by the static inclination at a multiple-lined field.⁸ As such, these movements appear to differ from the currently described movements in two significant respects. (1) They are much smaller (less than 1.0°). (2) They are involuntary. In order to determine how much of the measured cyclofixation was visually induced by the real stimulus line we conducted a control experiment. After training, subjects were instructed to relax and simply look for 30 sec at the real-line, which was held at different fixed lateral angles in 3.0° increments. This was done both with and without the usual vertical afterimage line. At the end of the 30 sec, photographs of the right (fixating) eye were taken. The time interval of 30 sec was comparable to the longest time required to obtain an afterimage/real-line match using voluntary torsion.

Nearly identical results were found whether or not the subject had an afterimage. They indicate that without voluntary effort there is essentially no effect; eye torsion remains nearly constant for any angle of the line. Only R. B. showed a slight trend, attaining a maximal torsional response of less than 1° . These results are similar to that found by Crone⁸ and demonstrate that in our stimulus situation optostatically induced eye torsion is very weak.

Binocular aspects. The training of torsion was an exclusively monocular task, with no training or measurement of the occluded left eye. It is of interest to know the rotational status of this occluded eye as the trained eye undergoes large torsional changes. For example, cyclotorsional eye movements have been reported to accompany vergence,¹ with extorsion increasing for increasing amounts of convergence. This relationship raises the

question as to whether our trained torsions are simply an expression of this relation or whether they indeed represent a new and separate type of eye movement.

To deal with this possibility, we separately photographed the rotations of each eye for different cyclofixations made with the right eye. We did this photographing of the right eye as described in the Methods section above and photographing the occluded left eye as it viewed darkness. During experimentation, M. N.'s left eye was exodeviated by 30° , necessitating the camera to be approximately positioned to photograph along the visual axis. Thus, for a cyclotorsional fixation made by the right eye as defined by a particular angle of the afterimage match, the rotations of either eye could be separately measured and compared. The degree of torsional conjugacy between the right and left eyes was determined by plotting the torsion of the viewing eye against the torsion of the occluded eye for different matching angles of the real-line. Fig. 3 shows a near-perfect correspondence between the cyclorotations of the two eyes in all three subjects.

Horizontal movements of the left eye were determined by measuring the relationship between the corneal reflex and the pupil center.¹⁰ This position remained constant to within $\pm 0.5^\circ$ (experimental error $\pm 0.2^\circ$) over the whole range of torsional movements of the right eye. This exceptional stability of horizontal eye position of the occluded eye during eye torsion effectively rules out any explanation of our results based on changes in vergence.* All our voluntary cyclotorsions

*All subjects demonstrated an exceptional degree of horizontal and vertical stability of the occluded eye and a near-perfect conjugacy of torsion. This was even true for M. N.'s left eye, which was exodeviated by 30° . Considering the presumed primary actions of the oblique and vertical muscles in 30° abduction,^{6, 19} it may be hypothesized that either the combination of neural inputs to the six muscles to produce torsion is greatly altered for M. N. or that the primary mechanical actions of the muscles remain invariant in an *eye-based coordinate system*. In the former hypothesis, torsion would be organized at a high level in the oculomotor system, thus requiring a "torsion command" system to rotate the eye around the visual axis, *independent of gaze direction*.

are conjugate wheel-like cycloversions which occur around the visual axes.

Subjective observations. During the training and testing of all voluntary cycloversions (including voluntary cycloversional slow pursuit and saccadic tracking—see below), subjects experienced sensations of lateral rolling. They also experienced during initial training occasional nausea, headache, and body fatigue. Most notable and most consistent was the sensation of the body turning in the same direction as the eye, with concomitant sensations of stationary objects appearing to rotate in the opposite direction when environmental cues were available. A more quantitative description of these and related illusions is presented elsewhere.⁵

Dynamic cycloversions

Voluntary conjugate eye movements can be divided into two distinct categories: slow pursuit and saccadic tracking. Because our trained cyclofixations were clearly voluntary, it was of interest to see whether their dynamic characteristics were comparable to voluntary horizontal and vertical movements, specifically in the degree to which they had the appropriate smooth and saccadic characteristics. Alternatively, it was also of interest to see whether the dynamics were comparable to the nystagmic pattern normally seen during reflexive cyclorotations.^{7, 8, 13}

Method. In order to characterize the ability to make voluntary dynamic cycloversions in detail, motion picture records were taken in one session each for two subjects, M. N. and C. H. This occurred after only 10 additional training sessions of 1 hr each. The subjects' ability to make large cyclofixations gave them the ability to make dynamic cyclorotary pursuit or tracking of a moving target within this short duration. Considered alone, the training of dynamic tracking was not difficult; however, it was made difficult by the bright illumination required for high-resolution photography. The over-all apparatus and procedure were also similar to the methods described earlier, with differences noted below.

Motion picture technique. Measures of dynamic torsion were made from photographs taken with a 16 mm Bolex H16 reflex movie camera running at either 24 frames/sec for smooth or 64 frames/sec

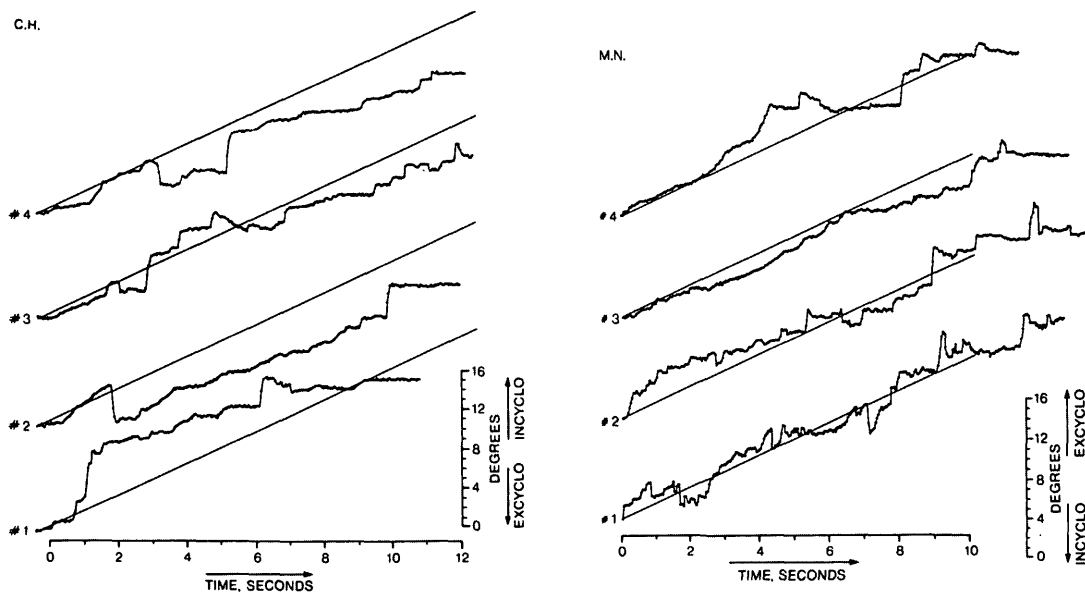


Fig. 4. Photographic analysis (24 frames/sec) of voluntary cycloverisional slow pursuit with complete visual feedback (rotating line and afterimage visible). Solid line represents a tracing moving at the correct velocity of $1.6^\circ/\text{sec}$. Numbers indicate order of tracing.

for saccadic testing. A 150 mm P. Angenieux zoom lens and 30 mm of extension tubes were used. Movies of the right eye were taken at 30 cm distance through a first-surface mirror in front of the subject at a 45° angle, placed 5.0° off the subject's visual axis. Two-Color Tran 650 watt flood lights at 100 cm distance provided the required constant illumination. During 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 Analyzer rear-projected a 10 times magnified image onto a horizontal table screen. Torsional movements of the eye were measured with the use of the limbal termination points of the two radial iris markings. The two termination points were chosen so that a line joining them would pass very close to the pupil center. The orientation of this line relative to a stationary vertical marker was used in determining objective cyclotorsion. Measurement error was $\pm 10'$ of arc.

Stimulus arrangements. Because of the large amount of illumination required to obtain high-resolution motion pictures, some stimulus alterations were required to ensure the simultaneous visibility of the real and afterimage line. Instead of a light target and afterimage being viewed against a dark background, the contrast of the over-all array was reversed. The target was a rotatable dark

line against a bright white field and the afterimage was viewed as negative afterimage against this field. Instead of a single flash, numerous consecutive flashes were required, this being necessary to obtain sufficient contrast for the afterimage. Rotations of the target line were produced automatically by driving the servomotor by means of a waveform generator, either at a constant velocity or in steps.

Results

Voluntary pursuit. In order to examine the characteristics of cyclorotary slow pursuit eye movements, the real-line was made to rotate at a constant angular velocity. Initially, observers were asked to make their afterimage "follow" the rotating real-line, reporting on their slow pursuit ability by noting the smoothness of the rotation of the afterimage. Some smooth pursuit was reported at the outset with perceptible improvement occurring over several practice sessions. Curiously, there was a relatively narrow range of velocities over which smooth pursuit was apparent, between 1° to $2^\circ/\text{sec}$. Outside this range the afterimage could be made to move only in steps, indicating the preponderance of saccades. It is of interest to note that the

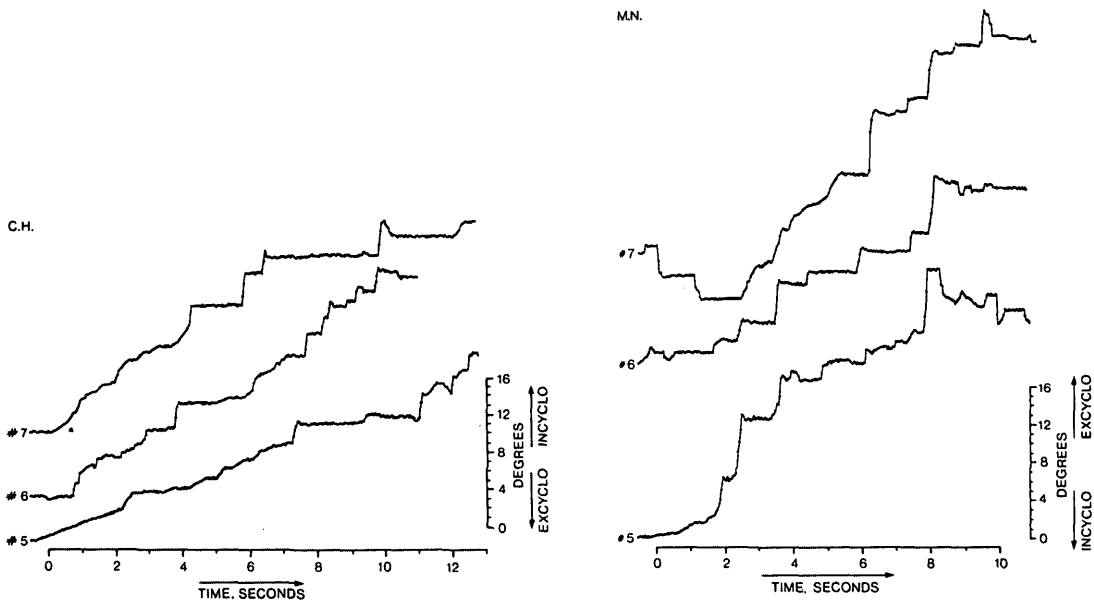


Fig. 5. Photographic analysis (24 frames/sec) of voluntary cycloversional slow pursuit with partial visual feedback (afterimage visible, no rotating line). Numbers indicate order of tracing.

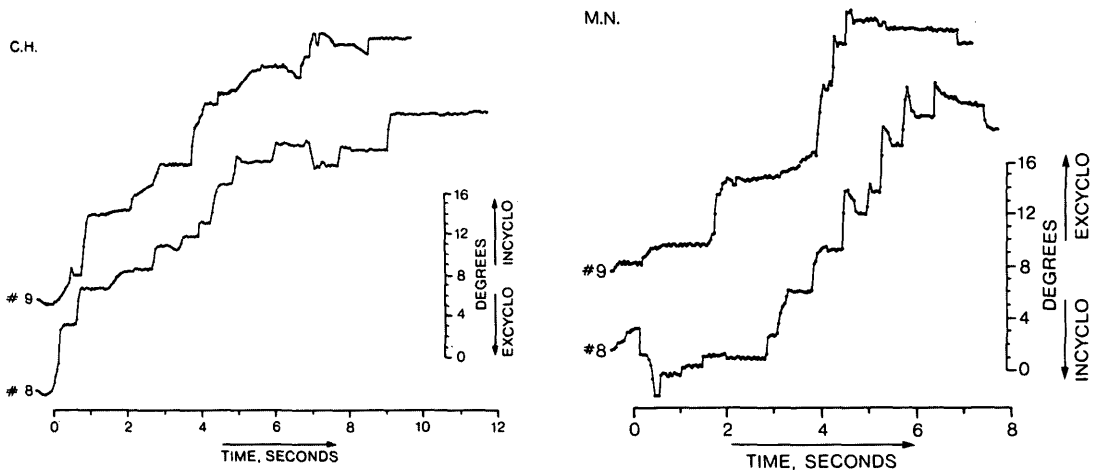


Fig. 6. Photographic analysis (24 frames/sec) of voluntary cycloversional slow pursuit with no rotary visual feedback (neither afterimage or real target line is visible). Numbers indicate order of tracing.

optimal velocity for optokinetic following of a rotating stimulus is also in this slow range.¹³ For a photographic analysis of pursuit, a constant 1.6°/sec angular velocity was used over a total rotation of 16°, rotating clockwise from -8° to +8° for M. N. and the reverse for C. H.

Three different conditions were used: (1) complete visual feedback utilizing both the

afterimage and the target line, (2) partial visual feedback with the afterimage only, and (3) no rotary or tilted visual feedback—this consisting of a single black fixation dot. Fig. 4 to 6 show time records of the torsional eye movements, obtained photographically, for the three conditions for each subject. The sloping solid line in Fig. 4 corresponds to a movement at the velocity of the target line.

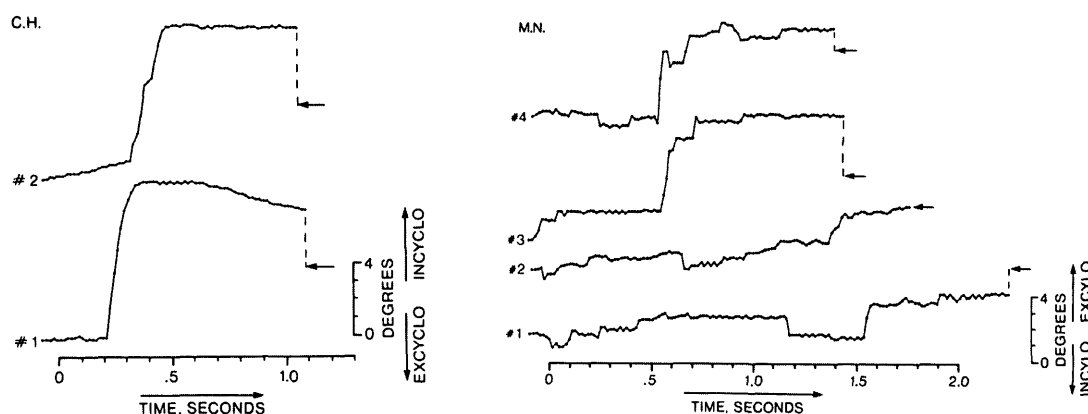


Fig. 7. Photographic analysis (64 frames/sec) of voluntary cycloverisional saccadic tracking: 4° step stimulus. Arrow represents "correct" destination of the saccadic eye movement. Numbers indicate order of tracing.

Traces are numbered in the order taken. With complete visual feedback both subjects demonstrated a moderate ability to make voluntary cyclotorsional slow pursuit movements. Particularly accurate are trace 2 for C. H. and trace 3 for M. N., where movements at the actual target velocity were common (see Fig. 4). Intermixed with these pursuit movements are small corrective saccades.

With partial visual feedback (Fig. 5), subjects had only a single afterimage line and a black fixation dot, and they were required to "imagine" a line moving at the same velocity as before (1.6°/sec). Under this condition, subjects had more difficulty, showing less time in performing smooth movements and showing more saccades instead. It should be noted, however, that C. H. was able to make some long, slow pursuit movements in the absence of a moving line using only the afterimage. Trace 5 begins with a movement having a velocity of 1.6°/sec. Her other traces 6 and 7 have episodes with a velocity of about 3°/sec. M. N. also shows some slow pursuit of about 3°/sec in his trace 7. Such findings might be considered analogous to experiments showing smooth horizontal tracking with afterimages alone.¹²

Ordinarily, horizontal and vertical pursuit eye movements cannot be made in the absence of perceived movement. Except under special circumstances,²² a stationary observer viewing a static scene is not capable of pro-

ducing any pursuit, producing only a series of saccades. As a further point of comparison between trained torsional pursuit and ordinary pursuit, we had our subjects attempt to make cyclotorsional pursuit movements without any stimulus other than a single fixation dot. Under these conditions, movements consisted mostly of a series of steplike saccades, with M. N. having peculiar overshoots (see below) but with little evidence of smooth eye movements (Fig. 6). This inability to make torsional pursuit in the absence of perceived torsional movement provides yet another comparison to the known characteristics of voluntary horizontal and vertical pursuit movements.

It should be emphasized that even though both subjects showed little evidence of smooth pursuit without a moving target, they could rotate their eyes over a large range, up to 24° (Fig. 6, M. N.), without any visual stimulus. This underscores the fact that the torsional eye movements are not visually induced. Subjects need *no* stimulus at all to voluntarily rotate their eyes.

Voluntary saccades. During the training and testing of voluntary cyclorotary saccades, the target line was moved in steps of 4°, 8°, and 16°. M. N. used a clockwise rotation from 0° to +4° or +8°, or -8° to +8°, whereas the movements were in the opposite direction for C. H. Subjects were instructed to track the vertical line using their afterimage. Motion

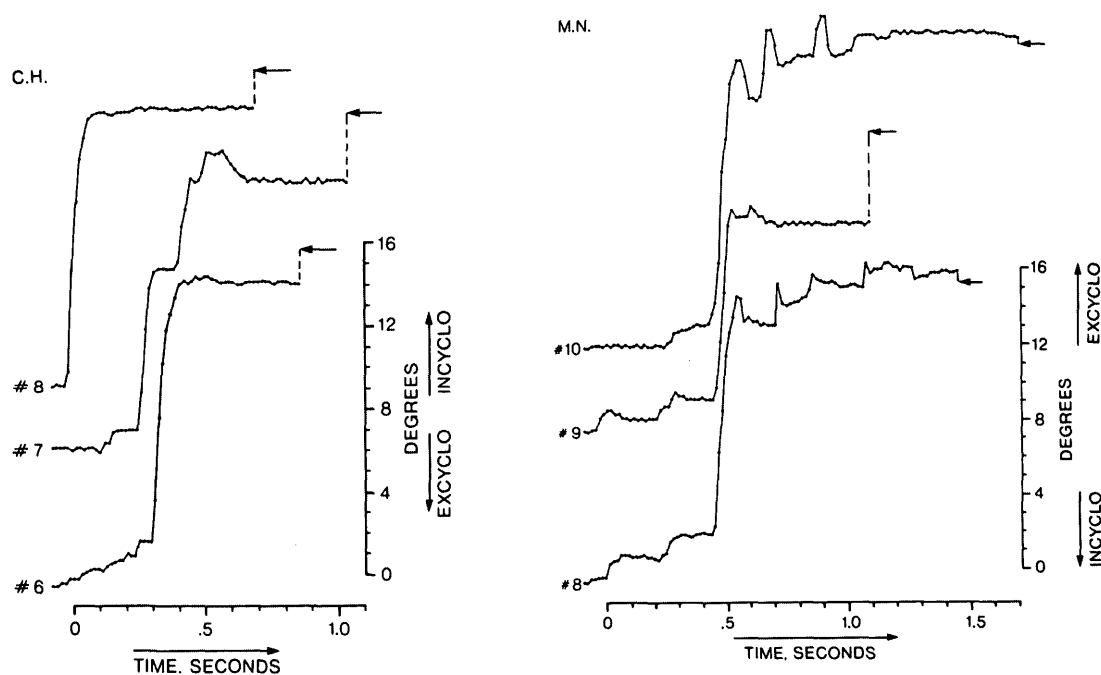


Fig. 8. Photographic analysis (64 frames/sec) of voluntary cycloversional saccadic tracking: 16° step stimulus. Arrow represents "correct" destination of the saccadic eye movement. Numbers indicate order of tracing.

picture speed was increased to 64 frames/sec, maximizing the temporal resolution that could be obtained photographically. Figs. 7 and 8 show sample records of the 4° and 16° saccades.

It is apparent that voluntary saccadic cycloversional eye movements exceeding 12° are possible (Fig. 8, C. H.). From the records it can be seen that the voluntary saccades can be single, sequential, or nearly overlapping. Accuracy of saccades, however, appears less than for ordinary saccades, showing errors as great as 4°. The records from M. N. were more irregular, some showing frequent drifts (0.2° to 1.0°/sec) with a magnitude of 1.0° or less.

During the 4° voluntary cycloversional saccadic tests (Fig. 7), either the subjects greatly overshoot the correct stimulus position 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 appropriate 4° saccade was virtually impossible to make and had to be coaxed to even attempt such a

movement. The 8° and 16° saccadic tasks were judged to be far easier. These results suggest a possible inability to accurately control cyclotorsional saccadic trackings of less than 4°.

C. H. demonstrated normal glissadic overshoots when compared to normal horizontal saccades,²³ and the saccadic tracking of M. N. often showed large dynamic overshoots of up to 2.0°, following the normal velocity-amplitude relationship for saccades² (see Fig. 8). Although M. N. is a unilateral intermittent exotropia, it should be remembered that these traces are for his nonstrabismic eye. Also, we found no unusual horizontal eye movements for either of his eyes when measured by an infrared photoelectric technique, accurate to 20'. We have one possible explanation. Bahill and Stark⁴ have found that the occurrence and magnitude of dynamic overshoots increases with fatigue. M. N. had reported feeling very tired for several days prior to and through the day of these tests. In addition, both subjects reported large amounts of saccadic suppression. Afterimages

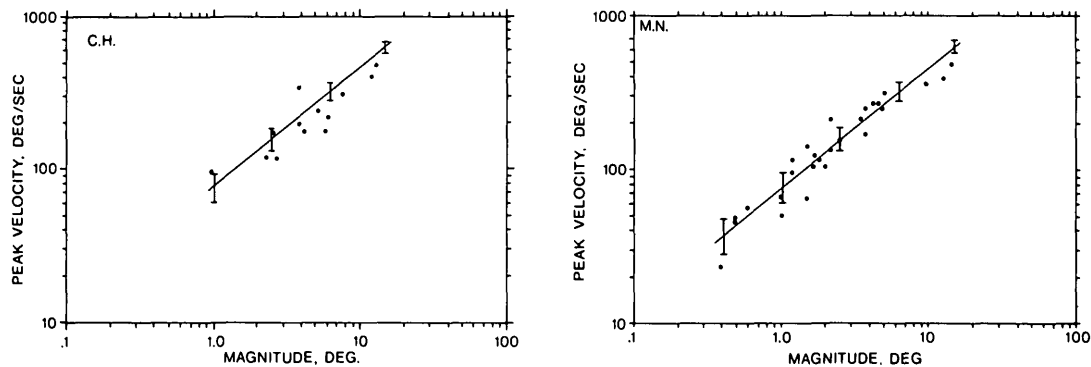


Fig. 9. Comparison of voluntary cycloverisional and horizontal saccades in terms of magnitude vs. peak velocity. Dots represent this analysis for voluntary cyclotorsional saccades. The regression line represents a best fit for a comparable analysis of horizontal saccades obtained by Bahill et al.³ with bars indicating the range of their data.

disappeared during and somewhat after voluntary saccades greater than about 4° or 5°, thus diminishing retinal feedback which related eye position to the subject. Unusual oculomotor control may have occurred because of these two factors.

Systematic analysis indicates that horizontal and vertical saccades are highly stereotyped. This is best understood by considering the well-documented magnitude vs. peak velocity function for normal saccades,^{3, 24} a relationship which emphasizes the fact that horizontal and vertical saccades do not come in all sizes and velocities but that for any given size there is a characteristic velocity and duration. The dots in Fig. 9 show peak velocities of torsional saccades as a function of amplitude. The velocities have been multiplied by a factor of 1.43, compensating for the fact that our frame rate of 64 frames/sec is effectively limited in its high-frequency response to 32 Hz. Such a limitation can be expected to reduce saccadic peak velocity by 30%,³ thereby requiring a multiplicative factor of 1.43 to obtain the best estimate of the true peak velocity. Comparative data from horizontal saccades are plotted as a regression line with error bars, these data being derived from Bahill et al.,³ utilizing a high-frequency recording system (1,000 Hz cutoff). What stands out is the remarkable congruence of the two sets of data, suggesting a common or analogous origin for both types of saccades.

TRAINED DYNAMIC CYCLOVERSION IS NOT VISUALLY INDUCED. Rotating stimuli can visually induce cyclotorsion.^{7, 8, 13} As a further control to clarify the voluntary nature of our cyclotorsional slow pursuit and saccadic tracking, we had subjects view the rotating real-line as in all previous test situations, instructing the subjects to relax and simply observe the rotating stimulus (either 1.6°/sec pursuit ramp; 4° or 16° saccadic step). This was done for both observers, with and without the afterimage line. Under all conditions no trace of systematic nystagmus or any movements were found. No movements exceeded 1°.

Discussion

Voluntary nature of the trained cycloverisions. Reflexive cyclotorsions have been known to exist for over 100 years. What is new* is the existence of a cyclotorsional eye movement which fails to fall into any class of reflexive movements, showing instead characteristics which are decidedly voluntary. Two sets of observations should further emphasize this point. First is the finding that neither static tilt nor rotary motion is sufficient to visually induce our reported cy-

*Although not reported as such, we note that Noji,¹⁷ in a supposed study of induced cycloverisions, used afterimages paired with real-lines, reporting increasing "induction" up to 15° only after 5 successive days of "exercise". Rather than induction, we consider this result to be the probable training of voluntary torsion.

clorotary movements. Second and equally important is the fact that large cyclorotary eye movements, up to 26.5° , can be made in the absence of any tilted or rotary stimulus whatever (Fig. 6). Vision alone cannot drive the large torsional movements; they require voluntary effort.

Plasticity and limits of plasticity in the oculomotor system. The emergence of voluntary eye torsion through training indicates an unsuspected plasticity of the human oculomotor system. For example, under ordinary circumstances voluntary fixations are thought to be governed by Listing's law such that, in terms of its resting position, the eye rotates with only two degrees of freedom, with the third degree of freedom (torsion) determined by the horizontal and vertical direction of gaze. The nonmechanical nature of this one degree of rotational constraint implies the existence of a supranuclear neural network, assuring a fixed and remarkably systematic degree of eye torsion for each gaze direction.^{15, 24} Clearly, the existence of voluntary torsion demonstrated in this paper indicates that such a seemingly "hard-wired" network can be modified or overridden.

It should be noted that despite the large degree of oculomotor plasticity demonstrated by our training procedures, there are some aspects of the newly trained movements which are obviously familiar and clearly not new. For example, the conditions under which one finds slow pursuit are similar, both for torsional as well as for normal pursuit, with greater amounts of slow pursuit apparent with greater amounts of movement information. For saccades, the magnitude vs. peak velocity relation affords the most systematic comparison. This relation is a continuous one for normal saccades²⁵ and is applicable to the fast phase of nystagmus as well.²⁰ What is of interest is the fact that our newly trained movements should also follow this rule very closely. We suggest that this similarity is not coincidental but reflects the fact that all saccades, including torsional saccades, are mediated by a primitive and relatively "hard-wired" neural network, originally designed for the quick phase of nystagmus.

Clinical applications. The success of our training procedure raises the issue as to whether other types of oculomotor organizations are also possible and, if this is so, whether or not such reorganization would have value in the treatment of eye movement disorders. The sensory feedback technique which we used to acquire this control is in principle similar to other methods which have used sensory feedback to gain control over responses which are thought to be involuntary; these include heart rate, visceral function, peripheral blood flow, and the permanent return of muscle control in patients with various manifestations of disturbed neuromotor control. (For a review of recent developments in sensory feedback, see Schwartz and Beatty.²¹) One of the key features for successful training of these involuntary responses is the availability of a *high-gain* sensory feedback signal indicating minute changes in direction of the desired motor response. With this information, the subject gradually gains access to previously inaccessible visceral or motor control mechanisms.

Considering this recent work on the training of involuntary responses and our own work on the training of voluntary torsion, it is of interest to determine whether other stereotyped oculomotor routines are also malleable. For example, both Hering's law and Listing's law are well-known rules of the oculomotor system, reflecting the fact that the pattern of innervation to the muscles is very orderly and seemingly permanent. Normally, this neural permanence is thought to be functional, enabling the muscles to direct the eyes in a precise and repeatable manner. In strabismus, and especially with incomitant strabismus, however, these laws, instead of being helpful, are harmful. What is required in the case of a muscle weakness is a new innervation pattern; the old pattern leads to symptoms. What is needed is a modification of neural patterns in the appropriate direction, i.e., a functional violation of Hering's law and Listing's law. The question is whether such fixed patterns of coordination can be reorganized.

Our results suggest that the limits of voluntary oculomotor control are as yet unknown. Since effortless voluntary torsion can be maintained over a significant range (6° to 8° minimum), it is possible that other eye movements can be trained as well. For example, voluntary cyclovergence might be applied to patients with superior oblique palsies, with the limits of such therapy determined by the specific feedback training procedure, patient motivation, and time.

We thank Drs. Lawrence Stark and Brian Brown for helpful comments. We especially thank subjects Matthew Noble and Candus Hedberg.

REFERENCES

- Allen, M. J.: Dependence of cyclophoria on convergence, elevation and the system of axes, *Am. J. Optom. & Arch. Am. Acad. Optom.* **31**:297, 1954.
- Bahill, T. A., Clark, M. R., and Stark, L.: Dynamic overshoot in saccadic eye movements is caused by neurological control signal reversals, *Exp. Neurol.* **48**:107, 1975.
- Bahill, T. A., Clark, M. R., and Stark, L.: The main sequence, a tool for studying eye movements, *Math. Biosci.* **24**:191, 1975.
- Bahill, T. A., and Stark, L.: Overlapping saccades and glissades are produced by fatigue in the saccadic eye movement system, *Exp. Neurol.* **48**:95, 1975.
- Balliet, R., and Nakayama, K.: An illusion of self rotation during voluntary torsion, *Science* (submitted, 1978).
- Boeder, P.: The cooperative action of extraocular muscles, *Br. J. Ophthalmol.* **46**:397, 1962.
- Brecher, G. A.: Die optokinetische Auslösung von Augenrollung und rotatoischem Nystagmus, *Pflügers Arch. Ges. Physiol.* **234**:13, 1934.
- Crone, R. A.: Optically induced eye torsion. II. Optostatic and optokinetic cyclovergence, *Albrecht von Graefes Arch. Klin. Exp. Ophthalmol.* **196**:1, 1975.
- Crone, R. A., and Everhard-Halm, Y.: Optically induced eye torsion. I. Fusional cyclovergence. *Albrecht von Graefes Arch. Klin. Exp. Ophthalmol.* **195**:231, 1975.
- Ditchburn, R. W.: *Eye Movements and Visual Perception*, Oxford, England, 1973, Clarendon Press.
- Helmholtz, H.: *Treatise on Physiological Optics*, translated from Third German edition, Southall, J. P. C., editor, New York, 1910, Dover Publications.
- Heywood, S., and Churcher, J.: Eye movements and the afterimage. I. Tracking the afterimage, *Vision Res.* **11**:1163, 1971.
- Kertesz, A. E., and Jones, R. W.: The effect of angular velocity of stimulus on human torsional eye movements, *Vision Res.* **9**:995, 1969.
- Miller, E. F.: Counterrolling of the human eyes produced by head tilt with respect to gravity, U. S. Naval School of Aviation Medicine Research Report No. 75, 1962.
- Nakayama, K.: Coordination of extraocular muscles. In Lennerstrand, G., and Bach-y-Rita, P., editors: *Basic Mechanisms of Ocular Motility and Their Clinical Implications*, Oxford, England, 1975, Pergamon Press, pp. 193-207.
- Nakayama, K., and Balliet, R.: Listing's Law, eye position sense, and the perception of the vertical, *Vision Res.* **17**:453, 1977.
- Noji, R.: Über optisch Erzwungene parallele Rollungen der Augen, *Arch. Ophthalmol.* **122**:562, 1929.
- Petrov, A. P., and Zenkin, G. M.: Torsional eye movements and constancy of the visual field, *Vision Res.* **13**:2465, 1973.
- Robinson, D. A.: A quantitative analysis of extraocular muscle coordination and squint, *INVEST. OPHTHALMOL.* **14**:801, 1975.
- Ron, S., Robinson, D. A., and Skavenski, A. A.: Saccades and the quick phase of nystagmus, *Vision Res.* **12**:2015, 1972.
- Schwartz, G. E., and Beatty, J.: *Biofeedback—Theory and Research*, New York, 1977, Academic Press, Inc.
- Steinbach, M. J.: Pursuing the perceptual rather than the retinal stimulus, *Vision Res.* **16**:1371, 1976.
- Weber, R. B., and Daroff, R. B.: Corrective movements following refixation saccades: type and control system analysis, *Vision Res.* **12**:467, 1972.
- Westheimer, G.: Saccadic eye movements. In Zikmund, V., Editor: *The Oculomotor System and Brain Function*, Bratislava, Czechoslovakia, 1973. Publishing House of the Slovak Academy of Science.
- Zuber, B. L., and Stark, L.: Micro saccades and the velocity amplitude relationship for saccadic eye movement, *Science* **150**:1459, 1965.