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Simonsz, H. J.; Wade, N. J.

Published in:
Strabismus

DOI:
[10.1080/09273972.2018.1539388](https://doi.org/10.1080/09273972.2018.1539388)

Publication date:
2018

Document Version
Peer reviewed version

[Link to publication in Discovery Research Portal](#)

Citation for published version (APA):

Simonsz, H. J., & Wade, N. J. (2018). Why did Donders, after describing pseudotorsion, deny the existence of ocular counterrolling together with Ruete, Volkmann, von Graefe and von Helmholtz, until Javal reconfirmed its existence? *Strabismus*, 26(4), 211-222. <https://doi.org/10.1080/09273972.2018.1539388>

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Why did Donders, after describing pseudotorsion, deny the existence of ocular counterrolling together with Ruete, Volkmann, von Graefe and von Helmholtz, until Javal reconfirmed its existence?

H.J. Simonsz, Dept. of Ophthalmology, Erasmus Medical Center Rotterdam
N.J. Wade, Psychology, University of Dundee, Dundee

Abstract

After the rapid spread of strabismus surgery by total tenotomy which had been proposed by the orthopedist Louis Stromeyer from Göttingen in 1838 and performed by the plastic surgeon Johann Friedrich Dieffenbach on October 26th and by the ophthalmologist Florent Cunier on October 29th, 1839, brilliant researchers studied the physiology of eye movements, resulting in the laws by Franciscus Cornelis Donders on pseudotorsion in tertiary positions of gaze and by Johann Benedict Listing that each eye position can be reached by rotation about an axis perpendicular to the primary and the new position gaze.

John Hunter had first described ocular counterrolling (OCR) with head tilt in 1786. The anatomist Alexander Friedrich von Hueck inferred from anatomical studies, however, OCR to be 28.6° OCR on head-tilt to right or left shoulder in 1838, based on the length of the tendon of the superior oblique muscle. Donders, Christian Georg Theodor Ruete, Albrecht von Graefe and Hermann von Helmholtz denied the existence of OCR for many years and thought that only pseudotorsion existed. Louis Emile Javal had myopia and astigmatism, and he re-established the existence of OCR in 1867 when he noticed that, on head tilt to either shoulder, the axis of astigmatism of his eyes no longer coincided with the axis of astigmatism of his glasses.

The occurrence of torsional eye movements had been entertained by anatomists on the basis of ~~extraocular muscle function. When it is contracted, it pulls the eye about its axis from the nose, and at the same time draws it forwards, and turns its Pupil downwards.... The action of this [second oblique] Muscle is to roll the Eye about its Axis from the Nose, and at the same time to draw it forwards, and direct its Pupil upwards.~~ However, experimental evidence of torsion was lacking until it was provided by John Hunter (1786) for static head tilt and by William Charles Wells (1794) for torsional nystagmus following body rotation. Ocular counterrolling (OCR) is a small torsional rotation of both eyes about the line of sight when the head is tilted towards the right or the left shoulder. OCR can be static, driven by the otoliths, comprising about 5° of torsional rotation of the eyes on head-tilt of around 40° towards either shoulder partly compensating for tilting the head with respect to gravity. For instance, a slow counterclockwise rotation of the eyes occurs when the head is tilted clockwise. OCR can also be dynamic, driven by the semicircular vestibular canals and image tilt, comprising a torsional optokinetic and vestibular nystagmus, for instance, a slow clockwise rotation while the head tilts counterclockwise - the eyes temporarily maintaining the torsional position of the environment to permit vision - interrupted by counterclockwise torsional jerks to catch up. The torsional jerks of the eyes can be easily seen when tilting the head of another person toward one of his shoulders. One should look closely at the blood vessels surrounding the cornea, or at the iris, while the head of the subject is tilted. Observing dynamic OCR of one's own eyes in a mirror is not possible, however, as the perception of the image is suppressed during the rapid phase of the torsional nystagmus. For static OCR, look at the position of the blood vessels relative to the orbital fissure and see whether their position is different on head-tilt to the right as compared to that to the left shoulder.

This is what Hunter saw more than two hundred years ago when he described OCR in 'The use of the oblique muscles', in a collections of papers called 'Observations on certain parts of the animal oeconomy' (1786): "Thus when we look at an object, and at the same time move our heads to either

shoulder, it is moving in the arch of a circle whose centre is the neck; and of course the eyes would have the same quantity of motion on this axis, if the oblique muscles did not fix them upon the object. When the head is moved towards the right-shoulder, the superior oblique muscle of the right-side acts and keeps the right-eye fixed on the object; and a similar effect is produced upon the left-eye by the action of its inferior oblique muscle: when the head moves in a contrary direction the other oblique muscles produce the same effect. This motion of the head may, however, be to a greater extent than can be counteracted by the action of the oblique muscles. Thus, for instance, while the head is on the left-shoulder, the eyes may be fixed upon an object, and continue looking at it while the head is moved to the right-shoulder, which sweep of the head produces a greater effect upon the eyeballs than can be counteracted by the action of the oblique muscles; and in this case we find that the oblique muscles let go the eye, so that it immediately returns into its natural situation in the orbit.”

His analysis was well ahead of time, for he not only appreciated the role of the oblique muscles in executing these eye movements, but inferred as well, that these torsional eye movements are necessary for maintaining vision while tilting the head (Nagel, 1871). To maintain vision, the eyes must be kept momentarily immobile with respect to the surroundings or object that is seen. This is obvious for horizontal and vertical eye movements, but it also applies to torsional eye movements.

That OCR does occur was subsequently shown by Wells (1794): “That the eye actually does roll upon its axis, is shewn by the following experiment: I placed a long thin rule parallel to the horizon, its edge being towards me, and gave it such a position, in other respects, that it was the only object intervening between my eyes and a bright sky. I afterwards fixed my eyes upon a mark in the middle of its edge, and having obtained in this way a long narrow luminous spectrum [afterimage], I turned myself, having my eyes pointed to a spot over my head, till I became giddy. I then stopped and directed my eyes to the middle of a perpendicular line drawn upon the wall of my chamber. A luminous line, the spectrum of the rule, now appeared upon the wall, crossing the real and perpendicular line at right angles, or nearly so. The two lines, however, did not for a moment preserve the same position with regard to each other, but continually moved round their common point of intersection, in such a manner that the extremities of the one alternately approached and receded from the extremities of the other... if we have made ourselves giddy while our eyes were directed to a point above us, the apparent motions do not continue nearly so long as if the giddiness had been produced while the head was erect, the body being turned the same number of times in both cases.... when we consider the mechanical resistance to the rolling of the eye upon its axis, and the feebleness of the oblique muscles, which alone can give it this motion, it is natural to expect that, when produced involuntarily, it should continue but for a very short time.” The afterimage technique introduced by Wells was to feature prominently in subsequent experiments on OCR.

The anatomist Alexander Friedrich von Hueck from Dorpat in Livonia (now Tartu in Estonia) described OCR (1838), but estimated the amplitude of torsional eye movement to be approximately 25° on head tilt to either shoulder: “Have a person standing upright fixate a vertically positioned object in front of him in the room, for example a door post, at a point the same level as the eyes, and observe meticulously the position of a horizontal small blood vessel in the conjunctiva comparing it with the position of the corresponding angle of the eye, for example outside next to the cornea of the right eye. Now let the observed person, while the point defined above remains fixated unalteredly, tilt the head towards the right shoulder, so that the right eye is now lower than the left eye (without turning the face sideways, or rotating the head too much, however) and one observes that the vessel defined previously moved upward, approaches the upper eyelid. When the head is now brought back into the upright position, the vessel resumes its previous position; when a person tilt the head on the other side, one sees that the vessel moves down and approaches the lower eyelid, resuming its previous position when putting the head upright. This is repeated every time when the head is tilted sideways, and every time to a similar amount; it occurs not only with straight horizontal direction of the visual axis, but also when the visual axis points towards the side, upward or downward; it occurs finally when looking with

one eye and when looking with both eyes. The phenomenon becomes very clear, when observing it in a mirror held before the eyes. When tilting the head quickly to and fro, it seems as if the eye remains fixed, and as if the head and the environment of the eye rotates about the eye, which actually then really is the case. Concerning the magnitude of this rotation, and believe that I can estimate that amount of head tilt at which the globe retains its original position, at which I saw the above-mentioned vessel to lay horizontally, at approximately 25 degrees amounting to 50 degrees for the entire rotation. When I tilt the head even more, the position of the globe changed only a little, and resumed its original position.”

Franciscus Cornelis Donders investigated these claims and denied the existence of OCR completely. How could Donders have been led astray? Firstly, he looked for the 25° that Hueck had supposedly found. Secondly, he did not see his own OCR when looking into a mirror. Thirdly, he had found pseudotorsion to occur in tertiary positions of gaze.

Donders had become interested in eye movements when he translated (1846) the 'Lehrbuch der Ophthalmologie' (1845) by Christian Georg Ruete, the founder of German ophthalmology (Fig. 2). Donders was a young doctor in the military in Utrecht, earned 800 guilders a year and did translation work to earn extra money. Donders started his article on eye muscle mechanics (1846) that later became Donders' Law by: “De werking en verrigting der oogspieren behoort tot die onderwerpen, welke door physiologen ten allen tijde met ijver en een zekere voorliefde zijn behandeld, en deze ijver vond in de voor eenige jaren zooveel gerucht makende operatiën tegen het scheelzien en de bijziendheid overvloedig voedsel.” (The action and effect of eye muscles is one of the subjects that have always been treated by physiologists with zeal and predilection, and this zeal has been nourished by the operations for strabismus and for myopia that caused so much uproar some years ago.)

Ruete (1845) had developed in Scharmbeck the first mechanical model of the eye and its muscles. He called it an 'ophthalmotrope'. Ruete also studied the rotation of his own eye about the visual axis. He was able to observe the rotation of his own eye about the visual axis by using an afterimage with the form of a + cross. A green afterimage was produced by looking at a red cross for a long time. He then looked at a screen in front of him to see whether the afterimage remained vertical when he looked right, left, up or down. Donders repeated these experiments and found that the afterimage tilted when he looked in tertiary positions of gaze, i.e. right-up, right-down, left-up or left-down, relative to the straight horizontal and vertical lines on the screen: He found that the amount of torsion depended upon the amount of elevation or depression and right or left gaze. In 1848 a German translation of Donders' article appeared which drew von Helmholtz' attention. He was very enthusiastic about Donders' discovery and proposed to call the definition of pseudotorsion 'Donders' law'. The reason for the tilt had not been recognized by Donders, however, it was von Helmholtz who explained the reason for its existence.

Pseudotorsion occurs in tertiary positions of gaze and is a mathematical consequence of globe rotation starting for a primary position. In tertiary positions of gaze, the vertical retinal meridian does not coincide with a vertical line in space, nor does the horizontal retina meridian coincide with a horizontal line in space. To illustrate this point: If the reader is sitting in front of one of the four walls of the room he is in, let him for a moment look at the left upper hand corner of this wall. The reader will perceive the left upper hand 90° corner of a wall in front of him as being larger than 90 deg. What, in this case, is horizontal and what is vertical? It is clear that the angle between the retinal horizontal and the vertical meridians is perceived as 90° at all times, no matter what the direction of gaze is. Hence, the retinal horizontal and vertical meridians cannot coincide with the left upper hand corner of the wall in front of us. The edges of the left upper hand corner are horizontal and vertical in space but, as the angle is perceived as larger than 90°, the rays of the angle cannot possibly coincide with horizontal and vertical retina meridians. In fact, both rays of the angle, projected on the retina, deviate with a small angle from the horizontal and vertical retinal meridian, one clockwise and one anti-clockwise. This small angle is called pseudotorsion and is defined by Donders' Law.

The only coordinate system for describing eye rotations that does not have these flaws is in terms of polar coordinates. In a polar coordinate system the position of the eye is determined by two angles: One angle defines the direction of eye movement out of the primary position and a second angle defines the angle of eye movement out of the primary position. In this coordinate system, all tertiary positions of gaze are reached by simple rotation about a single axis, perpendicular to the primary position and to the new position. This principle was first described by Johann Benedict Listing, a good friend of Ruete, who had collaborated with Ruete in studies on entoptic phenomena and cataract in Göttingen (1845; note that this reference does not contain Listing's Law).

Ruete (1853) therefore called this principle Listing's Law: "Aus der oben angegebenen normalen Stellung (Anfangsstellung, Primärstellung) des Auges wird das Auge in irgend eine andere, secundäre, durch die Cooperation der sechs Muskeln in der Weise versetzt, dass man sich diese Versetzung als das Resultat einer Drehung um eine bestimmte Drehungsaxe vorstellen kann, welche jederzeit, durch das Augencentrum gehend, auf der primären und secundären Richtung der optischen Axe zugleich senkrecht steht, so dass also jede secundäre Stellung des Auges zur primären in der Relation steht, vermöge welcher die auf die optische Axe projicirte Drehung wird. Diesem Princip zufolge lässt sich aus der bekannten Lage der drei auf je zwei antagonistische Muskeln bezüglichen Drehungsaxen für jede gegebene Secundärstellung des Auges der Wirkungsbetrag jedes Muskels, d.i. die Grösse seiner Verkürzung durch Rechnung bestimmen. Unter den vielfachen Consequenzen dieses Princip's verdient die hervorgehoben zu werden, dass nämlich das Auge beim Uebergange aus einer secundären Stellung in eine andere eine ihrer Grösse nach bestimmbare Drehung um seine optische Axe erfährt, welche nur in dem besonderen Fall null ist, wenn die drei Richtungen der optischen Axe in der primären und in den beiden secundären Stellungen in einer Ebene liegen." (In short, all secondary and tertiary positions of gaze can be reached by rotation about a single axis that is perpendicular to the primary position of gaze and to the new position of gaze... Among the many consequences of this principle, one needs particular emphasis, namely, that the eye will rotate about its optical axis in eye movements from one tertiary to another tertiary position of gaze, this rotation being zero only when the two tertiary positions of gaze and the primary position of gaze are all in a single plane.)

The Ophthalmic Collection of the former Netherlands Ophthalmic Hospital includes a copper model that illustrates this principle beautifully (Fig. 3). The name of the place of manufacture, Halle, is engraved in the model. Halle is near Leipzig, so it may have been Ruete or someone near Ruete who sent it to Donders. In Ruete's first ophthalmotrope (1845) the model eye was suspended in gimbals, i.e. the model eye rotated in a ring that itself could rotate about an axis that was perpendicular to the first axis, this method of suspension having been invented by Cardano in the sixteenth century. An improved version of his ophthalmotrope, presented by him in Leipzig in 1857, no longer employed suspension with gimbals (Fig. 4). The globe was simply pulled against a ring with screws by the 'muscles'.

Ruete did not employ a gimbal suspension in a second version of his ophthalmotrope (1857): this kind of globe suspension will not bring the eye in a tertiary position that complies with Listing's Law: Pseudotorsion occur in tertiary positions of gaze in accordance to Donders' Law. Ruete wrote that the ring with screws supporting the model eye represented the "fat pad behind the eye, the nutshell in which the eye was suspended", quite a modern concept for his time. Donders (1870 and 1876, Fig. 5) later presented his own ophthalmotrope to illustrate Donders' Law. In this model he used gimbal suspension on purpose, to make the pseudotorsion visible. This ophthalmotrope was equipped with a camera obscura, to obtain an image of, for instance, the left upper hand corner of the wall in front of us. This image was to be compared with the retinal meridians, which were represented by 4 copper bars surrounding the camera obscura.

What is the reason for one unique primary position, the starting point of eye rotation in Listing's Law or, in other words, why is there a primary position, from which all other eye positions can be reached by simple rotation about a single axis or, in other words, why is the primary position not in left upper

gaze, for instance? Von Helmholtz compared Listing's Law and the primary position being in approximate gaze ahead with the minimal energy condition in physics (1863). When the primary position is, approximately, the average position of the eye over the day, the least number of rotations are needed to rotate the eye. Most eye movements are directed radially from or to the primary position. During eye movement from one tertiary, left-down, for instance, to another tertiary position, right-down, for instance, Listing's law is fulfilled only if the rotation takes place about an axis that is tilted to Listing's plane by half the angle between the momentary eye position and primary position (von Helmholtz, 1863): hence an axis that changes during the eye movement.

The primary position was determined with afterimages (Ruete, 1853; Hering, 1868, p.74-83), it varied over time (von Helmholtz, 1867; Schubert, 1927), was in down-gaze during convergence (Donders, 1876) and varied with head position (Fischer, 1927).

In 1854, Fick first described a Cartesian coordinate system for eye position. In Fick's coordinate system, first the horizontal angle of a particular gaze position is described, and then the vertical angle (Figs. 6 and 7, middle left). It is an isoazimuth and isolatitude system, similar to the coordinate system used to designate a place on earth and similar to the system used in the Major Amblyoscope and Synoptometer.

Although the angles of the intersections of the latitude circles and the vertical meridians are all perceived by the observer as rectangular, the directions of the latitude circles and the vertical meridians will, nevertheless, not coincide with the horizontal and vertical meridians of the retina of the observer, they will both be tilted by the pseudotorsion described by Donders' Law (1846).

If this coordinate system is projected onto a screen in front of the observer (Fig. 7), it consists of vertical lines (projections of meridians) and horizontal hyperbolas (projections of latitude circles).

Von Helmholtz (1863, 1867) used the reverse of coordinate Fick's system: isolatitude horizontally and isoazimuth vertically (Figs. 6 and 7, top left). An equivalent of this coordinate system on earth would be to have the northpole in Columbia and the southpole in Indonesia. He argued that the trigonometric calculations were simpler when using this system, when vertical shifts in the reference point, the primary position, occurred.

The angles between the horizontal meridians and vertical latitude circles in the system of von Helmholtz are also perceived as rectangular by the observer at the center of the globe but, again, the directions of the horizontal and vertical lines do not coincide, in tertiary positions of gaze, with the horizontal or vertical meridian of the retina of the observer: They are now both tilted the other way.

In a coordinate system that is isoazimuth both ways (meridians both horizontally and vertically on the globe or, projected onto a screen, straight horizontal and vertical lines), the angles between the horizontal and vertical lines are perceived by the observer as larger than 90 deg (Figs. 6 and 7, bottom left). An example of the use of this coordinate system is the 'Tangentenskala', a frontoparallel screen with straight horizontal and vertical lines on it, introduced by Harms (1941).

Hess (1916) introduced a coordinate system with isolatitude horizontally and vertically (Figs. 6 and 7, top right) that became very popular as the 'Hess screen'. It is often used for measurements of the angle of strabismus in cases of eye muscle palsy. However, the angles between the horizontal and vertical lines of the Hess screen are perceived by the observer as smaller than 90 deg.

Von Helmholtz (1867) introduced the 'Directionskreise' (direction circles, Figs. 6 and 7, bottom right) representing true vertical and true horizontal for the eye in all directions of gaze. He found these using afterimage lines, horizontal and vertical on the retina. The direction circles are in between the isoazimuth and isolatitude coordinates. The direction circles consist of two families of circles (Fig. 8) having a common tangent, horizontal and vertical in the 'Occipitalpunkt' (occipital point), a point in space located behind the observer at a distance equal to the distance to the screen or the object of regard in front of the observer. As the common horizontal and vertical tangents intersect perpendicularly in the occipital point, all other intersections of any two members of the two families of

circles also intersect perpendicularly as the four tangents and the intersection of their two planes form two congruent triangles. A direction circle, as described by von Helmholtz, describes the eye movement that occurs when an observer strictly follows the direction of the vertical retinal meridian or the direction of the horizontal retinal meridian.

Ruete and Alfred Wilhelm Volkmann initially believed the description of OCR by Hueck in 1858 (von Graefe, 1854), but later denied its existence when pseudotorsion was described by Donders in 1846, and the amplitude of OCR claimed by Hueck was not found. Hence, Donders' denial of the existence of OCR (1848) was supported by von Graefe (1854) and von Helmholtz (1863), but all had to revoke later, including Donders (1875), when the existence of OCR was re-established by Louis Émile Javal in 1867. He noticed that on head-tilt, the axis of astigmatism of his eyes no longer coincided with the axis of astigmatism of his glasses. Skrebitzky was the guest of Donders in 1869, and Donders, doubting the view he had expressed earlier, asked him to reinvestigate the matter. Skrebitzky (1871) used afterimages to measure OCR, which method had been described by Ruete in 1846. He found 5° static OCR on a 45° head-tilt. Then Mulder, an assistant of Donders, was asked to study the matter and in 1875 a lengthy treatise on dynamic and static OCR appeared, together with a short article by Donders (1875), containing a description of Donders' law and a revocation of his earlier view on OCR.

OCR is accomplished by the concerted action of vertical rectus and oblique eye muscles. The superior rectus and superior oblique muscles of one eye, and the inferior rectus and inferior oblique muscles of the other eye contract, whereas their antagonists relax. This differential use of eye muscles, depending on head-tilt to either shoulder, has important consequences for patients with a palsy of the trochlear nerve that innervates the superior oblique eye muscle. A patient with a trochlear nerve palsy will prefer a head tilt that elicits OCR such that the paretic muscle is not needed. Then the angle of strabismus will be small and double vision absent. On head tilt towards the contralateral shoulder the angle of strabismus gets very large. This principle was formulated by Nagel (1871). Thirty years before the description of the head-tilt test by Hofmann and Bielschowsky in 1900, Nagel predicted the feasibility of such a diagnostic test that relied on OCR. He said: "Für die feinere Diagnostik der Augenmuskellähmungen wird die Prüfung der bei seitlicher Kopfneigung auftretenden Raddrehung eine willkommene Unterstützung und Vervollständigung sein und namentlich bei den der Analyse zuweilen grosse Schwierigkeiten bietenden kombinierten Augenmuskellähmungen wird sich vermutlich jene leicht auszuführende Prüfung als nützlich erweisen. Ist einer der die Raddrehung vermittelnden Muskeln funktionsunfähig, so wird an Stelle derselben eine leichte Ablenkung und ein sehr störendes Doppeltsehen eintreten müssen. Die Doppelbilder werden gegeneinander gedreht erscheinen, zugleich wird ein leichter Seiten- und Höhenabstand statthaben, da dem zweiten bei der Raddrehung beteiligten Muskei das Gegengewicht fehlt, welches die Wirkung auf die Richtung der Blicklinie annulliren sollte. Wahrscheinlich wird die Bewegungsstörung auch gross genug sein, um objectiv erkennbar zu sein."

For the diagnosis of a trochlear palsy, however, this test was first used in a patient by Baumeister (1874). It was elaborated in detail 26 years later by Hoffmann and Bielschowsky (1900). Baumeister was a lesser known pupil of Donders but also certainly brilliant. In the same supplement to the Annual Report of the Netherlands Ophthalmic Hospital from 1874 he also described the dependency of latent nystagmus upon the direction of gaze.

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LEGENDS

Fig. 1. The illustration from Hueck's: *Die Achsendrehung des Auges*. He studied the oblique muscle in geese and other animals.

Fig. 2. John Hunter, Alexander Friedrich von Hueck, Christian Georg Theodor Ruete, Johann Benedikt Listing (upper right), Franciscus Cornelis Donders and Louis Émile Javal.

Fig. 3. Ophthalmotrope from the Ophthalmologic Collection of the former Netherlands Ophthalmic Hospital in Utrecht, demonstrating Donders' and Listing's Laws. The primary position of gaze is at the left in the picture. The eye is represented by a small globe in the center of the model. Two wheels with spokes (representing the horizontal and vertical retina meridians) are mounted on the tips of an axis representing the direction of gaze. This axis can tilt about the oblique axis representing an axis in Listing's plane. At the front of the model (left in the picture) an arc representing a horizontal meridian, equivalent to a horizontal line on a flat screen, can be tilted upward: one can see that the horizontal retina meridian is tilted relative to the arc by Donders' pseudotorsion. At the back of the model, a vertical arc, representing a vertical meridian, equivalent to a vertical line on a flat screen, can be turned together with the second wheel with spokes: Donders' pseudotorsion is found in the opposite direction. The name of the place of manufacture, Halle, is engraved in the model. Halle is near Leipzig, so it may have been Ruete or someone near Ruete who sent it to Donders.

Fig. 4. Ruete's second ophthalmotrope. The eye is no longer suspended in gimbals like in Ruete's first ophthalmotrope, to comply with Listing's Law.

Fig. 5. Models to demonstrate and to quantify Donders' pseudotorsion. In this model Donders used gimbal suspension on purpose, to make the pseudotorsion visible. The version described by Donders in 1876 is shown here. The ophthalmotropes were equipped with a camera obscura, to obtain an image of, for instance, a screen with horizontal and vertical lines, to be compared with the retinal meridians, represented by 4 copper bars surrounding the camera obscura. The eye rotated in the inner ring, and the inner ring rotated in the outer ring of the gimbal suspension, the primary and secondary axes of rotation being perpendicular. The outer ring is in Listing's frontoparallel plane and it could rotate in its sleeve-like circular holder, so that the primary axis of rotation could tilt within Listing's plane. Hence, a tertiary position of gaze could be, incorrectly, reached by rotation about the primary horizontal and secondary vertical axes, resulting in pseudotorsion, or by tilting the primary axis of rotation in Listing's plane and subsequent rotation about the primary axis only, in compliance with Listing's Law.

Fig. 6 and 7. The six coordinate systems describing eye movements, depicted on a globe and (next page) their projections on a frontoparallel screen. The observer is at the center of the globe. In each figure, the direction of the horizontal and vertical meridian of the retina is represented by a bold cross. Upper left: the system used by von Helmholtz (1863, 1867) in his calculations: isolatitude horizontally and isoazimuth vertically. Middle left: the system used by Fick (1854), isoazimuth horizontally and isolatitude vertically, the coordinate system used on earth, in the Synoptometer and in the Major Amblyoscope. Lower left: the system used by Harms (1941), isoazimuth both horizontally and vertically. Upper right: the system used by Hess (1916), isolatitude both horizontally and vertically. Middle right: the polar coordinate system. Lower right: The 'direction circles' represent the true direction of the horizontal and vertical meridians of the retina in tertiary positions of gaze (von Helmholtz, 1867).

Fig. 8: A family of direction circles. The observer is at point O, looking in primary position at point A. All direction circles go through the occipital point A'. The occipital point is a point behind the observer, opposite to the primary position, at a distance equal to the distance to the screen or the object of regard in front of the observer. Here, one series of direction circles is shown with a common tangent through the occipital point. From Southall (1937).

Fig. 9: 3-D drawing of the eye movement that occurs when the direction of the vertical retinal meridian is strictly followed. A direction circle, described by von Helmholtz (1867) results. A is the primary position, A' is the occipital point and O is the observer. When the observer rotates his eye from Q to P following the vertical meridian of his retina, the path followed will be a direction circle with OG as axis of rotation. The horizontal and vertical retinal meridians are represented by the cross. From Southall (1937).

Fig. 1.

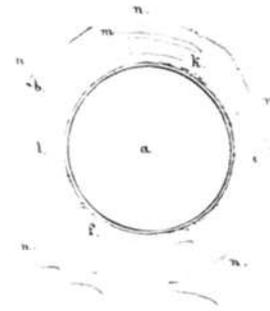
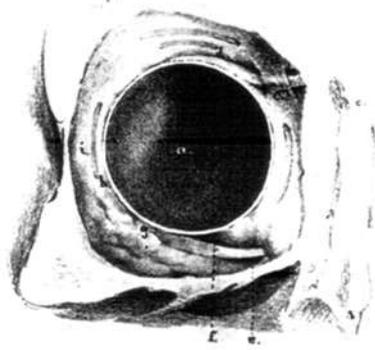
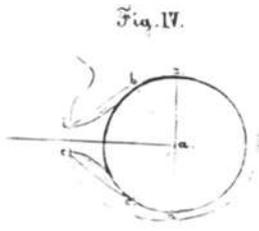


Fig. III.

