Extraocular muscle action from brain stimulation in the macaque

Robert S. Jampel

A study was made of the eye muscles activated by faradic stimulation of the frontal cortex, midbrain tegmentum, and oculomotor nerve of the macaque. The traditional view concerning the actions of the individual muscles was not confirmed. The vertical recti were found to be effective elevators and depressors of the eyes regardless of the position of the eye in the horizontal plane. At the brain levels stimulated, the vertical recti neither acted as adductors when the eye was partially adducted nor acted as torters. The superior oblique was an in-torter regardless of the position of the eye in the orbit and did not behave as an effective depressor when the eye was adducted or as an abductor when the eye was partially abducted. In these experiments the superior oblique was activated only from midbrain stimulation. The inferior oblique acted as an elevator in the primary and adducted positions and as an extorter when the eye was abducted from both cortical and midbrain sites. The horizontal recti produced precise, balanced eye movements from cortical stimulation without the collaboration of the vertical muscles. Cocontraction of the vertical muscles was not demonstrated. In oblique conjugate movements from cortical stimulation the participation of two muscles was demonstrated. Torsion of the globe was not produced by cortical stimulation. An individual muscle is capable, when acting independently, of bringing the eye to different end positions (goals). Two individual or groups of muscles are capable, under certain circumstances, of bringing the eye to the same end position. It is suggested that these observations can be explained if it is assumed that an extraocular muscle is composed of motor units that subserve different functions (in terms of goal and speed of eye movement) and exert unequal forces along the muscle insertion.

Traditional concepts of the actions of the extraocular muscles are founded on a mechanical analysis of anatomic data. These data were first published by Ruete in 1857, Fick in 1858, and Volkmann in 1869. Employing an X, Y, Z coordinate system of fixed reference points, measurements were made of the rotational center of the eye and the origins, the insertions, the angles of the insertions with various geometric planes of the globe, the cross-sectional areas, and the lengths of the extraocular muscles. The data were summarized by Zoth in 1900. Additional significant anatomic data and concepts concerning the check ligaments were provided by Motais in 1887. These data were utilized to build mathematical models, i.e., ophthalmotropes, and to determine the actions of individual and groups of muscles by means of vector analysis. Two schemes of extraocular muscle action originated from this analysis.
The first scheme concerns the actions of an individual muscle from the primary position when no other muscle is functioning (Fig. 1). The second scheme concerns the action of an individual muscle when the other muscles are innervated and the eye is in various positions of gaze (Fig. 2). The striking difference in the two schemes is in the action of the vertically acting muscles. In the first, the oblique muscles cause the eye to abduct, rotate, and move either up or down so that the eye attains the up-and-out or down-and-out positions, whereas in the second the oblique muscles produce pure vertical movement, when the eye is adducted by the medial rectus, so that the eye attains the up-and-in or down-and-in positions. The converse is true for the vertical recti. The subsidiary actions of the vertical recti and obliques as determined by vector analysis are given in Table I.

Krewson6 in 1950 and Boeder7 in 1961 subjected Volkmann’s anatomic data to more sophisticated mathematic analysis and drew new conclusions concerning the action of the inferior oblique muscle. Krewson demonstrated that the inferior oblique muscle starts as a partial adductor when the eye is adducted, and as the eye moves horizontally into a position of abduction its function changes to that of contributing to abduction. Boeder considered that the vertical recti and oblique muscles acted as pairs. By calculating the length of the muscle tendons in different ocular rotations and the total energy expended in any rotation, he concluded that the inferior oblique is not the predominant elevator when the eye is adducted. This traditional anatomic-mechanical approach represents a nice attempt to deduce function from morphology.

The purpose of this paper is to examine the validity of traditional vector analysis and the concepts that have arisen from its use. Eye movements were evoked in the monkey from 3 brain sites. The extraocular muscles responsible for these movements were determined by mechanical manipulation of the eye, selective detachment of the extraocular muscles, and employment of force-displacement transducers. Extensive review of the literature revealed that this approach had not been previously employed. Electromyography proved unsuitable since placement of the electrodes in the extraocular muscles of the monkey caused a gross distortion of the evoked eye movement.

### Methods

Twenty-two experiments were performed on 16 healthy primates, 14 monkeys (*Macaca mulatta*), and 2 baboons (*Papio papio*) under light ether anesthesia. Both of these animals have a neural

### Table I. The main and the subsidiary actions of the vertical muscles as determined by vector analysis

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<thead>
<tr>
<th>Vertical muscle</th>
<th>Action</th>
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<tr>
<td>Superior rectus</td>
<td>Elevation</td>
<td>Increases on abduction</td>
<td>Adduction and intortion</td>
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<td>Inferior rectus</td>
<td>Depression</td>
<td>Decreases on adduction</td>
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<tr>
<td>Inferior oblique</td>
<td>Elevation</td>
<td>Decreases on abduction</td>
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and muscular oculomotor apparatus similar to that of man. In each experiment the animal was intubated with an endotracheal catheter and placed in a specially designed chair with its head rigidly fixed by a three-pronged device (Fig. 3), or placed prone on an animal board with its head fixed by ear plugs. The ether anesthetic was administered through the endotracheal tube by means of an Epstein-McIntosh-Oxford inhaler. This device will deliver an even quantity of ether over an extended period of time and the level of anesthesia may be maintained without great fluctuations or varied to fit the needs of the experiment. During the period of the brain stimulation the level of anesthesia was maintained at the point at which voluntary ocular movements were abolished.

Faradic stimulation experiments were carried out at 3 different brain levels: the frontal cortex, the midbrain tegmentum, and the intracranial segment of the oculomotor nerve. In each case a craniotomy was performed under aseptic conditions. Precautions were taken so that the animal would survive the operative procedure and could be utilized for later experiments. The frontal cortex was exposed by removing the frontal bone, the midbrain tegmentum was stimulated by means of a Horsely-Clarke stereotaxic device, and the oculomotor nerve was exposed after a temporal craniotomy by gently retracting the temporal lobe of the brain.

The eyes were prepared by placing No. 6-0 black silk sutures at 3 and 9 o’clock on the corneal limbus (Fig. 4). These sutures were employed to serve as reference points from which to observe the eye movements, to mechanically displace the eye into various gaze positions, and to facilitate tenotomy of the extraocular muscles.

A stimulator* was employed to stimulate the frontal cortex, midbrain tegmentum, and oculomotor nerve. When stimulation at a given site produced a reproducible eye movement the following was done when considered appropriate: The eye was mechanically displaced into a different position in the orbit by means of the limbal sutures either before or during stimulation and the effect observed. The extraocular muscles were severed from the globe in different combinations before repeating a stimulus and the effect observed. This was not done in the experiments on the oculomotor nerve. The severed tendon of an extraocular muscle was attached to a force-displacement transducer* and the tension developed in the tendon by brain stimulation was measured.

The amplitudes of the eye movements were estimated in millimeter displacement of the limbal margins in any given direction. Since the macaque eye is between 55 and 65 mm. in diameter, each millimeter of movement represents between 5 and 7 degrees of arc.

Experimental results

Eye movements produced by stimulation of the cerebral cortex. Twelve experiments were performed on 6 macaques and 2 baboons. The areas stimulated in the frontal eye field are known to give rise to eye movements.10* Stimulus frequencies employed were 100 to 300 per second with pulse durations of 0.1 to 1 millisecond, and intensities of 2 to 7 volts. Unipolar stimulation was carried out in all cases with a platinum electrode insulated to the tip; the indifferent electrode was a platinum cylinder 5 mm. in diameter placed in the rectum. The eye movements studied were horizontal contralateral conjugate gaze and oblique contralateral conjugate gaze.

A. Horizontal contralateral conjugate gaze.

1. The effect of mechanically moving the eyes by means of limbal sutures into different positions in the orbit (Fig. 5). Regardless of the position of the eyes prior to stimulation, the final end position resulting from stimulation of

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*The Grass Instrument Company, Model No. 104A.

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*Grass Ft. 0.3 Grass Instrument Company.
Fig. 3. With the illustrated device a craniotomy may be performed with the monkey sitting up, prone, or supine. The central supporting bar of the device swivels in a universal socket and may be fixed in any position.

a cortical site was the same, and the route taken to achieve that final position was grossly the most direct. For example, if the homolateral eye was displaced upward and inward during stimulation, it would move straight down to the final position; and if displaced downward and inward, it would move up. If the eye homolateral to the stimulation was displaced upward and outward, it would move obliquely down and in to reach the final position; and if the eye was displaced downward and outward, it would move obliquely upward and inward. If the eye was mechanically abducted and extorted, it would simultaneously adduct and intort to reach the final adducted position.

2. The effect of severing the insertions of various extraocular muscles on the stability of horizontal conjugate gaze from cortical stimulation. Cutting the insertions of the vertical recti or oblique muscles had no grossly observable effect on the stability of horizontal conjugate gaze produced by stimulation of the frontal cortex. For example, cutting the superior rectus muscle or the inferior oblique muscle or both in either eye did not result in the introduction of a downward or a torsional movement of the eye in horizontal conjugate deviation, i.e., the two eyes remained in the horizontal plane and moved smoothly without vertical displacement or torsion to reach their end position. Also, cutting the insertion of the medial rectus in the homolateral eye resulted in the eye moving toward the midline (Fig. 5), but cutting the homolateral lateral rectus tendon did not cause the eye to “overshoot,” i.e., undergo a greater amplitude of movement than the contralateral eye.

When the detached tendons of the vertical muscles were connected to the force-displacement transducer during cortical stimulation, no contractile force was recorded.

B. Oblique contralateral conjugate deviations. These eye movements were more difficult to elicit and were more easily distinguished by repetitive cortical stimulation than the horizontal deviations.

Fig. 4. The eye of a baboon with No. 6-0 black silk sutures placed at 3 and 9 o’clock at the corneal limbus. This was done to facilitate mechanical displacement and tenotomy.
1. **Course of cortically evoked oblique ocular movements (Fig. 6, A).** These movements may be divided grossly into two phases, a horizontal phase and a vertical phase. The eye appeared to respond by first moving horizontally before moving vertically. Thus, in these movements the eye transcribed a right angle and did not move directly from the primary position to the final position, upward and inward or downward and inward. No torsional movements were observed.

2. **The effect of mechanically neutralizing the pull of the horizontal recti muscles with limbal sutures on the vertical component of oblique contralateral conjugate ocular deviations (Fig. 6, B).** In the cortically evoked oblique contralateral upward movements, if the homolateral eye was held in the position of forward gaze or abduction, it moved straight upward. The amplitudes of the upward movements were about the same (3 to 4 mm.) in the adducted and primary positions and less (2½ to 3 mm.) in the abducted position. No torsional ocular movements were induced by these mechanical manipulations. If the eye was mechanically intorted or extorted, it rotated back to its original position before elevating. Mechanical depression of the eye increased and mechanical elevation decreased the amplitude of elevation. In the contralateral eye, the observations were similar except that in abduction the upward movement was slightly less marked than in forward gaze and abduction. In oblique contralateral downward movements, maintaining the homolateral eye in the primary or abducted position resulted in downward movement without torsional movements. In the abducted position, the amplitude of depression was slightly less than in the adducted or straight forward positions.

3. **The effect of severing the insertions of the horizontal recti on the vertical component (Fig. 6, B).** The medial rectus in the homolateral eye was detached from its insertion and the eye was moved from the primary into the abducted position. Stimulation of the frontal eye field yielded an outward and upward movement of the contralateral eye. The homolateral eye moved to the midline and straight up without torting. Maintaining the eye with a limbal suture in the abducted position, opposing the inhibitory relaxation of the lateral rectus, resulted in a straight upward movement of that eye. The lateral rectus in the homolateral eye was then severed from its insertion and the eye was easily moved without opposition into various positions in the horizontal plane. In each case brain stimulation resulted in an upward eye movement. If the eye was mechanically depressed and intorted, it would extort to its original position and elevate. The amplitude of the upward movement was slightly less in the abducted position, but, unless the eye was mechanically intorted or extorted, no torsional movements were noted.

4. **The effect on the vertical component of severing the insertions of the superior and inferior rectus muscles.** The superior rectus in the homolateral eye was severed from its insertion. Stimulation of a site in the frontal eye field produced an outward-and-upward movement in the
Fig. 6. A, The path of the homolateral eye in a cortically produced oblique contralateral eye movement. The eye appears to move inward before moving upward, grossly transcribing a right angle. B, The paths of the homolateral eye from initial to final positions in cortically produced oblique contralateral gaze with the horizontal recti cut and the eye moved by means of limbal sutures into various positions. The movement was due in each case to the superior rectus muscle. C, The paths of the homolateral eye from initial to final position in cortically evoked oblique contralateral gaze with the horizontal recti cut and the eye moved passively into various positions. In this case the movement was due to the inferior oblique.

contralateral eye and an inward movement associated with a minimal elevation (about 0.5 mm.) of the homolateral eye. This slight elevation of the eye was eliminated following the severance of the inferior rectus muscle. However, spontaneous vertical nystagmus was observed in both eyes with a 3 to 4 mm. amplitude of movement above the horizontal plane and without a torsional component in spite of the fact that the superior rectus and inferior rectus muscles were cut in the homolateral eye. Spontaneous horizontal gaze to both sides was also noted without vertical instability. No torsional components were introduced to the cortically evoked eye movements by cutting the superior or inferior recti muscles or both. When these muscles were severed in the contralateral eye, stimulation of the frontal cortex produced an abduction but no upward deviation.

In another experiment, after severing the superior and inferior recti muscles in the homolateral eye, stimulation of an area in the frontal eye field resulted in abduction and elevation of that eye (Fig. 6, C). The relative position of the eye in the orbit was then changed with a limbal ligature. In the primary and abducted positions, the eye moved up about 3 mm. In the abducted position, there was an elevation of 2 mm. associated with an extortion of 20 degrees about a pivotal point at the lateral corneal limbus. Severance of the inferior oblique muscle from the globe eliminated this movement.

5. MUSCLE TENSION DEVELOPED IN COR-TICALLY PRODUCED EYE MOVEMENTS. The severed medial and lateral rectus tendons were attached to force-displacement transducers by means of sutures. The isometric force developed was from 7 to 10 Gm. The

*A lightly anesthetized monkey exhibits spontaneous eye movements. He will respond at times to noise and light by eye movement. The origin of these movements and the nature of the variables influencing them have not been exhaustively studied. They probably originate at a brainstem level.
muscle force could not be significantly increased by increasing the parameters of stimulation. Placing the medial rectus muscle under a tension of 10 Gm. prior to stimulation resulted in an increase in tension over the initial tension of 6 to 8 Gm. In this case the contralateral eye did not overshoot, i.e., move a greater amplitude than before obstructing the movement of the homolateral eye. A similar observation was made in a previous experiment by counteracting the adducting force of the homolateral eye with a limbal suture.

6. TORSIONAL EYE MOVEMENTS FROM CORTEXAL STIMULATION. In these experiments no torsional eye movements were elicited.

Eye movements evoked by stimulation in the midbrain tegmentum in the region of the oculomotor and trochlear nuclei and roots. Five experiments were performed on 5 primates—4 macaques, and 1 baboon. A penetrating unipolar steel electrode was employed and manipulated with a Horsely-Clarke stereotaxic apparatus. The stimulus parameters with 3 second trains and delays had a frequency of 100 per second, pulse duration 0.1 millisecond, and intensity 0.1 to 1 volt. It was possible to obtain responses for a considerable period of time (more than 90 minutes in one experiment) without apparent fatigue. The eye movements discussed subsequently were homolateral monocular movements.

1. Inward movement of the eye. The inward movement of the eye was the most frequent and most easily elicited response. Displacing the eye upward with a limbal suture prior to stimulation causing the visual line to be directed above the horizon did not add a vector of upward movement, and displacing the eye downward so that the visual line was directed below the horizon did not add a vector of downward movement. Severing the medial rectus muscle abolished this movement.

2. Inward-and-downward movement (Fig. 7, A). No torsional movement of the eye was observed with inward-and-downward motion. Severing the inferior rectus muscle abolished the downward component.

![Fig. 7. A, Three pathways of the inferior rectus from the primary to a final position evoked by midbrain and oculomotor nerve stimulation. B, Three pathways of the superior rectus from the primary to a final position evoked by midbrain and oculomotor nerve stimulation. C, The action of the inferior oblique muscle from midbrain stimulation in the adducted, primary, and abducted positions. The horizontal recti have been cut and the eye was moved into the initial positions just prior to stimulation. D, The action of the superior rectus from midbrain stimulation. The movement evoked prior to cutting the horizontal recti was up and out. Displacing the eye into the positions depicted caused a decrease in the amplitude of upward movement but did not introduce other vector forces. +, Initial position of the pupil. ⊗, Final position of the pupil. ↔, Direction of the movement.](http://iovs.arvojournals.org/pdfaccess.ashx?url=/data/journals/iovs/933632/ on 06/24/2017)
3. **Straight downward and oblique outward and downward movements (Fig. 7, A).** These movements were due to the contraction of the inferior rectus muscle. In either case, mechanical displacement of the eye from the primary position caused a decrease in the downward component. Thus, if stimulation caused the eye to move straight down, abducting or adducting it from the primary position resulted in a decrease in the downward component. The same phenomenon was observed in the oblique outward-and-downward movement. No torsional movements were induced by mechanically displacing the eye in the horizontal plane.

4. **Upward movement of the eye (Fig. 7, C).** Faradic stimulation of a site in the midbrain produced a straight upward movement of the globe. The medial and lateral recti were cut, and the eye was moved by means of limbal sutures into positions of adduction and abduction, and the midbrain restimulated. Next, the inferior rectus, superior rectus, superior oblique, and inferior oblique muscles were cut from the globe in that order. After each muscle was cut, the midbrain was restimulated. The only contracting muscle proved to be the inferior oblique. The movements noted were as follows: In the primary position and in the adducted position, the upward movement was 3 mm. No extorsion was noted in these positions. In the abducted position the eye moved up about 2 mm. and there was an eccentric extorsion of about 30 degrees around a pivotal point at the limbus. When the eye was mechanically intorted and moved into any relative position within the orbit, marked extorsion occurred equal to the amount of intorsion. When the eye was mechanically extorted no torsion occurred in any relative position of the eye and the vertical movement was not increased.

5. **Oblique upward and inward-and-upward movements (Fig. 7, B).** From other sites in the midbrain, stimulation produced oblique upward-and-inward and straight upward movement of the eye. Displacing the globe into different positions in the horizontal plane had the following effect: In abduction the upward motion was of less amplitude than in the primary or adducted positions. No torsional movements were introduced. The upward movement was due to the superior rectus and the inward to the medial rectus.

6. **Upward-and-outward movement.** Stimulation in the third nerve nucleus resulted in the eye moving obliquely upward and outward. The outward movement was about 3 mm. and the upward movement about 4 mm. There was no torsion. The eye was then moved into the cardinal positions by means of corneal limbal sutures. When the eye was adducted, adducted and elevated, or adducted and depressed, stimulation produced no ocular movement. When the eye was abducted beyond 3 mm. for the primary position, stimulation resulted in elevation but the amplitude of the elevation was decreased. Abduction of more
than 6 mm. resulted in abolition of the elevation (Fig. 7, D). From the resistance of the eye to displacement by the limbal suture it appeared that only the superior rectus muscle was functioning. This was proved when severance of the insertion of the superior rectus muscle completely abolished the ocular movement.

7. Intortion (Fig. 8, B). The response to stimulation in the region of the trochlear nucleus and roots was an intortion of the homolateral eye of about 50 degrees with a depression of the lower limbal margin of 3 mm. The intortion of the eye was characterized by an eccentric rotation inward occurring about a point fixed at the limbus, as depicted in Fig. 8, A, and by wheel torsion around the visual line. This ocular movement was associated with pupillary dilation from 3 to 7 mm., phonation, and increased diaphragmatic movements. Advancing the electrode ventrally 2 mm. eliminated the associated phenomena but preserved the intortion of the eye. The ocular movement was obtained repeatedly without attenuation during the 90 minutes in which the following observations were made.

The eye was moved into and maintained in various positions in the orbit by means of limbal sutures placed at 3 and 9 o'clock just before stimulation. In abduction intortion of the eye was slightly less than when the eye was in the primary position but no depression or re-enforcement of abduction was observed. In the up-and-out and down-and-out positions, intortion of the same magnitude as in horizontal abduction was noted. No depression or re-enforcement of abduction was noted.

In the straight up position, there was intortion of 45 degrees about a pivotal point fixed at the lateral corneal limbus with a depression of about 4 mm. In the straight-down position, there was wheel intortion without depression of the eye.

In adduction there was intortion with a downward component of the same magnitude as in the primary position (3 mm.). In the up-and-in position the magnitude of the intortion was decreased, whereas the downward component was increased to about 4 mm. In the down-and-in position there was a wheel intortion of about 50 degrees with no depression. If the two limbal sutures were held in such a manner as to prevent a downward movement, wheel intortion (rotation around the visual line) occurred whatever the position of the globe in the orbit.

The eye was then mechanically intorted. In abduction and in the up, down, and down-and-out positions the eye did not move with stimulation. In the primary position there was a 1 mm. downward displacement which was slightly increased when the eye was moved straight up. In adduction the downward movement was increased to 3 mm., and in the up-and-in position it was increased to about 6 mm. In the down-and-in position no movement was noted.

The inferior rectus muscle was then cut from its insertion on the globe and the above sequence repeated. No difference in response was noted. Next, the superior rectus muscle was cut from its insertion and the sequence repeated. This was followed by cutting the inferior oblique muscle. In each case the ocular movements were not affected. Finally, cutting the superior oblique tendon abolished the eye movement.

**Intracranial stimulation of the oculomotor nerve.** The intracranial segment of the left oculomotor nerve was successfully isolated in 5 primates—3 macaques, and 2 baboons. Stimulation frequencies employed were 30 to 100 per second, with pulse durations of 1 millisecond, and intensities of 0.1 to 1 volt. Different responses were obtained by varying the frequency and intensity of the stimulus and shifting the electrode to different positions on the surface of and within the parenchyma of the oculomotor nerve from the point at which it left the midbrain to that at which it entered the cavernous sinus. After stimulations were carried out the nerve was cut and a small segment extirpated. In each experiment this resulted in ptosis of...
the lid, wide pupillary dilation, and abduction of the eye which became manifest after the animal awakened from the anesthesia. Thus, it was certain that the ocular motor nerve had been isolated.

A summary of the responses obtained from stimulating the third nerve is contained in Table IV. Mechanical displacement of the eye before and during stimulation was performed and no significant alteration in the basic movement was observed.

Consideration of the experimental results

The oculomotor system was stimulated faradically at three levels in the nervous system: the frontal cortex, the oculomotor and trochlear nuclei and roots, and the intracranial segment of the oculomotor nerve. The frontal cortex was stimulated in sites known to produce horizontal and oblique contralateral conjugate gaze. The midbrain motor nuclei were stimulated reproducing in general the findings of Bender and Weinstein in regard to eye movements. The intracranial oculomotor nerve was stimulated under direct vision in the primate, apparently for the first time, though Lowenstein stimulated it indirectly using a Horsley-Clarke instrument. Problems concerning precise localization of the sites stimulated are not dealt with in this paper.

Continued repetitive stimulation of the frontal cortex (Table II) results in eventual extinction of the evoked eye movements, an example of cortical instability. The maximum time during which responses were obtained was about 30 minutes. On the other hand, responses were evoked from the midbrain motor nuclei and oculomotor nerve for as long as 90 minutes without apparent fatigue or alteration in the elicited eye movements.

In horizontal contralateral conjugate gaze evoked by stimulation in the frontal eye area the muscles responsible were the homolateral medial rectus and the contralateral lateral rectus. These muscles were capable of producing a smooth, stabilized, conjugate movement of full amplitude without a measurable contraction of the superior or inferior recti or obliques. (No contractile force was recorded with the transducer.) Simultaneous contraction (co-contraction) of the vertical muscles to stabilize the eye during contraction of the horizontal muscles could not be demonstrated. Thus, disrupting the vertical muscles by severing their tendons in different combinations had no effect on the stability of the horizontal movement, i.e., the eye did not wobble and was not displaced upward or downward. Also, disruption of the vertical muscles had no influence on the amplitude of the horizontal movement in adduction in the homolateral eye or in abduction in the contralateral eye. Thus, simultaneous contraction of the obliques did not appear to contribute to abduction and simultaneous contraction of the vertical recti to adduction. The horizontal recti produced a smooth, grossly linear, phasic or tonic movement directed to a consistent final position regardless of the initial position of the eyes prior to stimulation. Thus, if the eye was displaced upward and inward the medial rectus pulled the eye straight down, and if the eye was intorted in the primary position the medial rectus would extort the eye and pull it inward. It could not be demonstrated that the horizontal recti contribute to further elevation when the visual line is directed above the horizon or to depression when the visual line is directed below the horizon. If the homolateral medial rectus

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<th>Eye movement</th>
<th>Responsible muscles</th>
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<td>1. Horizontal conjugate gaze</td>
<td>Lateral and medial rectus</td>
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| 2. Oblique conjugate gaze | A. Lateral and superior rectus  
                             | Medial rectus and superior rectus  
                             | B. Lateral rectus and ?  
                             | Medial rectus and inferior oblique |
was severed, the eye moved to the midline (reciprocal innervation), but the contralateral eye did not overshoot, i.e., have a greater amplitude of movement than usual. Also, the contralateral eye did not overshoot when the homolateral medial rectus was mechanically prevented from contracting with a limbal suture or when the eye was forcefully abducted during stimulation against the adducting force of the medial rectus. If the lateral rectus in the homolateral eye was cut, contraction of the medial rectus produced a smooth linear movement of the eye of usual amplitude to a consistent final position regardless of the initial position of the eye.

In the oblique contralateral conjugate gaze evoked by frontal cortical stimulation the horizontal movement preceded the upward or downward movement. The muscles responsible for the inward-and-upward movement were the medial rectus and the superior rectus in the homolateral eye, and for the outward-and-upward movement the lateral and the superior recti in the contralateral eye, whereas the inward-and-downward movement was due to the medial rectus and inferior rectus, and the outward-and-downward to the lateral and the inferior recti. It was also possible, by stimulating cortical sites, to obtain upward movement that was produced by the inferior oblique muscle without contraction of the superior rectus or the occurrence of ocular torsion. Thus, in these cortically evoked upward movements either the superior rectus or the inferior oblique muscle, but not both functioning together, was found responsible for bringing the eye to a consistent elevated position. The superior rectus was more frequently responsible for the vertical component than the inferior oblique though the excursion produced by either had the same amplitude. Severing the superior rectus abolished the evoked upward component in one experiment, but spontaneous vertical nystagmus occurred that appeared to be due to the action of the inferior oblique muscle. The innervation for this spontaneous movement probably emanated from the brainstem levels.

In cortically evoked movements the actions of the superior rectus and inferior rectus were studied in the primary and abducted positions by mechanical manipulations with the limbal sutures and by cutting the tendons of the medial and lateral recti. The superior rectus moved the eye upward and the inferior rectus downward in the primary and abducted positions although the amplitude of the movement was slightly less in the latter position.

The isometric tension developed in the medial rectus from cortical stimulation ranged from 8 to 10 Gm. The tension could not be increased by increasing the parameters of cortical stimulation.

In these experiments torsional movements (rotations around the visual line) from cortical stimulation were observed only once and only after the eye was mechanically displaced. Slight extortion was noted when the inferior oblique contracted in the abducted position. No intortion was observed. Review of the literature on eye movements evoked from both the frontal and occipital lobes reveals no mention of torsional movements. This suggests that the innervations for torsion arise at brainstem levels.

Stimulation of sites within the oculomotor and trochlear nuclei and roots resulted in eye movements due to innervation of individual extraocular muscles (Table III). With constant stimulus parameters, the eye moved toward a constant end position. A vertical rectus, when acting by itself or with the medial rectus, could bring the eye to different end positions. The superior rectus yielded upward and upward-and-outward movement from the primary position and when acting with the medial rectus inward-and-upward movement. The inferior rectus responded with a downward or a downward-and-outward movement from the primary position, or, when acting with the medial rectus, an inward-and-downward movement. The in-
ferior oblique responded by straight upward movement from the primary positions and when the eye was adducted. When acting from the abducted position it produced an eccentric torsion around a pivotal point at the lateral limbus. A locus in the midbrain that produced extortion from the primary position was not found during these experiments. The superior oblique acted as an intorter regardless of the relative position of the eye (Fig. 8, B). This movement was called an eccentric intortion since it occurred about a pivotal point at the lateral limbal margin and involved some downward displacement of the lower limbal margin (Fig. 8, A). This downward displacement was minimal to absent when the eye was displaced downward. It could also be eliminated by holding the limbal sutures so that they roughly formed an isosceles triangle with the cornea as the base and with the vertex angle bisected by the visual line. In this way the eccentric intortion was converted into a wheel intortion. The downward displacement was greatest with the eye up and particularly when the eye was up and in. The maximum intorsion occurred with the eye down and in. In these experiments in the areas stimulated the superior oblique could not be made to respond by depressing the eye straight down regardless of the position of the eye in the horizontal plane.

Stimulation of the peripheral oculomotor nerve produced a broad spectrum of eye movements (Table IV) even though the superior oblique and lateral rectus was not innervated. The eye movement most easily obtained was adduction associated with lid elevation. Stimulation in a site with constant parameters resulted in the eye moving toward a consistent end position. By mechanical displacement it was not possible to induce significant new components in the eye movements.

Stimulation of the oculomotor nerve resulted in downward-and-inward, straight downward, and downward-and-outward movements of the eye of equal amplitudes. Since the superior oblique muscle was not innervated it follows that these movements were produced by the inferior rectus. Another movement elicited was adduction with intorsion. In this instance, according to traditional views, the superior rectus

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<th>Table III. Eye movements following stimulation of the oculomotor and trochlear nuclei and roots</th>
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<td>2. In and down</td>
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<td>3. Straight down</td>
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<tr>
<td>4. Out and down</td>
</tr>
<tr>
<td>5. Straight up</td>
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<tr>
<td>6. Up and out</td>
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<tr>
<td>7. Up and in</td>
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<tr>
<td>8. Intortion</td>
</tr>
</tbody>
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<table>
<thead>
<tr>
<th>Table IV. Eye movements following faradic stimulation of the intracranial segment of the oculomotor nerve</th>
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</thead>
<tbody>
<tr>
<td><strong>Eye movement</strong></td>
</tr>
<tr>
<td>1. In</td>
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<tr>
<td>2. In</td>
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<tr>
<td>3. In and up</td>
</tr>
<tr>
<td>4. Straight down</td>
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<td>5. In and down</td>
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<td>6. In and intorsion</td>
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<tr>
<td>7. Down and out</td>
</tr>
<tr>
<td>8. In and down, extortion</td>
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<tr>
<td>9. Up and out</td>
</tr>
<tr>
<td>10. Straight up</td>
</tr>
<tr>
<td>11. In and up, extortion</td>
</tr>
<tr>
<td>12. None</td>
</tr>
</tbody>
</table>
could be the only intorter, yet the eye was not displaced upward with stimulation. The same type of reasoning can be applied to other evoked eye movements revealing inconsistencies in the traditional views of the actions of the extraocular muscles.

**Discussion**

Eye movements were produced by faradic stimulation of the frontal cortex, the midbrain tegmentum, and the oculomotor nerve. The number of cells and fibers stimulated in these sites and the nature of the nervous impulses to the extraocular muscles are unknown. Also, only a small part of the total oculomotor activity was studied since impulses to the extraocular muscles are known to arise from many other sources. Even with these limitations certain generalizations and concepts arise from these experiments.

1. Eye movements are obtainable by brain stimulation which cannot be explained by traditional vector analysis. Mechanical displacement of the eye into different positions does not introduce significant new components into the basic movement evoked by brain stimulation. Vertical movements are frequently observed to be disassociated from torsional movements. Fender, in 1955, studied the minute excursions of the eyeball characteristic of ocular fixation but could not demonstrate the correlation of vertical movement and torsion predicted by traditional analysis.

2. A single muscle or a group of muscles is innervated to move the eye to a consistent end position. In attaining an end position the initial position of the eye does not influence the muscle or muscles innervated. This type of eye movement has been called goal directed by Hyde and Eliasson.

3. The function of a single or of a combination of extraocular muscles may be defined in terms of the speed of movement and the goal (end position). A vertical rectus either alone or in combination with the horizontal recti is capable of bringing the eye to numerous goals in vertical gaze depending upon the brain site stimulated. In this sense a vertical rectus can be viewed as having multiple functions.

4. Simultaneous contraction of antagonistic muscles (cocontraction) is not necessary for the stabilization of horizontal eye movements and does not contribute to the amplitudes of these movements. A horizontal rectus without the collaboration of any vertical muscle can move the eye to any goal in the horizontal plane precisely and smoothly, either tonically or phasically. Tamler, Marg, and Jampolsky did not find increased activity in the vertical recti by electromyography during voluntary following movements in human subjects.

5. A cortically evoked oblique conjugate movement is brought about by the contraction of two muscles. Torsion of the eye is effected by subcortical innervations.

6. Single muscles or groups of muscles acting independently can move the eye to the same goal depending upon the source of innervation. If a muscle is detached from the globe, another muscle, under certain circumstances, is capable of taking over its function.

A muscle is composed of many contractile units, i.e., motor units, which are its basic functional elements. The traditional view depends upon the assumption that the innervations to the extraocular muscles are identical for each function and differ only in quantity, and that the motor units in any one extraocular muscle are more or less the same and exert a uniform force evenly distributed along the entire width of the insertion. Thus, since the forces exerted are the same in each position of gaze and the muscle planes are known, a vector analysis can determine to what goal the eye will move.

These experiments do not support the traditional view. The final position of the eye is determined by the pattern of impulses leaving the central nervous system and is not dependent upon the position of the eye in orbit. The experimental observations are explained by considering...
that the vector forces exerted by the motor units comprising a muscle are unequal and vary with function as determined by central nervous system impulses.

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2. Fick, A.: Neue Versuche über die Augenstellungen, Moleschott, Untersuch. 5: 193, 1858.