

Pioneers of eye movement research

Nicholas J Wade

School of Psychology, University of Dundee, Dundee DD1 4HN, UK; e-mail: n.j.wade@dundee.ac.uk

Received 15 May 2010, in revised form 6 September 2010; published online 5 November 2010

Abstract. Recent advances in the technology affording eye movement recordings carry the risk of neglecting past achievements. Without the assistance of this modern armoury, great strides were made in describing the ways the eyes move. For Aristotle the fundamental features of eye movements were binocular, and he described the combined functions of the eyes. This was later given support using simple procedures like placing a finger over the eyelid of the closed eye and culminated in Hering's law of equal innervation. However, the overriding concern in the 19th century was with eye position rather than eye movements. Appreciating discontinuities of eye movements arose from studies of vertigo. The characteristics of nystagmus were recorded before those of saccades and fixations. Eye movements during reading were described by Hering and by Lamare in 1879; both used similar techniques of listening to sounds made during contractions of the extraocular muscles. Photographic records of eye movements during reading were made by Dodge early in the 20th century, and this stimulated research using a wider array of patterns. In the mid-20th century attention shifted to the stability of the eyes during fixation, with the emphasis on involuntary movements. The contributions of pioneers from Aristotle to Yarbus are outlined.

Keywords: afterimages, binocular eye movements, nystagmus, torsion, saccades, fixations, ocular stability, reading, picture viewing

1 Introduction

Aspects of behaviour that are universal and automatic (like eye movements) seldom warrant description unless their normal functions are disrupted by disease or accident. Moreover, the behaviours rarely have a well-defined history. This has certainly been the case for the study of eye movements, as attention to them has not matched that for most other aspects of vision. For example, in his classic book on the history of research on the senses and perception, Boring (1942) devoted much more space to the vagaries of vision (like illusions) than to the verities of oculomotor behaviour. This is surprising because the history of eye movement research provides a delightful discourse between description and measurement, between the subjective reports of effects and their objective measurement. In addition, the study of eye movements has, perforce, addressed the integration of vision and action. This integration is not restricted to the functions served by eye movements, but to the clues that patterns of eye movements provide for examining visual and cognitive phenomena (see Carpenter 1988, 1991; Findlay and Gilchrist 2003; Land and Tatler 2009; Tatler 2009; Tatler and Wade 2003; Wade 2007; Wade and Tatler 2005; Wade et al 2003). Moreover, the descriptions of oculomotor behaviour are based on the sense that is observing its own actions: eyes observing eye movements. One of the intriguing aspects of the history we are about to examine is that subjective impressions of their motor aspects were often taken as evidence of their occurrence (or absence) rather than observing the eyes of others. Subjective impressions (feelings) of displacements in the orbit were used as an index of whether the eyes had moved, and this became particularly significant in the context of vertigo.

Contemporary accounts of eye movements tend to fall under two headings—gaze stability and gaze shift (see Leigh and Zee 2006; Walls 1962). These divisions represent the distillations of centuries of study during which the dynamic features of oculomotor behaviour were only dimly appreciated. Indeed, a particularly striking feature of the history presented here is that ocular directions rather than ocular dynamics were the principal concerns until the late

19th century. In this historical context, the development of descriptions and measurements will be arranged in terms of binocularity, torsion, visual vertigo, reading and scene viewing, and finally stability during fixation. These will be described after a brief comment on the anatomy of the system that moves the eyes—the extraocular muscles.

Pioneers of research on eye movement either described or measured them in novel ways. Some of the pioneers are shown in [figure 1](#), but others of great importance are not displayed either because no portraits of them have been found (like Lamare) or perhaps none exist (like Porterfield and Wells).

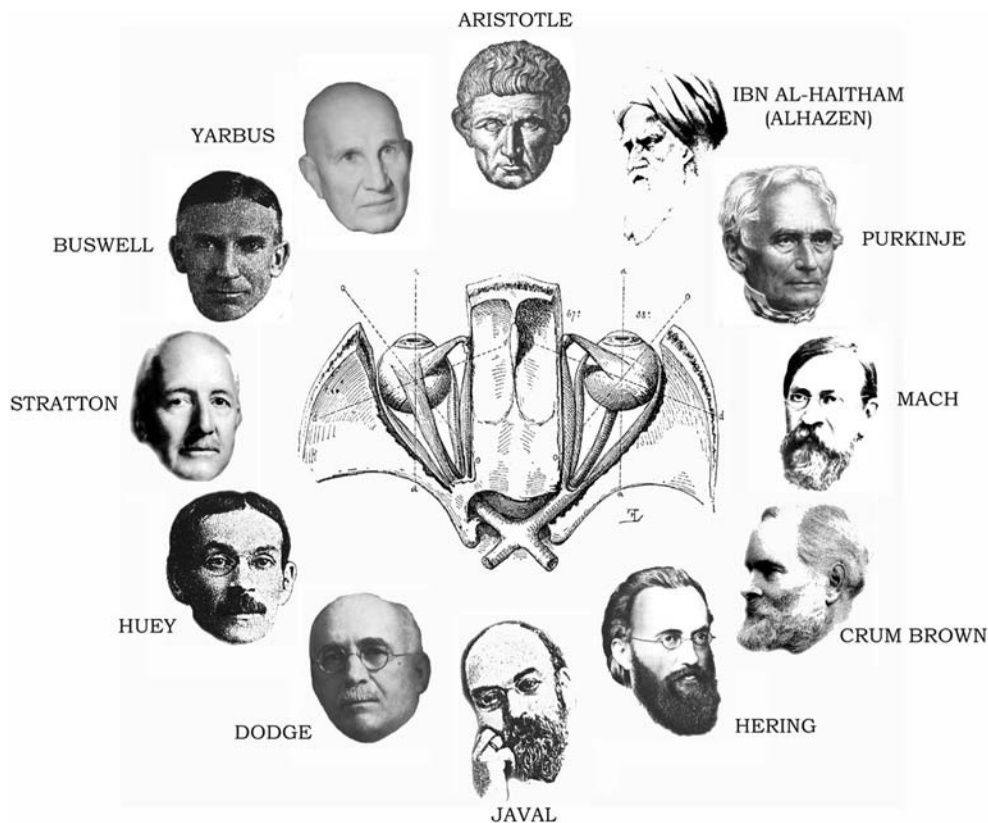


Figure 1. *Some pioneers of eye movement research.* They are arranged in a clockwise chronological sequence from Aristotle to Yarbus. The central diagram of the eyes and their musculature is from Landolt; it was published in 1879, the year in which Hering described the discontinuous movements of the eyes during reading (© Nicholas Wade).

2 Anatomy

The eyes move in order to locate objects of interest in the region of greatest visual resolution fovea. They are moved by muscles attached to the eyeball and the socket. The diagram at the centre of [figure 1](#) was taken from Landolt's (1879) *Manual of Examination of the Eyes*. The year in which it was published was important for discoveries about discontinuities of the eye movements, but not about ocular anatomy. The basic aspects of the extraocular musculature were known to Claudius Galen ([figure 2](#)) in the second century.

Misalignment of the eyes was recorded in antiquity, but its reported association with problems of binocular vision is more recent (see Duke-Elder and Wybar 1973; Hirschberg 1982; Maddox 1907; Shastid 1917; van Noorden 1996). The eye specialists in ancient Babylonia, Mesopotamia, and Egypt must have had a working knowledge of ocular anatomy in order to carry out the operations they are known to have performed; these were mostly on

cataracts. The records that have survived [such as the Ebers papyrus (see Hirschberg 1982)] relate mainly to the fees they charged and the penalties they suffered for faulty operations rather than the conditions they cured. Their skills and understanding would have been passed on to Greek physicians, who both developed and recorded them. Many Greek texts, through their translations, have been transmitted to us, but any illustrations that they might have included have not survived in their original form.

Galen was aware not only of the musculature, but also the rotations of the eye that they effected: “Well then, since there are four movements of the eyes, one directing them in toward the nose, another out toward the small corner, one raising them up toward the brows, and another drawing them down toward the cheeks, it was reasonable that the same number of muscles should be formed to control the movements” (May 1968, page 483). Similarly, Galen had described the oblique muscles that could produce eye rolling or ocular torsion: “Since it was better that the eye should also rotate, Nature made two other muscles that are placed obliquely, one at each eyelid, extending from above and below toward the small corner of the eye, so that by means of them we turn and roll our eyes just as readily in every direction” (May 1968, page 483). Thus, the three axes around which the eye can rotate were clearly described, but the emphasis was on the direction the eye would take following a rotation rather than on the rotations themselves. Despite the clear statement about torsion, evidence of it was to wait many centuries. The problem related to reconciling the anatomy of the eye muscles with the difficulty of observing small rotations of the eye around the optic axis. Torsion was contentious because it was difficult to detect, unlike misalignments of the eyes which have been commented on for many centuries. Deviations of the two eyes, like those that occur with squint or strabismus, are easy to detect, and it is this aspect of ocular direction that was reported upon at an early stage.

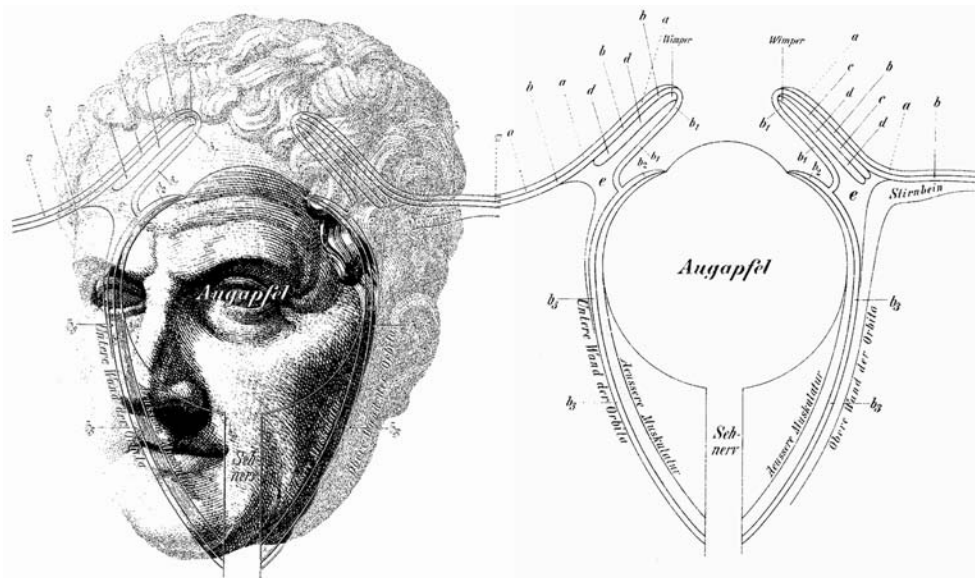


Figure 2. *Galen's eye.* The portrait of Claudius Galen (ca 130–200) was derived from an engraving in Pettigrew (1840a). The diagram of the eye (from Magnus 1901) was based on a description given by Galen, who provided details of the six extraocular muscles and their functions (© Nicholas Wade).

Most of Galen's dissections were on rhesus monkey (Singer 1956), although the results were subsequently adopted as applying to humans. Galen's anatomy informed science and medicine for well over 1000 years, largely due to the restrictions that were subsequently placed on dissections. It resulted in a reliance on his works on anatomy, which were recounted dogmatically until the time of Andreas Vesalius (1543). Greek anatomical wisdom

was retained by Islamic scholars, who translated many books into Arabic and eventually transmitted them to late mediaeval students (O’Leary 1949). Galen’s medical works were translated into Arabic by Hunain ibn Is-hâq (ca 807–877). The earliest surviving diagrams of the eye are to be found in Islamic manuscripts (see Meyerhof 1928; Polyak 1942, 1957), of which that by Hunain ibn Is-hâq is probably the oldest. It is essentially a functional diagram, since it adopts different viewpoints for different parts of the eye. This could be the reason why the pupil and the lens are shown in circular form, and the lens is situated in the middle of the eye. The extraocular muscles are also shown extended from the eyeball. The illustration was copied several times in the centuries that followed. Thus, Arabic accounts of the eye drew on Galen for inspiration, but their illustrations reflect a greater concern with geometry than with anatomy.

Representations of the extraocular muscles became more refined in medical texts, particularly after the gross anatomy of the eye was accurately drawn by Christoph Scheiner (1571–1650) in 1619. Distinctions were made between the internal and external musculature, although more attention was paid to the operation of the former in accommodation, than the latter in scene scanning. The Scottish physician, William Porterfield (ca 1696–1771), not only distinguished between these (introducing the term ‘accommodation’ in the process) but also displayed some appreciation of the dynamic aspects of eye movements:

The Motions of the Eye are either external or internal. I call *external*, those Motions performed by its four straight and two oblique Muscles, whereby the whole Globe of the Eye changes its Situation or Direction. And by its *internal* Motions, I understand those Motions which only happen to some of its internal Parts, such as the *crystalline* and *Iris*, or to the whole Eye, when it changes its spherical Figure, and becomes oblong or flat.... Now, though it is certain that only a very small Part of any Object can at once be clearly and distinctly seen, namely, that whose Image on the Retina is in the *Axis* of the Eye; and that the other Parts of the Object, which have their Images painted at some Distance from this same *Axis*, are but faintly and obscurely perceived, and yet we are seldom sensible of this Defect; and, in viewing any large Body, we are ready to imagine that we see at the same time all its Parts equally distinct and clear: But this is a vulgar Error, and we are led into it from the quick and almost continual Motion of the Eye, whereby it is successively directed towards all the Parts of the Object in an Instant of Time; for it is certain, that the Ideas of Objects, which we receive by Sight, do not presently perish, but are of a lasting Nature.... And this is the Reason why the Globe of the Eye moves so quickly, and that its Muscles have such a Quantity of Nerves to perform their Motions (Porterfield 1737, pages 160, 186–187).

It is the external motions that will be considered here, first in terms of eye position and then with regard to dynamic eye movements. It took many years before solutions to the “vulgar Error” of complete scene visibility were either entertained or given empirical support.

3 Binocular eye movements

One of the most distinctive features of eye movements is related to their binocularity—they tend to move together. Such conjoint motion is not always in the same direction, as was noted by Aristotle (figure 3a) more than 2000 years ago. He distinguished between version (movements in the same direction) and convergence eye movements. He also commented that there were certain movements that were not possible, namely, divergence beyond the straight ahead, and movements of one eye upward and the other downward. This reflected Aristotle’s belief that the two eyes operated as a unit rather than independently:

Why is it that we can turn the gaze of both eyes simultaneously towards the right and the left and in the direction of the nose, and that of one eye to the left or to the right, but cannot direct them simultaneously one to the right and the other to the left? Similarly, we can direct them downwards and upwards; for we can turn them simultaneously in the same direction, but not separately. Is it because the eyes, though two, are connected at one point, and under

one eye should move for the purpose of seeing while the other remains motionless, nor that one eye should strain to look at an object without the other straining to look at the same object, unless some obstacle or cover or some other accident intervened, thus hindering one of the eyes from participating in the act performed by the other. When both eyes are observed as they perceive visible objects, and their actions and movements are examined, their respective actions and movements will be found to be always identical (Sabra 1989, page 229).

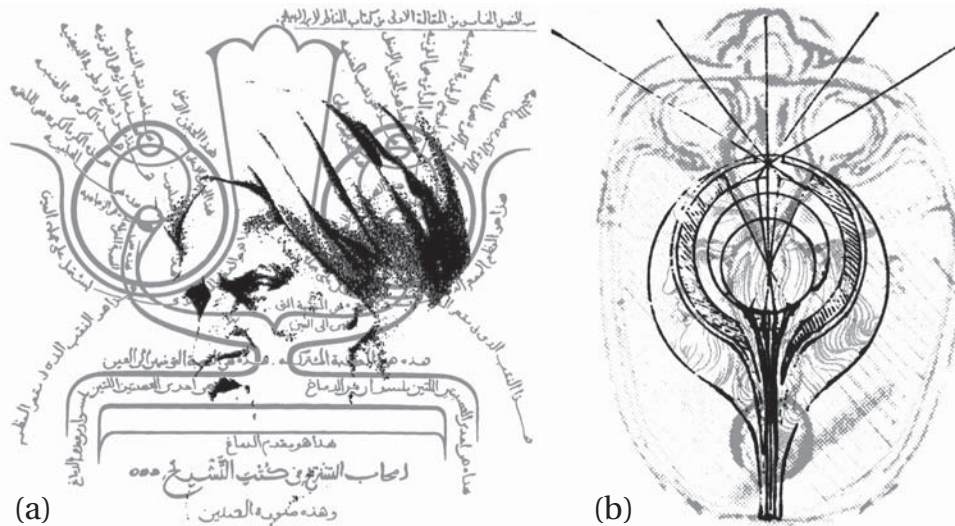


Figure 4. (a) *Binocular visionary*. All portraits of Ibn al-Haytham or Alhazen (ca 965–1039) are fanciful; this one is after an illustration in Duke-Elder and Abrams (1970), and the diagram of the eyes and visual pathways is from Polyak (1942). (b) *Leonardo's eye and brain*. The portrait of Leonardo da Vinci (1472–1519) is after an 1808 engraving in The Historic Gallery of Portraits and Paintings, and it is enclosed within his diagram of the eye (from McMurrich 1930); both are shown within a copy of his drawing of the visual pathways leading to the ventricles (MacCurdy 1938) (© Nicholas Wade).

Here we find one of the earliest indications that the actions of the eyes can be examined by observation rather than by introspection, although it was many centuries before it was put into practice. Theory rather than observation drove many of the interpretations. Galen believed that the origin of the visual pathways was located in the anterior ventricle of the brain, where the animal spirit could interact with the visual spirit, borne by the optic nerves. The optic nerves themselves came together at the optic chiasm, but each of the nerves remained on its own side. Three ventricles were enumerated in Galenic anatomy, and they were incorporated into late medieval philosophy as representing the sites of perception, reasoning, and memory (see Weisheipl 1980). The prevalence of this notion is evident in Leonardo da Vinci's analysis of binocular eye movements and his drawings of the visual pathways: the optic nerves lead directly into the first of the three ventricles (figure 4b). He wrote: "Saw a head in two between the eyebrows in order to find out by anatomy the cause of equal movements of the eyes, and this practically confirms that the cause is the intersection of the optic nerves" (MacCurdy 1938, page 186). Since the visual spirit was thought to pass from the ventricle to the eyes, it was generally believed that monocular vision was superior to binocular. This was because the visual spirit was then channelled to one eye rather than two. The common locus of the chiasm was also a factor in the interpretation of coordinated binocular eye movements, as is evident from the statement by Francis Bacon (figure 5a): "The eyes do move one and the same way; for when one eye moveth to the nostril, the other moveth from the nostril. The cause is motion of consent, which in the spirits and parts spiritual is strong" (Bacon 1857, page 628).

A more mechanistic interpretation was adopted by Robert Smith (figure 5b), a mathematician at Trinity College, Cambridge. In the context of eye movements Smith described a simple procedure for verifying the conjoint movements of the eyes. He was also able to relate eye positions to stimulation of corresponding retinal points and diplopia:

The habit of directing the optick axes to the point in view is so strong that it is very difficult to do otherwise; insomuch as when one eye is shut and the other is in motion one may feel by ones fingers laid upon the eye-lid, that the eye which is shut, always follows the motions of the eye that is open. But if by squinting or by depressing an eye with ones finger, the optick axes are not directed to the same point; in these cases objects appear double: now it is plain that their pictures are not painted upon corresponding places of the retinas (Smith 1738, pages 46–47).

Smith integrated several strands of interest in binocular vision: singleness of vision with two eyes was considered to be a consequence of stimulating corresponding points on the two retinas. First, distinct vision was restricted to the central region of the retina; secondly, both eyes moved in unison to retain correspondence; thirdly, this could be demonstrated by feeling the movements of the closed eye; and, finally, double vision occurs when one eye is moved out of alignment with the other. Such squinting can be induced artificially (by displacing one open eye with the finger), and it also occurs naturally.

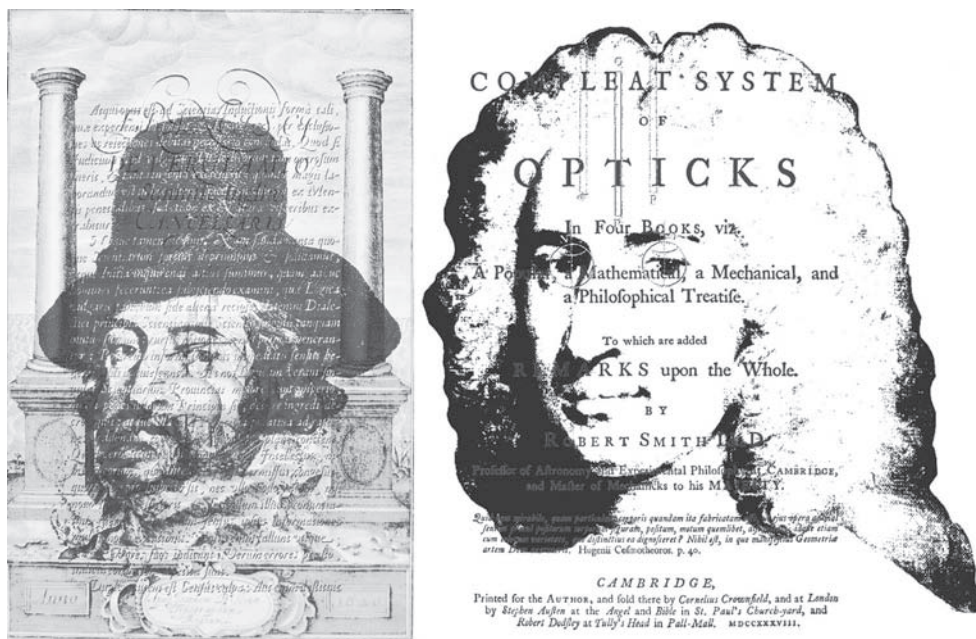


Figure 5. (a) *Bacon's Organum*. The portrait of Francis Bacon (1561–1626) is derived from an engraving in Knight (1837); he is depicted in text from the *Instauratio Magna* as well as its title page. It was part of the *Novum Organum*, the new instrument that was to replace Aristotle's *Organon*. The text describes the essentials of inductive science, and it cautions against placing too great a reliance on the senses because of the two fallacies to which they are prone: they either fail or they deceive. (b) *Smith's Opticks*. Robert Smith (1689–1768) was an ardent advocate of Newtonian optics; his portrait is accompanied by the title page of his *Opticks* (Smith 1738) as well as a diagram of the ruler illusion, seen when using two eyes (© Nicholas Wade).

By the time William Charles Wells (1757–1817), who was born in America but practised medicine in London, was writing about binocular visual direction, the conjoint motions of the eyes were an accepted fact. Moreover, he was able to support the statements with experiments using afterimages. The main point at issue was whether they were learned or innate:

The thing itself is universally acknowledged, though a dispute has arisen whether custom or an original property be the cause, that every voluntary motion of one eye, in persons who do not squint, is attended with a corresponding motion in the other. Now as all voluntary motions are produced by muscular action, it follows, that every state of action, in the muscles of one eye, has its corresponding state in those of the other, and that the two are constantly conjoined. When, therefore, the spot [afterimage] appears single to both eyes in their free positions, the states of action in the muscles must be such, that the direction, in which it is seen by one eye, coincides with that in which it is seen from its place, no change is hereby made in the action of its muscles; for the state of action in those of the free eye is confessedly the same as it was; and it will be attended with a corresponding state in those of the distorted eye; in proof of which it may be observed, that, whenever the pressure is removed, the distorted eye immediately returns to its former position, without the aid of any new muscular effort. The conclusion then is, that, since there has been no alteration in the action of its muscles, neither ought there to be any in the direction of the spot seen by it, which is the fact to be explained (Wells 1792, pages 71–72).

Wells introduced the use of afterimages and their apparent motion or stability as an index of whether the eyes had moved due to voluntary or involuntary muscular activity. This introduced another aspect to the study of eye movements, and it was taken up by Charles Bell (figure 6), both in terms of conjoint motion and the distinction between the consequences of voluntary and involuntary eye movements. With regard to the former he stated:

We can distort our eyes by an unnatural effort, but we cannot squint: that is to say, we can bring our eyes into such a forced situation that we cannot see anything distinctly; but we cannot keep one eye distinctly upon an object and turn the other from it. . . . This shows the strict correspondence betwixt the moving muscles of the eyeball. . . . Why should it be more difficult for a squinting person to learn to look straight when he pleases? The reason of the greater difficulty is obvious, that in making the eyes converge or diverge the will is acting upon both eyes equally; but to distort one eye inward or outward, and at the same time to keep the other fixed, is to me an absolute impossibility (Bell 1803, pages 359–360).

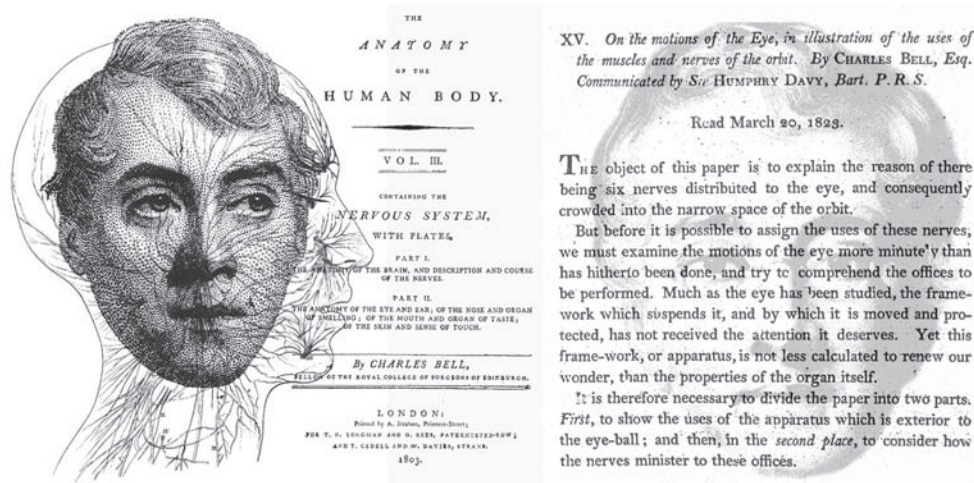


Figure 6. (a) *Bell's Anatomy*. Charles Bell (1774–1842) [after a frontispiece engraving in G Bell (1870)] is portrayed at the time when he moved from Edinburgh to London (about 1804); he is enclosed within his diagram of nerves of the head (from Bell 1844) and accompanied by the title page of his *Anatomy*, the other volumes of which were written by his brother, John Bell. (b) *The motions of Bell's eyes*. An older Bell (from Pettigrew 1840b) is shown with the first page of his article on eye movements in which he described experiments using afterimages and displacing the eye passively or actively (© Nicholas Wade).

Bell (1823) further developed the contrast between voluntary and involuntary eye movements by recourse to experiments like those performed by Wells (1792), without mentioning the latter:

there is an inseparable connection between the exercise of the sense of vision and the exercise of the voluntary muscles of the eye. When an object is seen, we enjoy two senses; there is an impression upon the retina; but we receive also the idea of position or relation which it is not the office of the retina to give. It is by the consciousness of the degree of effort put upon the voluntary muscles, that we know the relative position of an object to ourselves.... If we move the eye by the voluntary muscles, while the impression [of an afterimage] continues on the retina, we shall have the notion of place or relation raised in the mind; but if the motion of the eye-ball be produced by any other cause, by the involuntary muscles, or by pressure from without, we shall have no corresponding change of sensation (Bell 1823, pages 178–179).

Statements like those above regarding binocular eye movements were frequently repeated throughout the 19th century, but they were given more empirical support. Indeed, the origins of eye movement research were considered by some to belong to this period. Boring (1942) suggested that the monograph by Johannes Müller (figure 7), published in 1826, marked the onset of systematic studies. Carmichael (1926), meanwhile, argued that the article by Bell in 1823 was a more appropriate starting point. A stronger case can be made for crediting Wells (1792) with having conducted the first systematic studies of eye movements (see Tatler and Wade 2003; Wade and Tatler 2005).

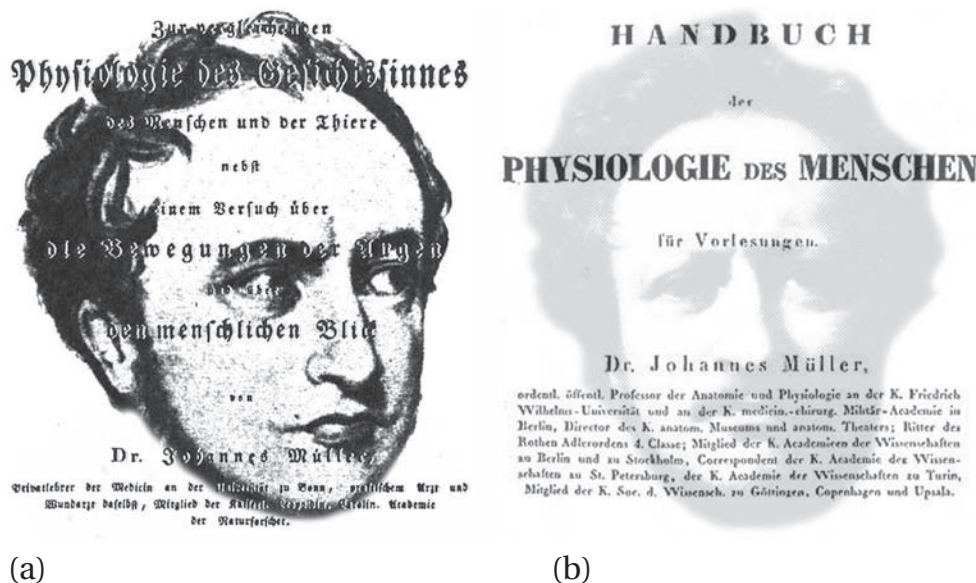


Figure 7. (a) *Müller's vision*. The portrait of Johannes Müller (1801–58) is derived from an illustration in Hirsch (1929); his book on the physiology of vision and movements of the eyes was concerned almost entirely with their binocular coordination. (b) *Müller's physiology*. Müller [after a lithograph in Stirling (1902)] is shown with the title page of his influential book on human physiology. In it he elaborated the doctrine of specific nerve energies as well as describing binocular eye movements (© Nicholas Wade).

Müller, who was to become professor of physiology in Berlin, published two books on vision in 1826: one (Müller 1826a) was on comparative physiology, in which he gave detailed descriptions of eye position following eye movements; the title page is shown in figure 7a. The other (Müller 1826b) was on subjective visual phenomena. A decade later, Müller provided a more extensive survey of vision in his *Handbuch der Physiologie des Menschen*; this book was translated into English as *Elements of Physiology* (Müller 1840, 1843). He was concerned with

relating binocular eye movements to binocular single vision and to the breakdown of the latter in squinting or strabismus:

Some of the most remarkable facts illustrating the association and antagonism of muscular actions are presented by the muscles which move the eyes. The corresponding branches of the third or motor oculi nerve of the two sides have a remarkable innate tendency to consensual action, a tendency which cannot be ascribed to habit. The two eyes, whether moved upwards, downwards, or inwards, must always move together; it is quite impossible to direct one eye upwards and the other downwards at the same time. This tendency to consensual motion is evidenced even from the time of birth (Müller 1843, pages 928–929).

Hermann Helmholtz (figure 8a) was one of Müller's students, and he also wrote extensively on eye movements. Indeed, this was the topic of his Croonian Lecture to the Royal Society in 1864 in which he wrote: "We cannot turn one eye up, the other down; we cannot move both eyes at the same time to the outer angle" (Helmholtz 1864, page 192). The difference between Aristotle and Helmholtz was that the latter could support the statement by experiment using afterimages. Helmholtz was to return to Berlin after positions in the universities of Königsberg (now Kaliningrad), Bonn, and Heidelberg. Eye movements proved to be one of the battle grounds between him and Ewald Hering (figure 8b), who made similar, but more subtle, statements about binocular eye movements (see Turner 1994), and these are now referred to as Hering's law of equal innervation:

The two eyes are so related to one another that one cannot move independently of the other: rather, the musculature of both eyes reacts simultaneously to one and the same impulse of the will. . . . It is possible for us to move both eyes simultaneously about different angles and with different speeds. . . and even to move one eye outward and inward while the other remains still. We are able to do this, not because we simultaneously give each eye a special innervation, but because in these movements each eye receives two different innervations. One is a turning movement of both eyes to the right or left and the other is inward or outward turning of both eyes. Since these two innervations of the two eyes work together in one eye and conversely in the other, the resultant movement in each eye must necessarily be different (Hering 1977, page 17).

Hering was a very productive and ingenious physiologist (see Baumann 2002) who worked in Leipzig, then Vienna, and finally in Prague. For him the two eyes moved as a single unit, and this union was not dependent upon learning or association, as Helmholtz maintained. Hering stated this point repeatedly, and he referred to the yoked actions of the two sets of eye muscles. His diagrams reflected this, too; the motions of each eye were referred to those of an imaginary eye between them. In the context of visual direction, the locus from which objects are seen was called the cyclopean eye. For binocular eye movements he referred to the directions relative to this 'imaginary single eye' as the binocular visual line. Fixations occur between movements of the eyes, and Hering showed a clear understanding of the functions that such movements served—that is, his concerns were not only with where the eye alights but with how it reaches that point. Technical constraints tended to restrict experimental studies to determining the orientation of the eye rather than how it moved.

One of the great advantages that both Helmholtz and Hering bestowed on eye movement research was the introduction of bite bars for controlling head position. A remarkable feature of experimental work in the 19th century was the reliance on data from a single observer. Helmholtz himself epitomised this tendency. In common with his contemporaries, he considered the processes of perception to be universal so that general principles could be derived from particular observations. Much of the polemic surrounding the heated debates in 19th-century visual science was based on the conviction that personal perception was pervasive; individual differences were only taken seriously in areas like colour blindness. Novel observations were accepted as fact when they were in turn seen by another investigator.

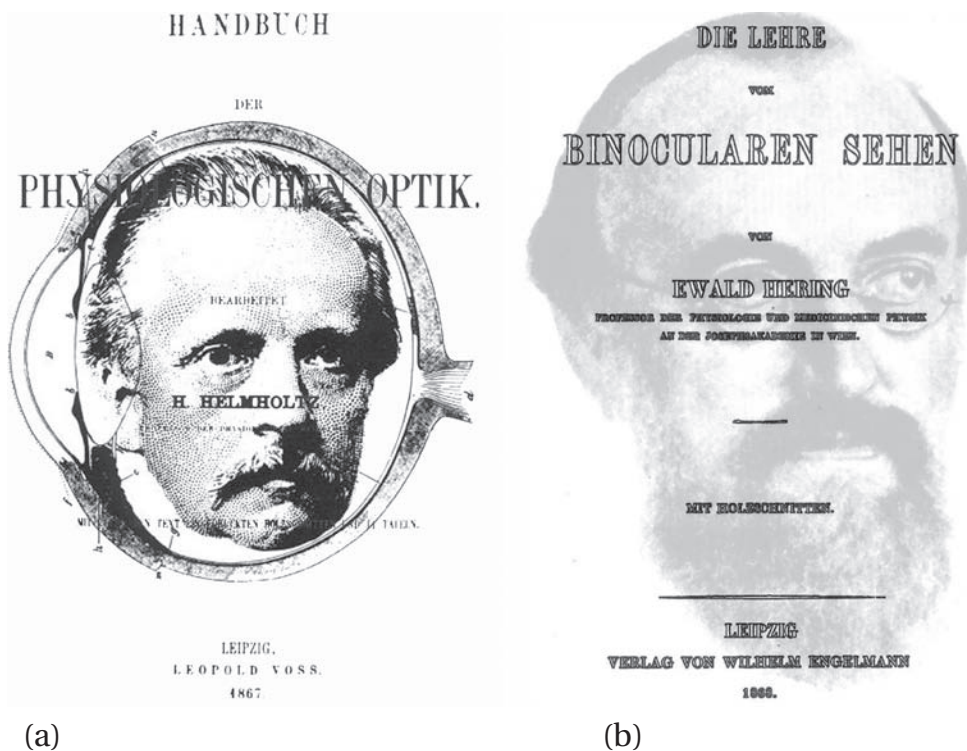


Figure 8. (a) *Helmholtz's Handbuch* (1867). The portrait of Hermann Helmholtz (1821–94) is after an engraving in Koenigsberger (1902); the diagram of the eye is from the *Handbuch*, the title page of which is also shown. (b) *Hering's Binocular Vision*. Ewald Hering (1834–1918) is shown with the title page of his book on binocular vision in which the principle of equal innervation was enunciated (© Nicholas Wade).

Helmholtz was at his most vulnerable when his observational skills were impugned (see Howard 1999). He set great store by his control of fixation and by his ability to assess his eye position with accuracy.

4 Torsion

In the mid-19th-century ocular torsion assumed considerable theoretical importance. Concern with the geometry of eye rotations and with the specification of their constraints led to the formulations of laws that could only be verified by means of measuring its magnitude. Although many were involved in this endeavour, the work was summarised and integrated by Helmholtz and Hering. A number of preliminary issues required resolving before the geometry of eye movements could be described with accuracy. The first concerned the centre of rotation of the eye. Despite the fact that small translations of the eye occurred, the centre of rotation was determined to be 13.6 mm behind the vertex of the cornea (Helmholtz 1867). The orbit of the eye can take a variety of locations as the head moves, and so a further question related to the position the head should adopt for experiments on eye movements. Helmholtz defined the planes of the head with regard to the symmetry between the two sides and the line joining the two eyes. The former was called the median plane, and the latter the transverse plane. The head was said to be upright when the median plane was vertical, and the transverse plane horizontal.

With the head in this erect position some reference position for the eyes was required as was some system of coordinates relative to which rotations could be described. The adoption of fixed axes around which the eye can rotate is arbitrary. Helmholtz described two systems: the Fick axis system in which the vertical axis is assumed to be fixed to the skull

and the Helmholtz system in which the horizontal axis is so fixed. When the eye moves from the primary position along a horizontal or a vertical axis, it assumes a secondary position; movements to any other (oblique) location involve the eye in a tertiary position.

One of the principal problems that Helmholtz and Hering addressed was the orientation of the eyes when they moved from the primary position. This was defined as the position of the eyes when they are horizontal and perpendicular to the axis between their centres of rotation (the interocular axis). The technique used for determining eye orientation was to generate a linear afterimage when the eye was in the primary position and match it with a real image in another direction. Helmholtz considered that the method had been introduced by Ruete (figure 9b) in 1845, whereas in fact it had been applied to dynamic torsional eye movements by Wells (1794a). Helmholtz remarked:

The best way of verifying these facts is by using after-images, as was originally suggested by Ruete. The way to do it is to stand opposite a wall covered with paper on which horizontal and vertical lines can be distinguished, the pattern, however, not being so sharply outlined as to make it difficult to see after-images on it. The best background is one of a smooth pale grey colour. Directly opposite the observer's eye, and on the same level with it, a black or coloured ribbon is stretched horizontally, two or three feet long; standing out in sharp contrast to the colour of the wall-paper.... Now let the observer look intently for a little while at the middle of the band, and then, without moving his head, turn his eyes suddenly to another place on the wall. An after-image of the band will appear there, and by comparing it with the horizontal lines of the wall-paper, the observer can see whether the after-image is horizontal or not. The after-image itself is developed on those points of the retina belonging to the retinal horizon; and during the motions of the eyes it indicates those parts of the visual field on which the retinal horizon is projected (Helmholtz 1925, page 45).

Frans Cornelis Donders (figure 9a) used this technique to measure the eye orientation in secondary and tertiary locations and provided a general relationship that Helmholtz (1867) elevated to the status of a law:

The law, given first by Donders and confirmed by all subsequent investigations, is that when the position of the line of fixation is given with respect to the head, the angle of torsion will invariably have a perfectly definite value for that particular adjustment; which is independent not only of the volition of the observer but of the way in which the line of fixation arrived in the position in question (Helmholtz 1925, page 44).

Thus, no matter what path the eye pursues to reach a given position, the degree of torsion will be the same.

Donders' law was formulated for movements of the eye from the primary position. Another lawful relationship was formulated by Johann Benedict Listing (1808–82), a mathematician who studied under Gauss at Göttingen. Whereas Donders' law stated that the eye always assumed the same orientation at a particular location, no matter how it had been reached, Listing's law specified the orientation that was adopted in a particular position. Listing did not publish an account of it himself but it was initially described in Ruete's (1853) book on ophthalmology. Again it was Helmholtz who named it Listing's Law; it was concerned with describing the axis about which the eye rotates from the primary position. Helmholtz described it in the following way:

Accordingly, for the case of a pair of emmetropic eyes with parallel lines of fixation, the law of their motion may be stated as follows: *When the line of fixation is brought from its primary position into any other position, the torsional rotation of the eyeball in this second position will be the same as if the eye had been turned around a fixed axis perpendicular to the initial and final directions of the line of fixation.* This is known as Listing's law of ocular movements, because it was first stated by him in this form (Helmholtz 1925, page 48, emphasis in original).

Both Donders's and Listing's laws apply for eye movements from the primary position, that is, with the eyes parallel and directed to the horizon. Empirical studies generally supported

the laws, and Helmholtz reported that eye rotations could be measured to within half a degree using the afterimage method. However, most eye movements are directed to objects that are nearer than optical infinity and so will involve some degree of convergence. Alfred Wilhelm Volkmann (1846) demonstrated that departures from the laws occur with convergence.

Maar is dan ten opzichte der psychische processen iedere quantitative behandeling uitgesloten? Geenszins! Een gewichtige factor scheen voor meting vatbaar: ik bedoel den tijd, die tot eenvoudige psychische processen wordt gevorderd. Voor de beslissing der vraag, of wij recht hebben, het in 't algemeen bewezen verband voor bijzondere gevallen toe te passen, met andere woorden, of we mogen aannemen, dat aan de verscheidenheid van ieder bijzonder gevoel, van iedere bijzondere voorstelling, van iedere uiting van den wil eene absoluut corresponderende verscheidenheid in de werking der hersenen is verbonden, schijnt de bepaling van dien tijd niet zonder gewicht. Sedert langen tijd stelde ik mij voor, daartoe pogingen te doen. In de zitting der Koninklijke Academie van wetenschappen van 24 Junij 1865 gaf ik een overzicht der eerste, onder medewerking van den Heer de Jaager en van eenige andere leerlingen der Utrechtsche Hoogeschool, dienangaande verkregen uitkomsten, die daarop uitvoeriger werden medegedeeld in de dissertatie van den Heer de Jaager over den *physiologischen tijd der psychische processen*. Met dienverstand tot deze proeven, zoo als trouwens de voorrede vermeldt, was van mij uitgegaan, de gevolgde methoden waren door mij aan de hand gegeven, en die proeven werden in het *physiologisch laboratorium* verricht en door mij bevestigd. Omstreeks dienzelfden tijd gaf ik, met aanwijzing der methoden, een overzicht der verkregen uitkomsten in eenige populairere voordrachten, te Utrecht en elders gehouden.



(a)

(b)

Figure 9. (a) *Donders's See*. Frans Cornelis Donders (1818–89) is best known in psychology for his work on reaction time and the text (from Donders 1869) in which his face is embedded describes this. He was an ophthalmologist who worked in Utrecht and wrote on accommodation as well as eye movements. (b) *Ruete's ophthalmotrope*. Christian Ruete (1810–67) was professor of ophthalmology first at Göttingen then at Leipzig. He employed afterimages to measure eye orientation and made a modified model of Helmholtz's ophthalmoscope. He is shown with his ophthalmotrope, as illustrated in Helmholtz (1867) (© Nicholas Wade).

The formulation of Donders' and Listing's laws enabled intricate instruments to be made that indicated the orientations of the eyes in various gaze directions. Ruete (figure 9b) made one such, called an ophthalmotrope, and Wilhelm Wundt (1862) produced a more complex model. Both displayed the understanding that had been achieved about the manner in which eye position was determined and also of the combined operation of the paired eye muscles. They were of considerable use in examining the pathology of eye movements and they emphasised the united activities of the two eyes. In addition, the ophthalmotropes indicated the importance that was placed on eye position following eye movements rather than the characteristics of the eye movements themselves.

Torsion was easier to observe as a consequence of inclining the head, and it is in this context that Scheiner (1619) hinted at its occurrence: "in an eye movement in which the middle part of the eye remains stationary, it is because it moves by a corresponding head rotation" (page 245). A more precise description was provided by John Hunter (1786), who outlined the function that the oblique muscles could serve; when the head was tilted to one side, they could rotate the eyes in their sockets in the opposite direction:

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 the inferior oblique muscle; when the head moves in the contrary direction, the other oblique muscles produce the same effect (Hunter 1786, page 212).

Bell (1823) argued on the grounds of anatomy and experiment “that the oblique muscles are antagonists to each other, and that they roll the eye in opposite directions, the superior oblique directing the pupil downwards and outwards, and the inferior oblique directing it upwards and inwards” (page 174). The experiments he conducted on rabbits and monkeys consisted of either noting changes in tension of the oblique muscles during eye movements or sectioning an oblique muscle in one eye and noting the consequences. Three years later, Müller (1826a) tried to measure torsion by marking the conjunctiva and noting any rotations of the marks. He was unable to see any and concluded that the eyes did not undergo torsion.

In contrast to Müller’s conclusion, observational studies by Alexander Friedrich Hueck (1838) lent support to the occurrence of torsion. Hueck, who like Volkmann was from Tartu, examined rotation of the eyes in the opposite direction to head tilt in more detail and tried to measure its magnitude. He stated that the eyes remain in the same relation to gravity for head tilts up to 28 deg—that is, there was perfect compensation for head inclination: “The observation of actual eye torsion shows that vertical diameter of the eyeball remains vertical if the head is inclined sideways by up to 28 deg, and therefore during this movement the image maintains its location unchanged. If we incline the head to the side by more than 28 deg, the eyeball can no longer retain its position with respect to the head rotation” (Hueck 1838, page 31).

Subsequent experiments have not fully supported Hueck’s claim: while rotation of the eyes does occur, its magnitude is only a fraction of the head tilt. This would now be called ocular countertorsion, and it has a gain of around 0.1 (Howard 1982). Thus, when the head is tilted laterally by 30 deg, the eyes rotate in the opposite direction by about 3 deg. It was because the magnitude of countertorsion is small that it was difficult to measure with any degree of precision, and there was much debate concerning its occurrence at all. A review of the 19th-century debates concerning countertorsion was provided by Willibald Nagel (1896), who was able to resolve the dispute regarding its occurrence in animals but not in humans. Howard and Templeton (1966) and Howard (1982, 2002) describe the techniques that have been applied to measure countertorsion in the 20th century.

Many years before these experiments had been conducted, Wells (1794a) examined dynamic torsion using the movement of afterimages relative to real images. He was disputing the claim that the eyes could not rotate around the optic axis:

But surely the parts which connect the eye-ball to the socket are sufficiently flexible to allow it to move in some degree round its axis; and, whoever bestows the least consideration upon the origin, progress, and termination, of the oblique muscles of the eye must perceive that they have the power of giving it such a motion. 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 (Wells 1794a, pages 906–907).

Wells was recording torsional nystagmus, and he compared it with the discontinuous eye movements that follow rotation of the body with an upright head. This he had studied earlier (Wells 1792), and it is in this context that nystagmus was first recorded with any degree of precision.

5 Nystagmus

Concerns with binocular coordination and torsion were related to the position of the eyes following some movement, and it was generally assumed that the eyes moved quickly but smoothly to new positions. An appreciation of the jerkiness of eye movements arose in the context of visual vertigo, particularly that generated by body rotation, where the eyes moved slowly in one direction and rapidly in the reverse. This is called nystagmus, and the term derives from the nodding movements of the head when in a drowsy state—the head drops slowly and then is jerked back. The similar smooth and jerky movements of the eyes can be elicited in a number of ways and are associated with a variety of maladies. That great French nosologist François Boissier de Sauvages de Lacroix (1772a) called one condition nystagmus; it involved uncontrolled back and forth movements of the eyes. He also discussed vertigo in his classification of diseases and described it as: “An hallucination which takes place when stationary objects appear to move and rotate around us... The cause of vertigo is nothing other than an impression on the retina which is equivalent to that excited by objects that paint their images successively on different parts of that membrane” (Sauvages de Lacroix 1772b, page 50). He drew parallels with persisting visual images when observing rapidly moving lights and suggested that the sensitivity of the retina was changed by the retrograde movements of blood in the vessels supplying it. He did discuss the effects of body rotation, and the possibility of unconscious eye movements during and after rotation was entertained. An alternative to speculating on processes in the retina or brain was to study the phenomenon of vertigo itself. Interest in vertigo was principally medical, and most observations upon it were made in that context.

Visual motion of the world following body rotation was described in antiquity. Perhaps the fullest accounts were given by Aristotle’s pupil Theophrastus (see Sharples 2003); he described the conditions that can induce dizziness, including rotation of the body, but he did not relate these to movements of the eyes. Porterfield (1759) did add an eye movement dimension to it, but he denied their existence following rotation—because he was not aware of feeling his eyes moving. That is, the index of eye movement he used was the conscious experience of it. He proposed that the post-rotational visual motion was an illusion in which the stationary eye is believed to be moving. Porterfield’s description stimulated others to examine vertigo and to provide interpretations of it, some of which involved eye movements. The most systematic studies were carried out by Wells (1792, 1794a, 1794b). He formed an afterimage (which acted as a stabilised image) before rotation so that its apparent motion could be compared with that of an unstabilised image when rotation ceased. His account was brief, simple, and insightful: “When we stop ourselves while giddy from turning, our eyes do not return to a state of rest along with our bodies, but continue to move for some time after. Of this, however, we are not conscious; and hence we imagine the relative motion between ourselves and objects at rest to be possessed by the latter” (Wells 1794a, page 902). The direction of the consequent slow separation of the two images and their rapid return (nystagmus) was dependent on the orientation of the head and the direction of body rotation.

Thus, Wells used afterimages to provide an index of how the eyes move by comparing them with real images. He confirmed his observations by looking at the eyes of another person who had rotated and then stopped. By these means he cast doubt on evidence derived from subjective impressions of how the eyes were moving. Wells described fast and slow phases of nystagmus and provided the first account of discontinuous eye movements in vertigo; he related the direction of visual vertigo to head position during rotation; and he found that nystagmus could be suppressed by attending to targets.

Jan Purkinje (figure 10) is best known to eye movement researchers through his descriptions of the images reflected from the surfaces of the eye. Light projected onto the eye reflects from the external surface of the cornea, the internal surface of the cornea, the external surface of the lens, and the internal surface of the lens. These reflections are known as Purkinje images, and they can be used to track eye position with great accuracy. Purkinje essentially repeated Wells's experiments on eye movements following body rotation, but was ignorant of them (see Purkinje 1820, 1825). Indeed, Purkinje's experiments were inferior to those of Wells, but both adopted interpretations of visual vertigo in terms of eye movements. Purkinje added a novel method for studying vertigo and eye movements—galvanic or electrical stimulation of the ears. The technique was amplified by Eduard Hitzig (figure 11a). He examined eye and head movements during galvanic stimulation of the ears and likened nystagmus so produced to a fisherman's float drifting slowly downstream and then being snatched back (Hitzig 1871).

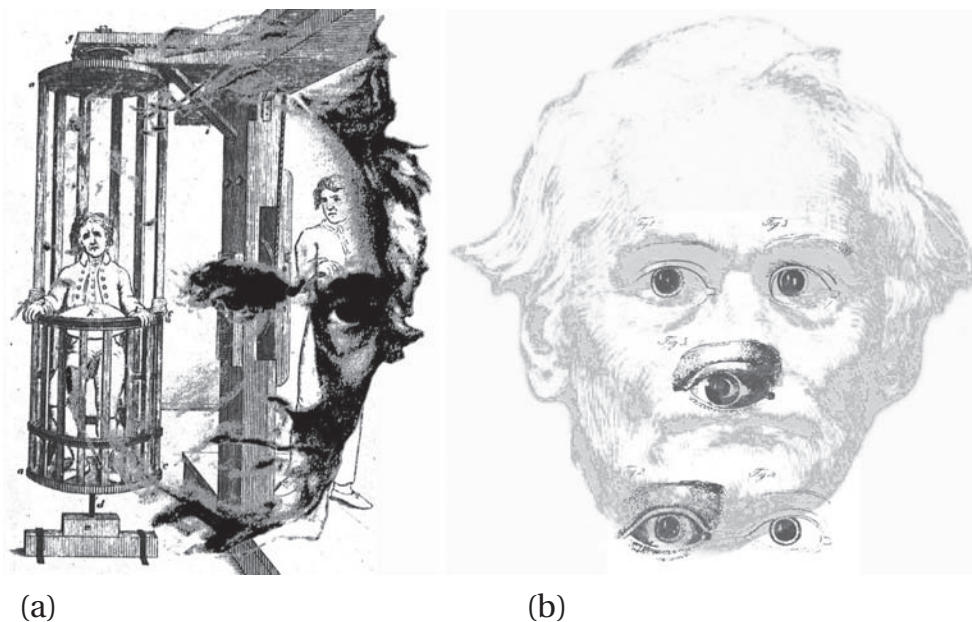


Figure 10. The two portraits of Jan Evangelista Purkinje (1787–1869) are after illustrations in Psotníčková (1955). (a) *Purkinje's Schaukel*. Purkinje is shown together with a rotating device of the type used in his experiments on vertigo [after an illustration in Kruta (1969)]. (b) *Purkinje images*. The reflections of a candle flame from the structures of the eye. The images were described and illustrated by Purkinje in 1823 (see John 1959). Purkinje carried out his experiments in Prague, prior to his appointment (in 1823) as a physiologist at the University of Breslau (now Wrocław) (© Nicholas Wade).

Wells rotated his body voluntarily, but Purkinje was able to enlist the assistance of a rotating device. It was a form of human centrifuge, the first model of which had been devised by Erasmus Darwin (1801) as a treatment for insanity (Wade et al 2005). Purkinje adapted it for generating vertigo in an experimental setting, but it continued to be used clinically—not as a treatment for the insane but as a test of vestibular function. Indeed, the rotating chair is now called the Bárány chair, after Robert Bárány (figure 11b). In the early 20th century, two

Ueber die beim Galvanisiren des Kopfes entstehenden Störungen der Muskelinnervation und der Vorstellungen vom Verhalten im Raume.¹⁾

Von

EDUARD HITZIG.

I. Literatur.

Schon den älteren Experimentatoren im Gebiete der galvanischen Elektrizität war es bekannt, dass bei Application von einigermaßen intensiven Strömen in der Gegend des Kopfes Schwindelempfindungen eintreten können. So erwähnt Augustin²⁾ einen einschlägigen Versuch:

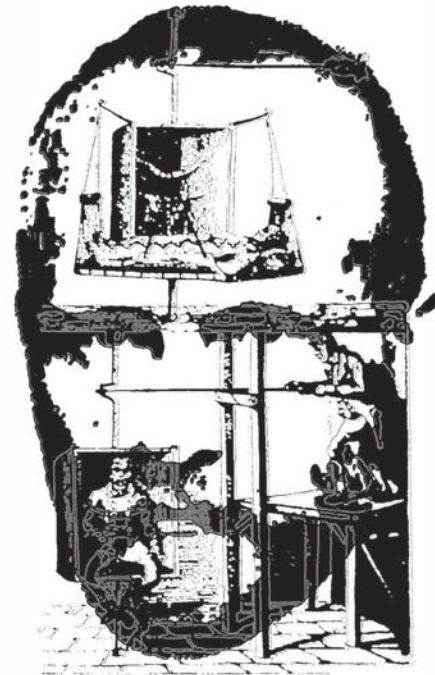
„Umwickelt man die Ohren mit Draht, befeuchtet sie mit Salzwasser und taucht dann die Spitzen jenes Drahtes in die Wassergläser, worin die an den Extremitäten der Säule befestigten Ketten liegen, so wird einem schwindlich und man sieht elektrische Blitze.“

Bereits im Jahre 1827 wurde dieser Gegenstand aber von Purkinje³⁾ in einer bei den neueren Autoren leider in Vergessenheit gerathenen Abhandlung ausführlicher behandelt. In

1) Die erste Mittheilung von den in dieser Abhandlung angeführten hauptsächlichsten Thatsachen machte ich der Berliner medizinischen Gesellschaft in ihrer Sitzung vom 19. Januar 1870. S. Berl. Klin. Wochenschr. 1870. Nr. 11.

2) Versuch einer vollständigen systematischen Geschichte der galvanischen Elektrizität und ihrer medizinischen Anwendung von Dr. F. L. Augustin. Berl. 1803. S. 129.

3) Rust's Magazin für die gesammte Heilkunde etc. Bd. XXIII. Berl. 1827. S. 297.



(a)

(b)

Figure 11. (a) *Electrical stimulator*. Eduard Hitzig (1838–1907) [after an illustration in Polyak (1957)] applied galvanic currents to the side of the head and noted the direction of the ensuing nystagmus. The text is the first page of his article describing and illustrating the eye movements; the experiments were conducted while he was in Berlin. (b) *Bárány's chair*. Robert Bárány (1876–1936) devised a rotating chair for studying semicircular canal function. It was very similar to the chairs devised for the treatment of maniacs early in the 19th century; the one shown here was derived from an illustration in Hallaran (1818). Bárány studied vertigo in Vienna before moving to Uppsala University (© Nicholas Wade).

aspects of eye movements and vertigo attracted clinical attention. The first was the use of post-rotational nystagmus as an index of vestibular function, and the second was stimulating the semicircular canals with warm and cold water so that the direction of eye movements they induce could be easily observed. These characteristics of nystagmus were defined more precisely by Bárány (1906, 1913), who was awarded the Nobel Prize in 1914 for his vestibular researches.

The 1870s was the decade of added interest in eye movement research because of its assistance in determining semicircular canal function. Post-rotational eye movements were measured and related to hydrodynamic theory, which was proposed independently by Ernst Mach, Josef Breuer, and Alexander Crum Brown (figure 12). Breuer (1874) provided a similar description of post-rotational nystagmus to Wells, but he was able to relate the pattern of eye movements to the function of the semicircular canals. Breuer argued that during rotation the eyes lag behind the head in order to maintain a steady retinal image; then they make rapid jerky motions in the direction of head rotation. The eye movements reduce in amplitude and can stop with rotation at constant angular velocity. When the body rotation ceases, the eyes rotate in the same direction as prior head rotation, and the visual world appears to move in the opposite direction interspersed with rapid returns. He also stated, like Wells, that there is no visual awareness during these rapid returns. This is a clear reference to both fast eye movements and to saccadic suppression, although he did not use the term 'saccade'.

Afterimages were also employed by Mach (1873, 1875; and see Young et al 2001), who rediscovered Wells's method for examining post-rotational eye movements. Mach (figure 12a)

developed his own model for examining the perception of motion. With this device, he was able to investigate both visual orientation during tilt and the effects of rotation. He demonstrated that vertigo can be induced by visual stimulation alone. Mach made the explicit connection between Purkinje's experiments on vertigo and the function of the semicircular canals. In addition to observing an afterimage, he applied the time-honoured technique of placing a finger by the side of the eye and of using pressure figures as stabilised retinal images. However, perhaps the clearest descriptions of eye movements during and following body rotation were given by Crum Brown (1874, 1878), who provided diagrams of the steady head and jerky eye movements. Wells's account of the dynamics of eye movements following rotation was beautifully refined by Crum Brown, although no reference was made to Wells. Like most other historians of the vestibular system, Mach, Breuer, and Crum Brown all championed Purkinje as the founder of experimental research linking eye movements to vestibular stimulation.

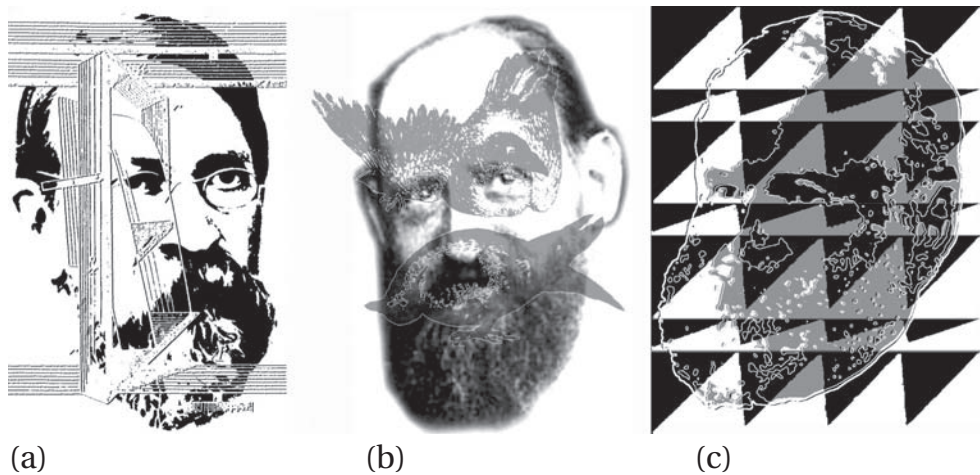


Figure 12. (a) *Mach's chair*. Ernst Mach (1838–1916, after a photograph in Schmitz 1983) is shown together with his device for rotating the body around different axes (from Mach 1875). Mach was a physicist at the University of Prague. (b) *Breuer's pigeons*. Josef Breuer (1842–1925) confirmed the influence of semicircular canals on the posture of pigeons by ablation studies, the pigeons illustrated are after a figure in Kruta (1969). He also performed experiments with humans using afterimages. Breuer worked with Hering at the University of Vienna. (c) *Crum Brown's nystagmus*. Alexander Crum Brown (1838–1922) [after a portrait in Comrie (1932)] was able to record the slow movements of the eyes and their rapid return (nystagmus) during body rotation, as well as the adaptation that occurs; the saw-tooth patterns are derived from Crum Brown's (1878) diagrams. He was professor of chemistry at Edinburgh University (© Nicholas Wade).

6 Saccades

The term 'saccades' was introduced to eye movement research by Émile Javal (figure 13), who was founder and director of the ophthalmology laboratory at the Sorbonne, Paris. It derives from a French word referring to certain rapid movements of a horse during dressage. The English translation of 'saccade' is 'jerk'. As indicated in the previous section, vestibular researchers had recognised the discontinuity of eye movements for some time, and Crum Brown (1878) both described and illustrated them. However, it was not until Crum Brown's (1895) general consideration of eye and head movements that writers in English used the term 'jerk' to describe these eye movements. Importantly, Crum Brown recognised that such discontinuous eye movements were not confined to post-rotational

nystagmus, and despite what we might feel, our eyes always move by these jerks as we look around the world. Crum Brown gave a graphic description of eye movements in general:

We fancy that we can move our eyes uniformly, that by a continuous motion like that of a telescope we can move our eyes along the sky-line in the landscape or the cornice of a room, but we are wrong in this. However determinedly we try to do so, what actually happens is, that our eyes move like the seconds hand of a watch, a jerk and a little pause, another jerk and so on; only our eyes are not so regular, the jerks are sometimes of greater, sometimes of less, angular amount, and the pauses vary in duration, although, unless we make an effort, they are always short. During the jerks we practically do not see at all, so that we have before us not a moving panorama, but a series of fixed pictures of the same fixed things, which succeed one another rapidly (Crum Brown 1895, pages 4–5).

Here, Crum Brown offered an eloquent description of eye movements in which he demonstrates an understanding not only that the eyes move in a series of jerks but also that these vary in size, and that vision only occurs during the intervals between these jerks. Crum Brown used the term ‘jerk’ to describe these movements, the English equivalent of Javal’s ‘saccades’ (figure 13).

The term saccades is now so widely applied to the rapid sweeps of the eye that it is of interest to determine the origins of its initial assignment. Raymond Dodge suggested that the term should be used by writers in English because “German and Scandinavian writers are commonly using the descriptive class term ‘saccadic’ to denote the rapid eye movements for which we have only the arbitrary name of ‘type I’” (Dodge 1916, page 422). While saccade is now a specialist term applied to a particular set of eye movements, at the time that it was used by Javal it was an unremarkable French word, in common usage, meaning ‘jerk’ or ‘twitch’.

6.1 Eye movements in reading

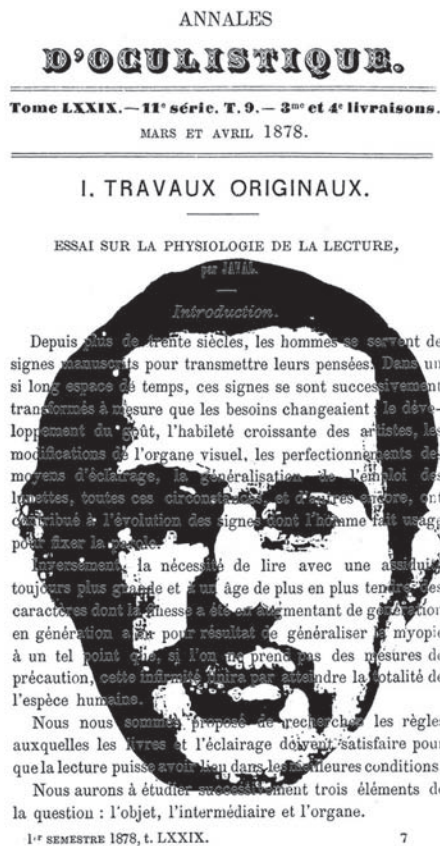
Porterfield (1737) provides a link between nystagmus and saccades, although he used neither of these terms and his analysis was logical rather than psychological. He did examine vertigo as well as reading, and he understood the requirement for rapid eye movements in reading:

Thus in viewing any Word, such as MEDICINE, if the Eye be directed to the first Letter M, and keep itself fixed thereon for observing it accurately, the other Letters will not appear clear or distinct. . . . Hence it is that to view any Object, and thence to receive the strongest and most lively Impressions, it is always necessary we turn our Eyes directly towards it, that its Picture may fall precisely upon this most delicate and sensible Part of the Organ, which is naturally in the *Axis* of the Eye (Porterfield 1737, pages 184–185).

Porterfield did not provide empirical support for the ideas he developed. He also appreciated the historical background in which his researches were placed. Moreover, he applied his understanding of eye movements to a wide range of phenomena, including visual vertigo. It was from vertigo that the first signs of discontinuous eye movements derived: the fast and slow phases of nystagmus were demonstrated with the aid of afterimages. Afterimages were also to play an important role in appreciating the discontinuity of eye movements generally. The studies took place in 1879, the same year in which Javal first used the term saccades.

Hering published an extensive account of eye movements in 1879. It was a long chapter in Hermann’s *Handbuch der Physiologie*, the title page of which is shown in figure 14a; the chapter was translated into English as a book (Hering 1879a, 1942). Most of the book is addressed to eye position, but Hering did make a general observation on eye dynamics:

In ordinary seeing the visual point constantly changes its position; for, in order to recognize the outer objects, we must examine one after another, all their separate parts and endeavor to perceive them with utmost acuity. This can be accomplished only by bringing their images upon the two retinal centers. With small objects the mere turning of the eyeballs in their



(a)

252 JAVAL.

surpris de la rapidité avec laquelle les myopies fortes continuent à progresser (1).

Il vient heureusement un moment où le myope, lisant sans lunettes, ne peut plus lire sans déplacer la tête ou le livre; c'est alors que l'excès du mal produit un bien; dès qu'il s'est habitué à ces mouvements, le myope n'a plus besoin de faire varier son accommodation en lisant, et sa myopie devient stationnaire.

Si ces idées théoriques sont exactes, les personnes que leur myopie contraint à lire de très près devront s'appliquer à suivre les lignes par des mouvements de la tête ou du livre; c'est le conseil que je ne manque pas de leur donner; je les engage aussi, quand elles lisent des brochures, à les courber de manière à produire un cylindre vertical dont l'axe passe approximativement par le centre de rotation de leur œil, et jusqu'ici les faits m'ont paru assez favorables: aucun de ceux à qui j'avais donné ces conseils n'est venu se plaindre d'une augmentation de myopie.

Mais il ne faut pas s'attendre à voir tous les myopes recourir aux conseils d'un médecin; cherchons donc à modifier les livres de manière à diminuer le nombre des cas de myopie progressive. Le moyen résulte avec évidence de tout ce que nous venons de dire: il faut éviter les lignes longues. L'expérience est d'ailleurs là pour nous donner raison; c'est dans les pays où les livres et les journaux sont imprimés avec les lignes les plus longues que la myopie progressive sévit avec la plus grande intensité.

A ceux qui disent complaisamment que le degré de civilisation d'un peuple peut se mesurer au nombre des myopes qu'il révèle aux statisticiens, nous répondrons que l'économie outrée de lumière, l'emploi de caractères gothiques trop petits et souvent usés, imprimés sur un papier gris et transparent, sont des causes bien suffisantes pour faire apparaître la myopie chez les enfants, et que l'abus de la lecture, au détriment de la réflexion et de l'observation des faits réels, joint à l'emploi de

(1) D'après des recherches entreprises par M. Lamare dans notre laboratoire, l'œil subit même plusieurs saccades dans le courant de chaque ligne, environ une par 15 à 18 lettres de texte: il est probable que, chez le myope, à chacune de ces saccades de l'œil répond une variation brusque de l'accommodation.

(b)

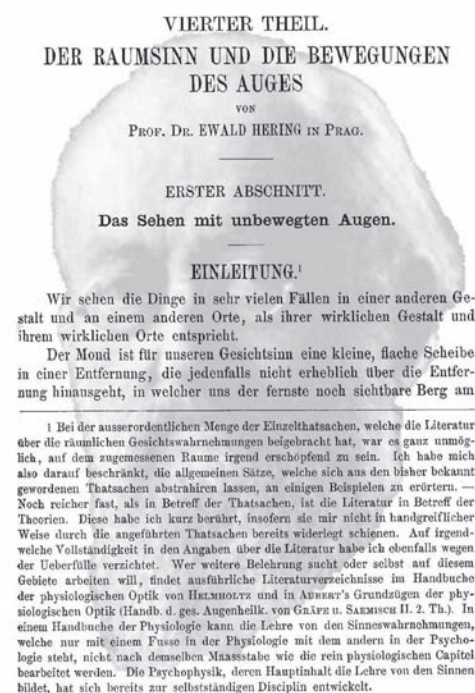
Figure 13. (a) *Reading Javal*. Between 1878 and 1879, Louis Émile Javal (1839–1909) wrote eight articles on the physiology of reading; the title page of the first one is shown. The portrait reflects the ambiguity associated with Javal and his research on reading: one source (Schmitz 1983) states that it is a portrait of Javal by Toulouse Lautrec, whereas Sugana (1973) states that it is a portrait of Lautrec by (another) Javal! The latter is likely to be correct. (b) *Saccadic suppression*. An authentic portrayal of Javal [modified from Taylor (1937)] in text from the penultimate page of his final article (Javal 1879); saccades are mentioned in the footnote (© Nicholas Wade).

sockets suffices. But if the object of regard is of large dimensions, we resort to turning the head, and if necessary, the upper body, and finally even changing our location. Rarely do we devote our attention to one spot, even for the duration of a second. Rather does our glance spring from point to point, and in its wanderings it is followed slavishly by the visual point, in whose movements we have greater agility than in any other movement, for no organ is so continuously used as the visual organ (Hering 1942, page 83).

Hering's chapter seems to have diverted interest from his brief but insightful experiments on eye movements during reading, published in the same year (Hering 1879b), the first page of which is shown in figure 14b. While the *Handbuch* chapter was being prepared for publication, Hering's attention was drawn to an article by Hueter (1878). In it Hueter made a passing observation that sounds could be heard when a rubber tube was applied to the closed eyelid. He suggested that the sound was generated by blood flow through the capillaries in the lids. Hering (1879b) presented evidence to indicate that the sounds were a consequence of muscle contractions. He attached a rubber tube to a cigar holder and listened to the sounds produced when it was placed on the eyelids: he "heard a surprisingly strong and whirring roar" (page 137). When he placed the device on the eye of curarised dogs or rabbits, the sounds ceased even though the blood flow continued. Having determined that

the sounds reflected muscular contractions, Hering applied the technique to the eye lid of an open eye. Even when he tried to keep his eyes still, he heard the sounds: “Throughout one’s observations, one hears quite short, dull clapping sounds, which follow each other at irregular intervals” (page 145). Hering was able to use his experience with afterimages to establish that the sounds were correlated with eye movements by comparing them: “every clapping sound corresponds to a displacement of the afterimage” (page 145). This was confirmed by movements of floaters, which occurred with the clapping sounds.

Hering’s study is significant not only because he compared afterimage movements with the sounds of muscular movements, but also because he applied the technique to reading: “One can observe the clapping sounds very clearly during reading. Although the eyes appear to glide steadily along the line, the clapping sounds disclose the jerky movement of the eyeball” (1879b, page 146). The sounds were louder when the eye moved from the end of one line to the beginning of the next, and they were evident when observers read lines of text; however, the sounds disappeared if subjects were instructed to fixate a stationary target. It is also of note that he used the term ‘jerks’ (*Rucke* in German) because it is equivalent to using the term ‘saccades’ to describe rapid eye movements if he had been writing in French. Thus, Hering described the discontinuity of eye movements and recognised the class of rotations that we now refer to as saccadic. He was amongst the first to offer a description of the discontinuity of eye movements outside the context of vestibulo-ocular reflexes.



(a)



(b)

Figure 14. (a) *Hering's Spatial Sense*. Hering published a long chapter on the spatial sense and eye movements in 1879, the title page of which is shown. The portrait was derived from a photograph kindly supplied by Leo Hurvich. (b) *The sounds of eye movements*. In the same year a shorter article on muscle sounds appeared, the first page of which is shown. It was in this article that Hering related the muscle sounds to jerky eye movements during reading. His portrait is derived from an illustration in Lesky (1965) (© Nicholas Wade).

Hering’s report of his experiments was published in the same year as Javal gave a brief description of ‘saccades’ during reading. Javal is generally considered to have instigated

research in eye movements during reading. In fact, Javal said virtually nothing about eye movements in his eight essays on the physiology of reading, published in 1878 and 1879 (see Wade and Tatler 2005, 2009). Saccades were only mentioned in passing on the penultimate page of his final article (which is shown in figure 13b). These were not the only attempts to measure eye movements at that time. Most employed afterimages and compared their displacements to real images. Javal (1878) used this technique to establish that the eye glided horizontally across lines of text with no vertical deviations. Measurements of eye movements during reading were carried out in Javal's laboratory by Lamare and reported in passing by Javal: "Following the research of M Lamare in our laboratory, the eye makes several saccades during the passage over each line, about one for every 15–18 letters of text. It is probable that in myopes the eye reacts with a rapid change in accommodation with every one of these saccades" (Javal 1879, page 252). Javal tried, unsuccessfully, to attach a pointer to the eye so that eye movements could be recorded on a smoked drum. He also tried, with a similar lack of success, to measure the deflections of light from a mirror attached to the eye. Throughout, his concern was with distinguishing between horizontal and vertical eye movements. It was Lamare who observed and recorded the jerky or saccadic movements during reading in 1879. However, he did not describe his experiments until thirteen years later. He tried various methods, including observing the eyes of another person, but:

The method that gives the best results is one by which the movements are heard via a drum with an ebonite membrane in the centre and to which a small tube is attached; the tube is in contact with the conjunctiva or eyelid and is connected to both ears by rubber tubes... The apparatus yields distinctive sounds which an assistant can count and add, and note for each line. The return movement of the eyes to the beginning of a line gives a longer and louder noise that is easy to recognise; one counts the number of *saccades* from the start of the line to be able to *note* the number of divisions that occur in a line (Lamare 1892, page 357, original emphasis).

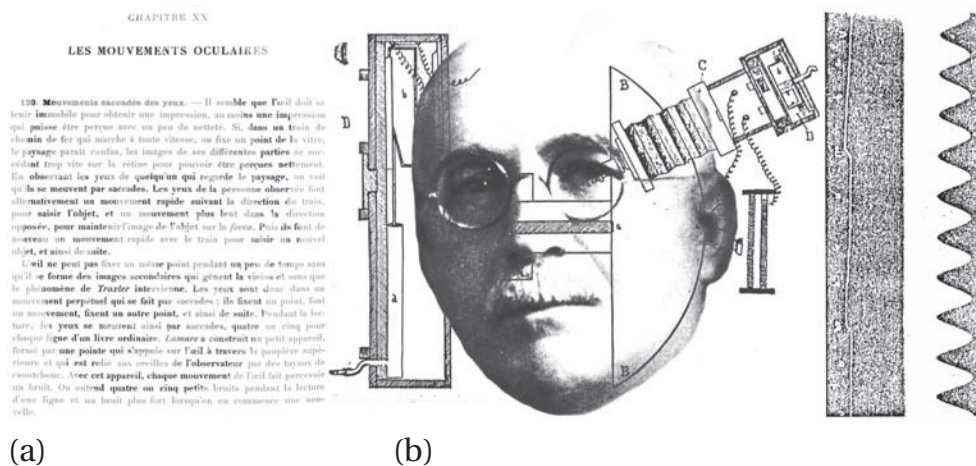


Figure 15. (a) *Tscherning's Optique*. The portrait of Marius Hans Erik Tscherning (1854–1939) after a [frontispiece photograph in Tscherning (1900)] is embedded in the first page of his chapter on eye movements in his *Optique Physiologique* (1898). (b) *Dodge's camerawork*. Raymond Dodge (1871–1942) [after a portrait in Murchison (1930)] carried out some of the most elegant early studies on eye movements and reading. In 1901, together with Cline, he developed a photographic recording method of tracing the movements during reading; the camera device is shown here as is the photographic tracings on the right (© Nicholas Wade).

Lamare's intricate technique for recording eye movements was clearly described by Javal's successor as director of the ophthalmological laboratory at the Sorbonne, Marius Hans Erik Tscherning (figure 15a): he did not mention Javal in the context of his brief description

of saccadic eye movements in his *Optique Physiologique* (Tscherning 1898); the book was translated into English two years later. He noted:

The eyes are, therefore, in perpetual motion which is made by jerks: they fix a point, make a movement, fix another point, and so forth. While reading, the eyes move also by jerks, four or five for each line of an ordinary book. Lamare constructed a small instrument, formed by a point which is supported on the eye across the upper eyelid, and which is fastened to the ears of the observer by rubber tubes. With this instrument each movement of the eye causes a sound to be heard. We hear four or five sounds during the reading of one line, and a louder sound when we begin to read a new line (Tscherning 1900, page 299).

Lamare's technique bears a remarkable similarity to that employed by Hering in 1879; indeed, Hering remarked that he had been aware of the muscle sounds for years. Thus both Hering and Lamare should be accorded the credit for demonstrating the discontinuity of eye movements in reading. It is of interest to note that Tscherning's (1898) book used the word 'saccades', which was translated as 'jerks' in the English edition (Tscherning 1900).

A mechanical means of measuring nystagmus was tried by Rähmann (1878) and later Ahrens (1891) applied similar methods to reading. Ahrens attempted to record eye movements directly by placing an ivory cup on the cornea and attaching a bristle to it; movements could be registered by the displacements of the bristle on a revolving smoked drum. He was not able to obtain any detailed recordings of eye movements, but his method was adopted by Delabarre (1898) at Brown University and Huey (1898, 1900) at Clark University to record eye movements during reading. Edmund Huey (figure 16) noted that: "the most casual observation showed that the eye moved along the line by little jerks and not with a continuous steady movement" (Huey 1898, page 583). He then went on to record eye movements with a similar system (figure 16a) to that used by Delabarre. Both methods used plaster-of-Paris eye-cups, which required the eye to be anaesthetised with cocaine. Huey refined the technique and was able to register discontinuous eye movements during reading. Huey also refined the controls necessary for eye movement recording. The head was stabilised by head clamps and an individual bite-bar; a calibration recording was made initially, with the eye moving from one end of the line to the other; he also used a time marker.

Huey (1898) appears to have been the first writer in English to cite Javal's work, although it was with reference not to eye movements but to accommodation while reading. In a later article, Huey (1900) elaborated on Javal's description of eye movements during reading and indicated that he had corresponded with Javal. Huey also made reference to Lamare's studies: "Lamare, working with Javal, finding that the movement of the eye in reading was not continuous, but by little jerks (*par saccades*), devised the following method for counting these" (Huey 1900, page 285). Huey then gave a brief account of Lamare's auditory method of detecting eye movements. Javal was not cited in Huey's (1901) second article on reading.

Several years later, in his book *The Psychology and Pedagogy of Reading* (the title page of which is shown in figure 16b), Huey provided an historical account of research on eye movements and reading. It is in this book that Huey established Javal as the founder of research in this area:

As you watch the reading [of another person], you notice, too, that the eyes do not move continuously from left to right along the line, but proceed by a succession of quick, short movements to the end, then return in one quick, usually unbroken movement to the left. You find all this very evident. And yet most of those who have studied the eye have curiously failed to note that the movement was discontinuous; and up to 1879, when Professor Javal called attention to it, I find no mention of the fact in the literature. Indeed, I have not myself seen mention of these reading movements until 1898, except in the writings of Javal and some other French authors who took up his discovery, and in a paper published in 1895 by Professor Alexander [Crum] Brown, of Edinburgh. It is a curious instance of the failure of scientists to make first-hand observations except along certain lines that have become habitual. . . .

Professor Javal, of the University of Paris, seems, as has been said, to have been the first to note the actual character of the eye's movements in reading. He concluded that there was a pause about every ten letters, and thought that this was about the amount that could be seen clearly at one fixation. He found that after reading he had after-images of straight gray lines corresponding to the parallel lines of print, and concluded that the eye's fixation point did not leave the line as it moved forward in reading. . . . While not all of Professor Javal's observations are conclusive, he deserves more than does anyone else the credit for making the initial discoveries in this field, and for initiating a considerable number of later studies (Huey 1908, pages 15–16, 18).

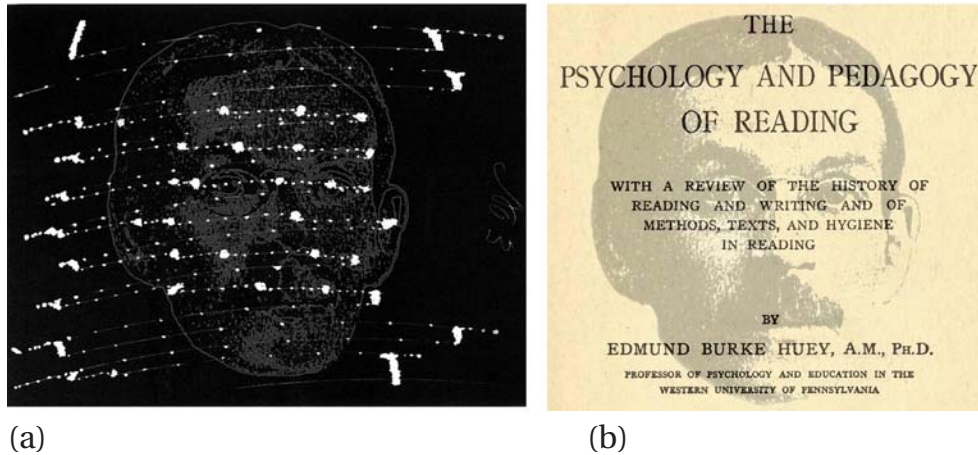


Figure 16. (a) *Reading Huey's record.* Edmund Huey (1870–1913) recorded eye movements during reading with a lever attached to a plaster eye-cup which moved a pen over a rotating smoked drum. The tracing on the smoked drum was photographed and then engraved (Huey 1900). A dimly defined portrait of Huey hovers behind the tracing. (b) *Huey's history.* The same portrait of Huey [derived from Taylor (1937)] is combined with the title page of his book in which Javal was championed as the first person to record saccadic eye movements during reading (© Nicholas Wade).

It is perhaps this last statement, assigning credit to Javal, that has led others, on the basis of Huey's writing, to accord Javal the honour of having conducted the experiments on eye movements and reading rather than Lamare. Hering's work was ignored completely.

As the 20th century began, there was a proliferation of eye-tracking technologies. The lever devices of Delabarre and Huey were limited by their mechanical properties: they applied additional force to the eye, and their inertia resulted in considerable overshoots in the eye movement traces recorded. Alternative devices were developed rapidly in which direct attachment between eye and recording surface was not required. Orschansky (1899) attempted to record light reflected from a mirror attached to the surface of an eye-cup, and variants of this principle were used throughout the 20th century. The key figure in the development of such devices was Dodge (figure 15b). He carried out his initial studies on eye movements with Benno Erdmann at the University of Halle in Germany, and he continued them on his return to America, particularly at Wesleyan University, Connecticut. Dodge appreciated the errors and pitfalls of self-observation when describing eye movements and perception in the same way that Wells had distrusted Porterfield's recourse to subjective experience more than 100 years earlier. Consequently, Dodge employed the use of an assistant to observe his eye movements, or to be observed:

It will be clear that when the eye moves as rapidly as possible from one fixation point to the other nothing new is seen; but it will seem that, when the eye moves more slowly, the entire line is seen very distinctly. If the observer takes the precaution to have some one watch his

eyes, as recommended, he will find that what in self-observation passes for slow movements of the eyes is in reality broken by one or more clearly defined full stops (Dodge 1900, page 457).

Dodge then developed photographic devices that required no attachment on the eye and that were more comfortable for the participants (Dodge and Cline 1901; Dodge 1903, 1904). After Dodge's development of the photographic eye tracker there followed something of a revolution in eye movement research and a proliferation of new experiments in this field (see Taylor 1937). Other researchers developed similar convenient and effective eye trackers, and research extended beyond the domain of reading. Researchers began to consider whether the newly described saccade-and-fixate strategy applied to tasks other than reading, and it was soon realised that this was the case. The proliferation of eye-tracking devices at the end of the 19th century went hand-in-hand with a rapid evolution of ideas about the link between fixations, saccades, perception, and cognition. An immediate application of the recognition of saccades and fixations was to consider how our apparently smooth and continuous visual experience could be reconciled with oculomotor behaviour that was anything but smooth and continuous.

6.2 Eye movements in picture viewing

Soon after the discovery of saccades and fixations during reading, George Malcolm Stratton (figure 17a) considered whether the places that the eyes were brought to rest might correlate with the perceptual experience of illusions. Stratton carried out his initial work in Wundt's laboratory at Leipzig and continued his research at the University of California. He employed a photographic technique to examine eye movements when viewing simple geometrical patterns (Stratton 1902). This was an important new direction for eye movement research and served to highlight the importance of saccades outside the context of reading. Stratton was surprised by the discontinuity of eye movements recorded: "The eye darts from point to point, interrupting its rapid motion by instants of rest. And the path by which the eye passes from one to another of these resting places does not seem to depend very nicely upon the exact form of the line observed" (Stratton 1902, page 343). Stratton's work is significant because it attempted to bridge the gap between visual phenomena (illusions), cognition (aesthetic judgements), and the underlying mechanisms (eye movements and fixations). Moreover, his studies signified a shift of emphasis in approaches to understanding the link between oculomotor behaviour and perception. Where his predecessors had primarily considered perception with respect to the movements of the eyes, Stratton's work shows a transition from this approach to an emphasis upon the locations selected for fixation.

The transition is most evident in Stratton's (1906) article exploring the relationship between eye movements and perception when viewing simple patterns and line illusions. He placed emphasis not only on the movements of the eyes but on the locations at which the eyes paused for fixations: "One is struck by the almost grotesque unlikeness between the outline observed and the action of the eye in observing it. For the most part the eye moves irregularly over the figure, seeking certain points of vantage from which the best view of important features may be obtained. And these positions are marked by the eye's momentary resting there" (Stratton 1906, page 94). Despite this shift of emphasis in the direction of fixations, Stratton was unable to reconcile viewing behaviour with the aesthetic experience: "The sources of our enjoyment of symmetry, therefore, are not to be discovered in the form of the eye's behaviour. A figure which has for us a satisfying balance may be brought to the mind by most unbalanced ocular motions" (Stratton 1906, page 95). It is clear from Stratton's closing remarks in his article on eye movements and symmetry that he appreciated the gulf between perception and cognition and that he was aware that his work was defining new questions in vision that would be addressed in the future.

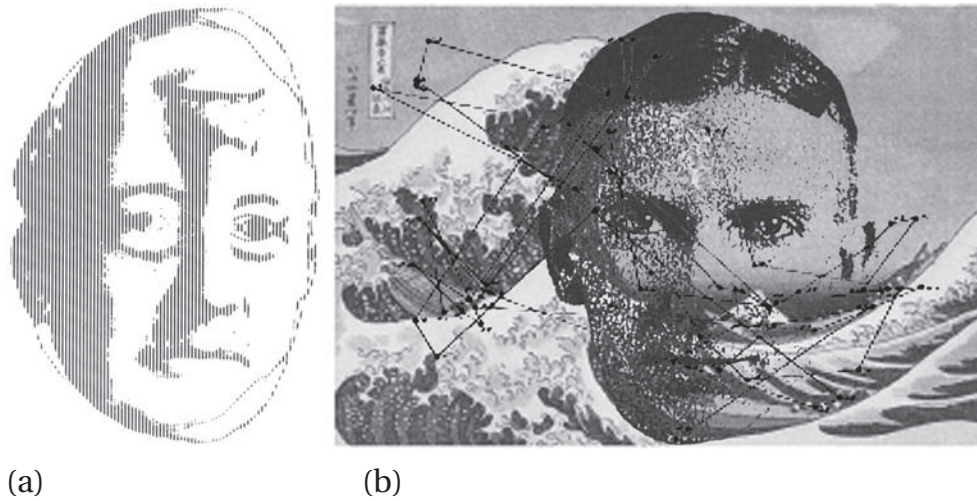


Figure 17. (a) *Inverted visionary*. George Malcolm Stratton (1865–1957; modified from a portrait kindly provided by Karen De Valois) is better known for his experiments on inverted vision than for his studies of eye movements. He employed photographic techniques for examining eye motion paths over geometrical shapes. (b) *Waves of eye movements*. Guy Buswell (1891–1994) [after a portrait in Taylor (1937)] together with eye movement records of one observer viewing “The Wave” painted by Hokusai; black circles represent fixations, and the lines indicate the saccades that moved the eye from one fixation to the next (from Buswell 1935) (© Nicholas Wade).

It is the question of what drives the selection of particular locations upon which to fixate that was eventually to assume unrivalled prominence in both eye movement and attention research late in the 20th century. Perhaps the key figure in the emergence of this area of research was Guy Buswell (figure 17b) at the University of Chicago. While Buswell's (1937) research on reading is probably his most renowned work, it was from his study of eye movements when viewing pictures that one of his major contributions to eye movement research arises. The latter work was published in his impressive monograph *How People Look at Pictures* (Buswell 1935). He reported eye movement data recorded from 200 participants each viewing multiple pictures, such that his data comprised almost 2,000 eye movement records, each containing a large number of fixations. This volume of eye movement data is impressive by modern standards, but particularly so given the technology at the time and the need to transform manually the horizontal and vertical position of the eye indicated in the eye movement records into precise locations on the pictures viewed. This work was the first to explore systematically eye movements of observers while viewing complex pictures, rather than text or simple geometrical patterns, and represented something of a revolution in eye movement research. It is interesting to note that while Buswell's work is heralded as a key study in eye movement research, the character of the eye movements themselves was not the topic of much consideration: rather it was about the placement of the fixations between them.

Buswell's monograph explored a wide range of issues regarding the eye movements made while viewing pictures, including some surprisingly modern concerns: he looked at the overall distribution of fixations on pictures; he compared the first few fixations on a painting with the last few; he compared the durations of fixations made early in viewing with those made near the end of viewing; he looked at how fixation duration changed with viewing time; he compared the consistency between different observers when viewing the same picture; and he looked at the influence of instructions given to observers upon their eye movements when viewing a picture. Buswell made density plots of where all participants fixated when viewing pictures and showed that not all locations and objects in pictures

are fixated, with particular ‘centres of interest’ where fixations are concentrated. He also appreciated that there could be quite large individual differences in where people fixate when viewing pictures.

The differences that were present in the locations fixated by individuals when viewing each image were also reflected in the durations of the fixations, with a large variation between observers in their average fixation duration on each picture. Buswell’s investigation of individual differences extended to exploring differences between artistically trained individuals and those without training, between children and adults, and between Western and Oriental participants. In all cases, differences between the groups were small: “The average differences between the groups were so much less than the individual differences within each group that the results cannot be considered significant” (Buswell 1935, page 131). Differences were found in the eye movement data that emerged over the course of viewing a picture for some time. The regions fixated on in the picture were more consistent between observers for the first few fixations than for the last few on each picture. He also found that fixation duration increased over the course of viewing a picture for some time.

Buswell devoted a chapter of the book to looking at the influence of the characteristics of the picture on where eyes fixate. This work is very reminiscent of that conducted some years earlier by Stratton, although he did not cite Stratton’s work. In places Buswell appeared to argue that eye movements do tend to follow contours in pictures. This is contrary to Stratton’s suggestion that eye movements do not seem to be particularly influenced by the form of the figure being viewed. However, other aspects of Buswell’s data suggested less concordance between eye movements and the characteristics of the picture. When he showed participants more basic designs and patterns he found that: “The effect of different types of design in carrying the eye swiftly from one place to another is apparently much less than is assumed in the literature of art. . . . The writer should emphasize that the data from eye movements are not to be considered as evidence either positively or negatively for any type of artistic interpretation” (Buswell 1935, page 115). Like Stratton, Buswell felt that the pattern of eye movements was insufficient to explain our visual experience, and so he highlighted the need to appeal to cognitive explanations of vision.

Perhaps the most often overlooked aspect of Buswell’s work was his investigation of how different instructions given to observers prior to viewing an image can influence the locations selected for fixation during viewing. For example, when presented with a picture of the Tribune Tower in Chicago, eye movements were first recorded while the participant viewed the picture “without any special directions being given. After that record was secured, the subject was told to look at the picture again to see if he could find a person looking out of one of the windows of the tower” (Buswell 1935, page 136). Very different eye movement records were obtained in these two situations, demonstrating that cognitive factors such as the viewer’s task can have a strong effect upon how a picture is inspected.

The question of the factors underlying fixation placement was revived by Alfred Yarbus (figure 18) at Moscow in his research during the 1950s and 1960s (translated into English in Yarbus 1967). Within this work, Yarbus conducted an experiment where a single observer was shown the same painting (Repin’s *An Unexpected Visitor*) seven times, but with a different question asked before each viewing. This elegant experiment confirmed Buswell’s earlier observation that the instructions given to an observer can radically change the places that the observer fixates. Yarbus’s demonstration has become a classic in eye movement research and is frequently cited as an unequivocal demonstration that high-level factors can overshadow any low-level, stimulus-driven guidance of attention (see Tatler et al 2010). Moreover, in his measurements of eye movements when looking at pictures of people, Yarbus (1967) established a feature that has become a canon of face perception. Fixations are focussed on

the eyes and mouth, and this triangular scanning pattern was demonstrated on photographs of faces. The scan paths superimposed on a portrait of Yarbus, shown on [figure 18b](#), right, are those that he measured when looking at a full-face photograph of “Girl from the Volga” (Yarbus 1967, [figure 115](#)).

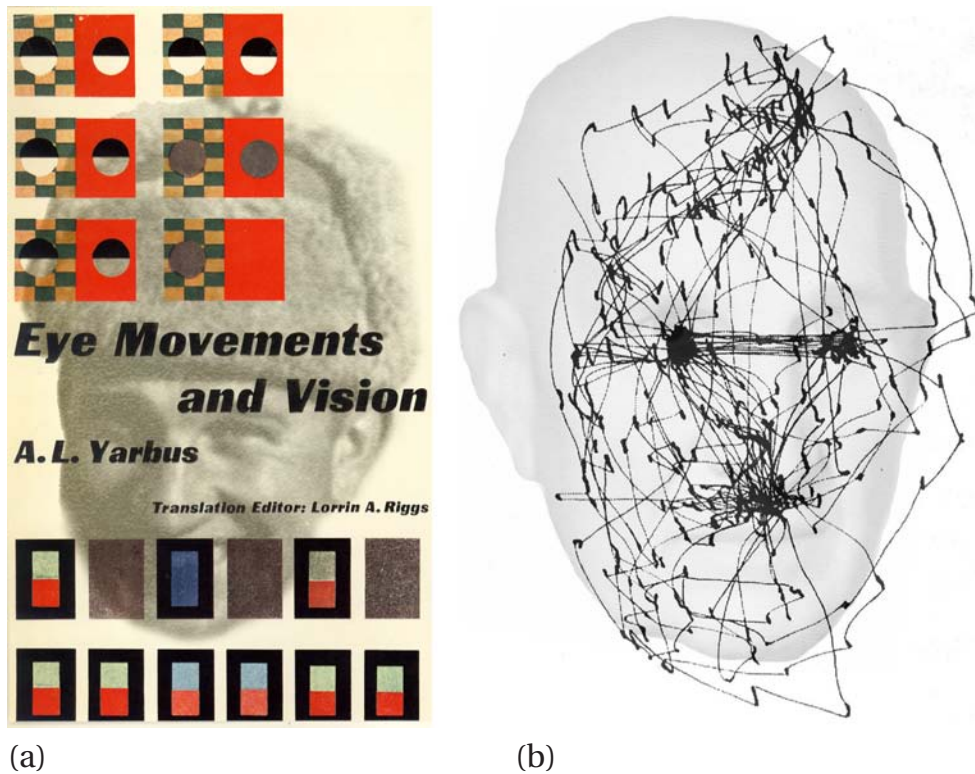


Figure 18. (a) *Yarbus translated*. Yarbus is shown during his military service, taken around 1944, together with the cover of the English version of his book. (b) *Scanning Yarbus*. Yarbus, photographed during the 1980s, with the pattern eye movements he recorded when scanning a face. The two photographs from which the portraits of Alfred Luk’yanovich Yarbus (1914–86) were constructed were kindly supplied by Galina Rozhkova (© Nicholas Wade).

6.3 Fixational eye movements

Yarbus devoted much more of his book to examining conditions in which the eyes do not move. Indeed, much of the research in mid-20th century was concerned with this issue. It was fuelled by the desire to determine whether involuntary eye movements had a deleterious effect on visual acuity. The idea is an old one, as James Jurin (1684–1750) suggested that complex objects could be resolved in more detail “if the eye be supposed to fluctuate ever so little” (Jurin 1738, page 151). It was possible to examine this hypothesis with images that were stabilised with respect to the retina. Yarbus developed a full-fitting contact lens which retained its position by suction. With this optical system, he found that “in any test field, unchanging and stationary with respect to the retina, all visible differences disappear after 1–3 sec, and do not reappear in these conditions” (Yarbus 1967, page 59). There were some differences in the results obtained in other laboratories examining stabilised retinal images, and the source of these was examined by Barlow (1963). He used a full fitting contact lens and a suction cap after the manner of Yarbus in order to compare their possible slippage; an afterimage was used as a perfectly stabilised target. The suction cap was more stable than the full-fitting contact lens, but neither was free from some slippage. His conclusion was that “Good-quality images stabilized as well as possible ... ‘blur’ and lose contrast rapidly: detail

and texture cease to be visible, and do not reappear” (Barlow 1963, page 50). It is of interest to note that the benchmark of ocular stability was the afterimage—the phenomenon that provided the initial insights into the ways the eyes moved.

The photographic recording techniques developed by Dodge and others were not precise enough to resolve very small eye movements. From the early 1950s optical techniques were employed to measure them and also to present stimuli that were optically stabilised on the retina; that is, they moved with movements of the eyes. Three research groups were very active in this initial phase, Ditchburn and Ginsborg at Reading University, and Riggs and Ratliff at Brown University, and Barlow at Cambridge. During fixation the eyes undergo high frequency, low amplitude tremors, onto which are superimposed slow drifts and rapid flicks or microsaccades. These were demonstrated by sets of complex compensatory optical systems or with contact lens devices (see Ditchburn 1973). The pattern of involuntary eye movements can be seen in figure 19a superimposed on the portrait of Floyd Ratliff, one of the pioneers who used such devices (Ratliff 1952). Ratliff and Riggs (1950) employed an optical lever system and photography to record the involuntary motions of the eye during fixation. They found small rapid motions of about 17.5 seconds of arc at 30–70 Hz, slow motions of irregular frequency and extent, slow drifts and rapid jerks. Barlow (1952) placed a droplet of mercury on the cornea and photographed the eye during motion and fixation; the instabilities during fixation were small but measurable. He confirmed his photographic measurements by comparing them with afterimages.

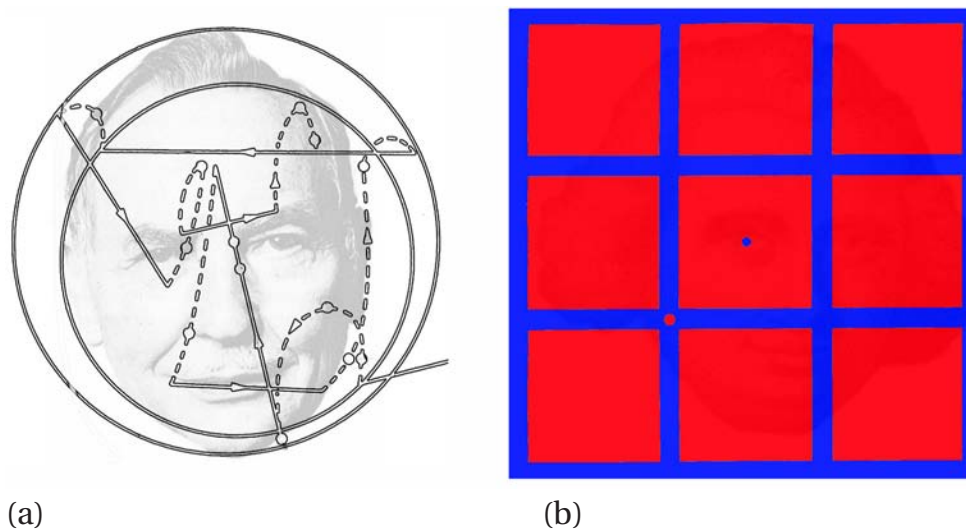


Figure 19. (a) *Unsteady gaze*. Floyd Ratliff (1919–99) [after an illustration in Zemon (2002)] within a pattern of involuntary eye movements during fixation; the high-frequency tremor is superimposed on the slow drifts (dashed lines), with intermittent microsaccades (after Ditchburn 1973). (b) *Darwin's grid*. Maintaining steady fixation on the central blue dot for about 30 s and then fixating the red dot will result in an afterimage of the grid; when subjects try to maintain fixation on the red dot, the afterimage will appear to move around as a consequence of involuntary eye movements. Within the grid is a low contrast portrait of Erasmus Darwin (1731–1802), which is derived from an illustration in *The European Magazine and London Review* 1795 (© Nicholas Wade).

Verheijen (1961) described how the effects of involuntary eye movements can be experienced by the simple expedient of generating an afterimage and then trying to maintain fixation. By fixating on the central blue dot in figure 19b for long enough to generate an afterimage (around 30 s) and then attempting to fixate on the red dot, the minor involuntary movements of the eyes will be expressed in shifts of the negative afterimage. It will be evident from carrying out this task that it is difficult to maintain fixation. Another consequence

follows from prolonged fixation, and it was described by Erasmus Darwin: “On looking long on an area of scarlet silk of about an inch in diameter laid on white paper... the scarlet colour becomes fainter, till at length it entirely vanishes, though the eye is kept uniformly and steadily upon it” (Darwin 1794, page 19). Not only does the colour fade, but peripheral targets disappear. He made this discovery in the context of his experiments on afterimages, which demanded prolonged fixation of colour patches in order to render them visible. The intensity of the colour declined until the whole patch ceased to be visible. This can also be experienced with [figure 19b](#), as it contains a low contrast portrait of Erasmus Darwin; the blue dot is at the centre of Darwin’s right eye, and the peripheral parts of the portrait will fade from view as fixation is maintained.

The instability of the eyes was noted from studies employing afterimages. It had long been recognised that even when apparently fixating stably, the eye is rarely truly still. However, it is not always evident whether some of the early writers were referring to instability during fixation or general movements of the eyes. For example, André Du Laurens (1558–1609) noted that “the eye standeth not still but moveth incessantly” (Du Laurens 1599, pages 28–29). It is perhaps more likely that the small involuntary eye movements were described by Edmé Mariotte (1620–84); he is better known for his account of the blind spot than for his observations on eye movements. He made brief reference to such instabilities, suggesting that they were involuntary: “The *Eyes* are always in motion, and very hard to be fixt in one place, though it be desired” (Mariotte 1683, page 266). This conclusion was probably reached by careful observation of the eyes of another person. Darwin’s son, Robert Darwin ([figure 20](#)), amplified this with regard to forming afterimages:

When we look long and attentively at any object, the eye cannot always be kept intirely motionless; hence, on inspecting a circular area of red silk placed on white paper, a lucid crescent or edge is seen to librate on one side or the other of the red circle: for the exterior parts of the retina sometimes falling on the edge of the central silk, and sometimes on the white paper, are less fatigued with red light than the central part of the retina, which is constantly exposed to it; and therefore, when they fall on the edge of the red silk, they perceive it more vividly. Afterwards, when the eye becomes fatigued, a green spectrum [afterimage] in the form of a crescent is seen to librate on one side or other of the central circle, as by the unsteadiness of the eye a part of the fatigued retina falls on the white paper (Darwin 1786, page 341).

These effects can be observed in [figure 20](#); the coloured regions are not circles of silk but a portrait of Robert Darwin (the son of Erasmus Darwin and father of Charles). Instabilities during fixation on the black dot can be seen at the edges of the blue oval. When fixation is shifted to the black dot on the right, a complementary afterimage will be seen, and Darwin will have recovered from his prior jaundice! Both Erasmus and Robert Darwin wrote on afterimages (or ocular spectra as they were then called) and used them as an index of eye movements (see Wade 2002, 2010). Erasmus Darwin (1794) included a chapter on ‘motions of the retina’ in his *Zoonomia*, and it is principally concerned with experiments employing afterimages. It is of interest that the afterimage remains the benchmark for determining the accuracy of optical image stabilisation.

Extending the roll call of pioneers to the 1960s introduces many more names than can be listed here. Excellent accounts of the research on eye movements in the last six decades can be found in Carpenter (1988, 1991), Eggert (2007), Findlay and Gilchrist (2003), Land and Tatler (2009), Legge (2006), Leigh and Zee (2006), and Tatler (2009).

7 Conclusion

Several paradoxes are posed by investigations of eye movements when considered in an historical context. Oculomotor behaviour constitutes a fundamental feature of our exploration of the world. We are aware that our own eyes move, and we can readily

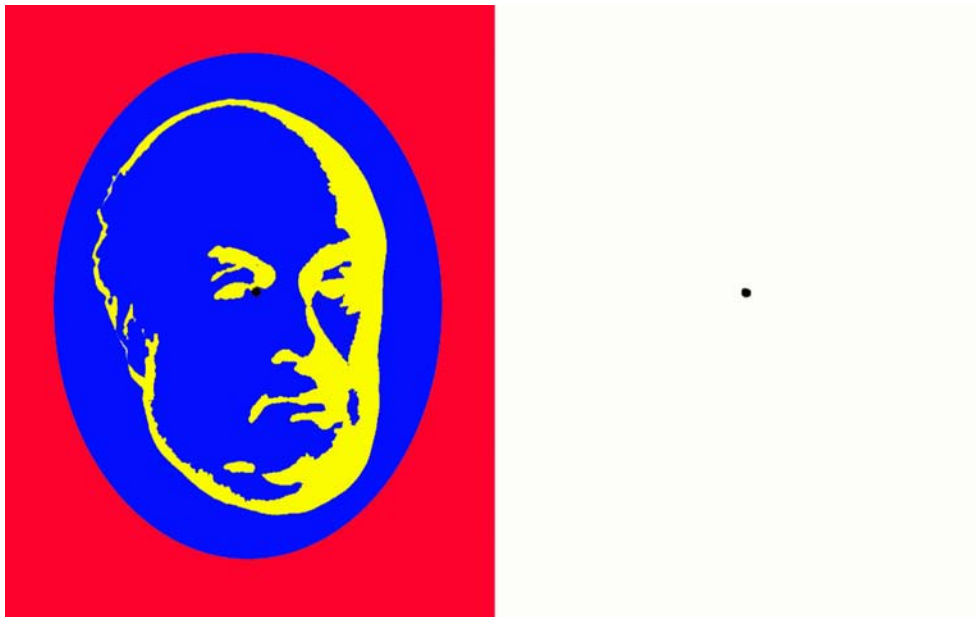


Figure 20. *Ocular spectra.* If you fixate the black dot on the portrait of Robert Waring Darwin (1766–1848) for about 30 s and then fixate the black dot on the right, a complementary afterimage will be seen. During adaptation, yellowish crescents will be seen beyond the boundaries of the blue ellipse, again signalling the instability of the eyes during attempts to maintain steady fixation (© Nicholas Wade).

detect movements in the eyes of those we observe. This awareness was, however, partial. Throughout the long descriptive history of studies of eye movements, a vital characteristic of them remained hidden from view, both in ourselves and in our observations of others. The rapid discontinuous nature of eye movements is a relatively recent discovery, as are the small involuntary movements that accompany fixation. For most of recorded history, the eyes were thought to glide over scenes to alight on objects of interest, which they would fix with unmoved accuracy.

Another paradox is that initial knowledge about eye movements derived from generating stimuli that did not move with respect to the eye when the eye moved. The first of these was the afterimage, which, since the late 18th century, has been applied to determining the ways the eyes moved. More complex photographic recording devices appeared a century later, and the assistance of computers was incorporated three quarters of a century later still. Nonetheless, the insights derived from the skilful use of afterimages have tended to be overlooked in the histories of eye movements. One of the reasons that less attention has been paid to studies using afterimages is that they became tainted with other ‘subjective’ measures of eye movements as opposed to the ‘objective’ recording methods of the 20th century. A second factor was that the early studies were concerned with vertigo, which resulted in involuntary movements of the eyes.

The objective eye trackers developed in the late 19th and early 20th centuries allowed crucial new insights into the true nature of eye movements. Researchers were unanimously surprised by what they found; eye movements were not as smooth and continuous as they subjectively appeared. These new devices for measuring eye movements accelerated interest in their nature. The technological advancements allowed new questions to be addressed and indeed identified new and unexpected questions in the psychology and physiology of eye movements and their relation to cognition and visual experience. Eye-tracking technology continues to evolve, and with it, so do the range of questions that can be

addressed. Increasingly, the eyes are measured when inspecting objects in three-dimensional space, and it is probable that these applications will have the most profound influence on our understanding of this most integrated aspect of active vision.

Acknowledgements. I am grateful to Galina Paramei and Marco Bertamini for inviting me to deliver an address to the AVA meeting that was held in Liverpool Hope University in March 2010, and I thank Ben Tatler for many stimulating discussions of early eye movement research. I would also like to express my appreciation to two anonymous reviewers for their constructive comments on the original manuscript.

References

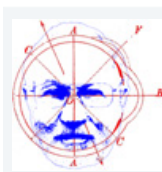
- Ahrens A, 1891 *Die Bewegung der Augen beim Schreiben* (Rostock: University of Rostock) ◀
- Bacon F, 1857 *The Works of Francis Bacon* Eds J Spedding, R L Ellis, D D Heath (London: Longman, Simpkin, Hamilton, Wittaker, Bain, Hodgson, Washbourne, Bohn, Richardson, Houlston, Bickers and Bush, Willis and Southeran, Cornish, Booth, and Snow) ◀
- Bárány R, 1906 “Untersuchungen über den vom Vestibularapparat des Ohres reflektorisch ausgelösten rhythmischen Nystagmus und seine Begleiterscheinungen” *Monatsschrift für Ohrenheilkunde* **40** 193–297 ◀
- Bárány R, 1913 “Der Schwindel und seine Beziehungen zum Bogengangapparat des inneren Ohres. Bogengangapparat und Kleinhirn (Historische Darstellung. Eigene Untersuchungen.)” *Naturwissenschaften* **1** 396–401 doi:10.1007/BF01490389 ◀
- Barlow H B, 1952 “Eye movements during fixation” *Journal of Physiology* **116** 290–306 ◀
- Barlow H B, 1963 “Slippage of contact lenses and other artefacts in relation to fading and regeneration of supposedly stable retinal images” *The Quarterly Journal of Experimental Psychology* **15** 36–51 doi:10.1080/17470216308416550 ◀
- Baumann C, 2002 *Der Physiologe Ewald Hering (1834–1918)* (Frankfurt: Hänsel-Hohenhausen) ◀
- Bell C, 1803 *The Anatomy of the Human Body volume 3* (London: Longmans, Rees, Cadell and Davies) ◀
- Bell C, 1823 “On the motions of the eyes, in illustration of the uses of the muscles and of the orbit” *Philosophical Transactions of the Royal Society of London* **113** 166–186 doi:10.1098/rstl.1823.0017 ◀
- Bell C, 1844 *The Anatomy and Philosophy of Expression as Connected with the Fine Arts* 3rd edition (London: John Murray) ◀
- Bell G J, 1870 (Ed.) *Letters of Sir Charles Bell, Selected from his Correspondence with his Brother George Joseph Bell* (London: John Murray) ◀
- Boring E G, 1942 *Sensation and Perception in the History of Experimental Psychology* (New York: Appleton-Century) ◀
- Breuer J, 1874 “Über die Funktion der Bogengänge des Ohrlabyrinthes” *Wiener medizinisches Jahrbuch* **4** 72–124 ◀
- Buswell G T, 1935 *How People Look at Pictures: a Study of the Psychology of Perception in Art* (Chicago, IL: University of Chicago Press) ◀
- Buswell G T, 1937 *How Adults Read* (Chicago, IL: University of Chicago Press) ◀
- Carmichael L, 1926 “Sir Charles Bell: A contribution to the history of physiological psychology” *Psychological Review* **33** 188–217 doi:10.1037/h0072659 ◀
- Carpenter R H S, 1988 *Movements of the eyes* 2nd edition (London: Pion) ◀
- Carpenter R H S (Ed.) 1991 *Vision and Visual Dysfunction. Volume 8. Eye Movements* (London: Macmillan) ◀
- Comrie J D, 1932 *History of Scottish Medicine, volume 2* (London: Baillière, Tindall and Cox) ◀
- Crum Brown A, 1874 “Preliminary note on the sense of rotation and the function of the semicircular canals of the internal ear” *Proceedings of the Royal Society of Edinburgh* **8** 255–257 ◀
- Crum Brown A, 1878 “Cyon’s Researches on the Ear. II” *Nature* **18** 657–659 doi:10.1038/018657a0 ◀
- Crum Brown A, 1895 *The Relation between the Movements of the Eyes and the Movements of the Head* (London: Henry Frowde) ◀
- Darwin E, 1794 *Zoonomia; or, the Laws of Organic Life, volume 1* (London: Johnson) ◀
- Darwin E, 1801 *Zoonomia; or, the Laws of Organic Life, volume 4* 3rd edition (London: Johnson) ◀
- Darwin R W, 1786 “New experiments on the ocular spectra of light and colours” *Philosophical Transactions of the Royal Society of London* **76** 313–348 doi:10.1098/rstl.1786.0016 ◀
- Delabarre E B, 1898 “A method of recording eye movements” *American Journal of Psychology* **9** 572–574 doi:10.2307/1412191 ◀

- Ditchburn R W, 1973 *Eye-Movements and Visual Perception* (Oxford: Clarendon Press) ◀
- Dodge R, 1900 "Visual perception during eye movement" *Psychological Review* **7** 454–465 doi:10.1037/h0067215 ◀
- Dodge R, 1903 "Five types of eye movement in the horizontal meridian plane of the field of regard" *American Journal of Physiology* **8** 307–329 ◀
- Dodge R, 1904 "The participation of eye movements and the visual perception of Motion" *Psychological Review* **11** 1–14 doi:10.1037/h0071641 ◀
- Dodge R, 1916 "Visual motor functions" *Psychological Bulletin* **13** 421–427 doi:10.1037/h0074240 ◀
- Dodge R, Cline T S, 1901 "The angle velocity of eye movements" *Psychological Review* **8** 145–157 doi:10.1037/h0076100 ◀
- Donders F C, 1869 "Over de snelheid van psychische processen" *Nederlandsch Archief voor Genees- en Natuurkunde* **4** 117–145 ◀
- Duke-Elder S, Abrams D, 1970 *System of Ophthalmology, volume 5* (London: Kimpton) ◀
- Duke-Elder S, Wybar K, 1973 *System of Ophthalmology, volume 6* (London: Kimpton) ◀
- Du Laurens A, 1599 *A Discourse of the Preservation of the Sight: of Melancholic Diseases, of Rheumes, and of Old Age* translated by R Surphlet (London: The Shakespeare Association) ◀
- Eggert T, 2007 "Eye movement recording methods" in *Neuro-ophthalmology: Neuronal Control of Eye Movements* Eds A Straube, U Büttner pp 15–34 (Basel: Karger) ◀
- Findlay J M, Gilchrist I D, 2003 *Active Vision: the Psychology of Looking and Seeing*. (Oxford: Oxford University Press) ◀
- Hallaran W S, 1818 *An Enquiry into the Causes Producing the Extraordinary Addition to the Number of Insane, Together with Extended Observations on the Cure of Insanity: with Hints as to the Better Management of Public Asylums*, 2nd edition (Cork: Edwards & Savage) ◀
- Helmholtz H, 1864 "The Croonian Lecture. On the normal motions of the human eye in relation to binocular vision" *Proceedings of the Royal Society of London* **13** 186–199 doi:10.1098/rspl.1863.0046 ◀
- Helmholtz H, 1867 "Handbuch der physiologischen Optik" in G Karsten (Ed.) *Allgemeine Encyclopädie der Physik, volume 9* (Leipzig: Voss) ◀
- Helmholtz H, 1925 *Helmholtz's Treatise on Physiological Optics, volume 3* translated by J P C Southall (New York: Optical Society of America) ◀
- Hering E, 1868 *Die Lehre vom binocularen Sehen* (Leipzig: Engelmann) ◀
- Hering E, 1879a "Der Raumsinn und die Bewegungen des Auges" in *Handbuch der Physiologie der Sinnesorgane, volume 3* Ed. L Herrmann pp 341–601 (Leipzig: Vogel) ◀
- Hering E, 1879b "Über Muskelgeräusche des Auges" *Sitzberichte der kaiserlichen Akademie der Wissenschaften in Wien. Mathematisch-naturwissenschaftliche Klasse* **79** 137–154 ◀
- Hering E, 1942 *Spatial Sense and Movements of the Eyes* translated by C A Radde (Baltimore: American Academy of Optometry) ◀
- Hering E, 1977 *The Theory of Binocular Vision* translated by L Stark, B Bridgeman (New York: Plenum Press) ◀
- Hirsch A (Ed, 1929 *Biographisches Lexikon der hervorragenden Ärzte aller Zeiten und Völker, volume 4* (Berlin: Urban and Schwarzenberg) ◀
- Hirschberg J, 1982 *The History of Ophthalmology, volume 1* translated by F C Blodi (Bonn: Wayenborgh) ◀
- Hitzig E, 1871 "Über die beim Galvanisiren des Kopfes entstehenden Störungen der Muskelinnervation und der Vorstellung vom Verhalten im Raume" *Archiv für Anatomie, Physiologie und wissenschaftliche Medizin* 716–771 ◀
- Howard I P, 1982 *Human Visual Orientation* (New York: Wiley) ◀
- Howard I P, 1999 "The Helmholtz-Hering debate in retrospect" *Perception* **28** 543–549 doi:10.1068/p2805ed ◀
- Howard I P, 2002 *Seeing in Depth, volume 1* (Toronto: Porteous) ◀
- Howard I P, Templeton W B, 1966 *Human Spatial Orientation* (London: Wiley) ◀
- Howard I P, Wade N J, 1996 "Ptolemy's contributions to the geometry of binocular vision" *Perception* **25** 1189–1202 doi:10.1068/p251189 ◀
- Hueck A, 1838 *Die Achsendrehung des Auges* (Dorpat: Kluge) ◀
- Hueter C, 1878 "Versuche zur Begründung einer Auscultation für chirurgisch-diagnostischen Zwecke" *Centralblatt für medicinischen Wissenschaften* **51** ◀
- Huey E B, 1898 "Preliminary experiments in the physiology and psychology of Reading" *American Journal of Psychology* **9** 575–586 doi:10.2307/1412192 ◀
- Huey E B, 1900 "On the psychology and physiology of reading. I" *American Journal of Psychology* **11** 283–302 doi:10.2307/1412745 ◀

-
- Huey E B, 1901 "On the psychology and physiology of reading. II" *American Journal of Psychology* **12** 292–312 doi:10.2307/1412280 ◀
- Huey E B, 1908 *The Psychology and Pedagogy of Reading* (New York: Macmillan) ◀
- Hunter J, 1786 *Observations on certain Parts of Animal Economy* (London: Published by the author) ◀
- Javal L, 1878 "Essai sur la physiologie de la lecture" *Annales d'Oculistique* **80** 240–274 ◀
- Javal L, 1879 "Essai sur la physiologie de la lecture" *Annales d'Oculistique* **82** 242–253 ◀
- John H J, 1959 *Jan Evangelista Purkyně: Czech Scientist and Patriot 1787–1869* (Philadelphia: American Philosophical Society) ◀
- Jurin J, 1738 "An essay on distinct and indistinct vision" in *A Compleat System of Opticks in Four Books* Ed. R Smith pp 115–171 (Cambridge: Published by the author) ◀
- Knight C, 1837 *The Gallery of Portraits: with Memoirs, volume 7* (London: Charles Knight) ◀
- Koenigsberger L, 1902 *Hermann von Helmholtz, volume 1* (Braunschweig: Vieweg) ◀
- Kruta V, 1969 *J E Purkyně (1787–1869) Physiologist. A Short Account of his Contributions to the Progress of Physiology with a Bibliography of his Works* (Prague: Czechoslovak Academy of Sciences) ◀
- Lamare M, 1892 "Des mouvements des yeux dans la lecture" *Bulletins et Mémoires de la Société Française d'Ophthalmologie* **10** 354–364 ◀
- Land M F, Tatler B W, 2009 *Looking and Acting: Vision and Eye Movements in Natural Behaviour* (Oxford: Oxford University Press) ◀
- Landolt E, 1879 *A Manual of Examination of the Eye* translated by S M Burnett (London: Bailliere, Tindall and Cox) ◀
- Legge G E, 2006 *Psychophysics of Reading in Normal and Low Vision* (London: Routledge) ◀
- Leigh R J, Zee D S, 2006 *The Neurology of Eye Movements*, 4th edition (New York: Oxford University Press) ◀
- Lejeune A, 1956 *L'Optique de Claude Ptolémée dans la Version Latine d'après l'Arabe de l'Émir Eugène de Sicile* (Louvain: Université de Louvain) ◀
- Lesky E, 1965 *Die Wiener medizinische Schule im 19. Jahrhundert* (Graz: Böhlau) ◀
- MacCurdy E, 1938 *The Notebooks of Leonardo da Vinci, volume 1* (London: Cape) ◀
- Mach E, 1873 "Physikalische Versuche über den Gleichgewichtssinn des Menschen" *Sitzungsberichte der Wiener Akademie der Wissenschaften* **68** 124–140 ◀
- Mach E, 1875 *Grundlinien der Lehre von den Bewegungsempfindungen* (Leipzig: Engelmann) ◀
- Maddox E E, 1907 *Tests and Studies of the Ocular Muscles*, 3rd edition (Philadelphia: Keystone) ◀
- Magnus H, 1901 *Die Augenheilkunde der Alten* (Breslau: Kern) ◀
- McMurrich J P, 1930 *Leonardo da Vinci the Anatomist (1452–1519)* (Baltimore: Williams & Wilkins) ◀
- Mariotte E, 1683 "An account of two letters of Mr. Perrault and Mr. Mariotte, concerning vision" *Philosophical Transactions of the Royal Society* **13** 266–267 ◀
- May M T, 1968 *Galen On the Usefulness of the Parts of the Body* (Ithaca, New York: Cornell University Press) ◀
- Meyerhof M, 1928 *The Book of the Ten Treatises on the Eye, Ascribed to Hunain ibn Is-Hâq (809–877 AD)* (Cairo: Government Press) ◀
- Müller J, 1826a *Zur vergleichenden Physiologie des Gesichtssinnes des Menschen und der Thiere, nebst einen Versuch über die Bewegung der Augen und über den menschlichen Blick* (Leipzig: Cnobloch) ◀
- Müller J, 1826b *Über die phantastischen Gesichterscheinungen* (Coblenz: Hölscher) ◀
- Müller J, 1840 *Elements of Physiology, volume 1* translated by W Baly (London: Taylor and Walton) ◀
- Müller J, 1843 *Elements of Physiology, volume 2* translated by W Baly (London: Taylor and Walton) ◀
- Murchison C (Ed, 1930 *A History of Psychology in Autobiography, volume 1* (Worcester, MA: Clark University Press) doi:10.1037/11401-000 ◀
- Nagel W A, 1896 "Über kompensatorische Raddrehungen der Augen" *Zeitschrift für Psychologie und Physiologie der Sinnesorgane* **12** 331–354 ◀
- Noorden G K, 1996 *Binocular Vision and Ocular Motility*, 5th edition (St. Louis: Mosby) ◀
- O'Leary De L, 1949 *How Greek Science passed to the Arabs* (London: Routledge) ◀
- Orschansky J, 1899 "Eine Methode die Augenbewegungen direct zu untersuchen" *Zentralblatt für Physiologie* **12** 785–785 ◀
- Pettigrew T J, 1840a *Medical Portrait Gallery, volume 3* (London: Whittaker) ◀
- Pettigrew T J, 1840b *Medical Portrait Gallery, volume 4* (London: Whittaker) ◀
- Polyak S L, 1942 *The Retina* (Chicago: University of Chicago Press) ◀

- Polyak S, 1957 *The Vertebrate Visual System* (Chicago: University of Chicago Press) ◀
- Porterfield W, 1737 “An essay concerning the motions of our eyes. Part I. Of their external motions” *Edinburgh Medical Essays and Observations* **3** 160–263 ◀
- Porterfield W, 1759 *A Treatise on the Eye, the Manner and Phænomena of Vision, volume 2* (Edinburgh: Hamilton and Balfour) ◀
- Pspotníčková J, 1955 *Jan Evangelista Purkyně* (Prague: Orbis) ◀
- Purkinje J, 1820 “Beyträge zur näheren Kenntniss des Schwindels aus heautognostischen Daten” *Medicinische Jahrbücher des kaiserlich-königlichen öesterreichischen Staates* **6** 79–125 ◀
- Purkinje J, 1825 *Beobachtungen und Versuche zur Physiologie der Sinne. Neue Beiträge zur Kenntniss des Sehens in subjectiver Hinsicht* (Berlin: Reimer) ◀
- Rähmann E, 1878 “Über den Nystagmus und seine Ätiologie” *Albrecht von Græfes Archiv für Ophthalmologie* **24** 237–317 doi:10.1007/BF01945601 ◀
- Ratliff F, 1952 “The role of physiological nystagmus in monocular acuity” *Journal of Experimental Psychology* **43** 163–172 doi:10.1037/h0062338 ◀
- Ratliff F, Riggs L A, 1950 “Involuntary motions of the eye during monocular fixation” *Journal of Experimental Psychology* **40** 687–701 doi:10.1037/h0057754 ◀
- Ross W D (Ed.) 1927 *The Works of Aristotle, volume 7* (Oxford: Clarendon) ◀
- Ruete C G T, 1845 “Die Physiologie in ihrer Anwendung auf die Augenheilkunde” in *Handwörterbuch der Physiologie, volume 3 part 2* Ed. R Wagner pp 234–338 (Baunschweig: Vieweg) ◀
- Ruete C G T, 1853 *Lehrbuch der Ophthalmologie, 2nd edition* (Braunschweig: Vieweg) ◀
- Sabra A I, 1989 *The Optics of Ibn Al-Haytham. Books I-III* (London: The Warburg Institute) ◀
- Sauvages de F B, 1772a *Nosologie Méthodique, ou distribution des maladies en classes, en genres et en especes, suivant l'esprit de Sydenham, & la méthode des botanistes, volume 4* (Lyon: Bruyset) ◀
- Sauvages de FB, 1772b *Nosologie Méthodique, ou distribution des maladies en classes, en genres et en especes, suivant l'esprit de Sydenham, & la méthode des botanistes, volume 7* (Lyon: Bruyset) ◀
- Scheiner C, 1619 *Oculus, hoc est fundamentum opticum* (Innsbruck: Agricola) ◀
- Schmitz E-H, 1983 *Handbuch zur Geschichte der Optik, volume 3* (Bonn: Weyerborgh) ◀
- Sharples R W, 2003 “On dizziness” in *Theophrastus of Eresus on Sweat, on Dizziness, and on Fatigue* Eds W W Fortenbaugh, R W Sharples, M G Sollenberger pp 169–250 (Leiden: Brill) ◀
- Shastid T H, 1917 “History of ophthalmology” in *The American Encyclopedia and Dictionary of Ophthalmology, volume 11* Ed. C A Wood pp 8524–8904 (Chicago: Cleveland Press) ◀
- Singer C, 1956 *Galen on Anatomical Procedures* (London: Oxford University Press) ◀
- Smith A M, 1996 *Ptolemy's Theory of Visual Perception: An English Translation of the Optics with Introduction and Commentary* (Philadelphia: The American Philosophical Society) ◀
- Smith R, 1738 *A Compleat System of Opticks* (Cambridge: Published by the author) ◀
- Stirling W, 1902 *Some Apostles of Physiology in Four Books* (London: Waterlow) ◀
- Stratton G M, 1902 “Eye-movements and the aesthetics of visual form” *Philosophische Studien* **20** 336–359 ◀
- Stratton G M, 1906 “Symmetry, linear illusions and the movements of the eye” *Psychological Review* **13** 82–96 doi:10.1037/h0072441 ◀
- Sugana G M, 1973 *The Complete Paintings of Toulouse-Lautrec* (London: Weidenfeld and Nicolson) ◀
- Tatler B W, 2009 *Eye Guidance in Natural Scenes* (Hove, UK: Psychology Press) ◀
- Tatler B W, Wade N J, 2003 “On nystagmus, saccades, and fixations” *Perception* **32** 167–184 doi:10.1068/p3395 ◀
- Tatler B W, Wade N J, Kwan H, Findlay J M, Velichkovsky B M, 2010 “Yarbus, eye movements, and vision” *i-Perception* **1** 7–27 doi:10.1068/i0382 ◀
- Taylor E A, 1937 *Controlled Reading* (Chicago: University of Chicago Press) ◀
- Tscherning M, 1898 *Optique Physiologique* (Paris: Carré and Naud) ◀
- Tscherning M, 1900 *Physiologic Optics* translated by C Weiland (Philadelphia: Keystone) ◀
- Turner R S, 1994 *In the Eye's Mind: Vision and the Helmholtz-Hering Controversy* (Princeton: Princeton University Press) ◀
- Verheijen F J, 1961 “A simple after image method demonstrating the involuntary multi-directional eye movements during fixation” *Journal of Modern Optics* **8** 309–312 doi:10.1080/713826390 ◀
- Vesalius A, 1543 *De Humani Corporis Fabrica* (Basel: Oporini) ◀
- Volkmann A W, 1846 “Sehen” in *Handwörterbuch der Physiologie, volume 3 part 1* Ed. R Wagner pp 265–351 (Baunschweig: Vieweg) ◀
- Wade N J, 2002 “Erasmus Darwin (1731–1802)” *Perception* **31** 643–650 doi:10.1068/p3106ed ◀

- Wade N J, 2007 "Scanning the seen: vision and the origins of eye movement research" in *Eye Movements: A Window on Mind and Brain* Eds R P G van Gompel, M H Fischer, W S Murray, R L Hill pp 31–61 (Oxford: Elsevier) ◀
- Wade N J, 2010 "The Darwins and Wells: From revolution to evolution" *Journal of the History of the Neurosciences* **19** 85–104 doi:10.1080/09647040903504807 ◀
- Wade N J, Norrsell U, Presly A, 2005 "Cox's chair: 'a moral and a medical mean in the treatment of maniacs'" *History of Psychiatry* **16** 73–88 doi:10.1177/0957154X05046093 ◀
- Wade N J, Tatler B W, 2005 *The Moving Tablet of the Eye: The Origins of Modern Eye Movement Research* (Oxford: Oxford University Press) ◀
- Wade N J, Tatler B W, 2009 "Did Javal measure eye movements during reading?" *Journal of Eye Movement Research* **5** 5–7 ◀
- Wade N J, Tatler B W, Heller D, 2003 "Dodging the issue: Dodge, Javal, Hering, and the measurement of saccades in eye movement research" *Perception* **32** 793–804 doi:10.1068/p3470 ◀
- Walls G, 1962 "The evolutionary history of eye movements" *Vision Research* **2** 69–80 doi:10.1016/0042-6989(62)90064-0 ◀
- Weisheipl L A (Ed.) 1980 *Albertus Magnus and the Sciences: Commemorative Essays* (Toronto: Pontifical Institute of Mediaeval Studies) ◀
- Wells W C, 1792 *An Essay upon Single Vision with two Eyes: together with Experiments and Observations on several other Subjects in Optics* (London: Cadell) ◀
- Wells W C, 1794a "Reply to Dr. Darwin on vision" *The Gentleman's Magazine and Historical Chronicle* **64** 794–797 ◀
- Wells W C, 1794b "Reply to Dr. Darwin on vision" *The Gentleman's Magazine and Historical Chronicle* **64** 905–907 ◀
- Wood W, 1880 *Portraits of the One Hundred Greatest Men in History, volume 4* (London: Sampson Low, Marston, Searle, and Rivington) ◀
- Wundt W, 1862 *Beiträge zur Theorie der Sinneswahrnehmung* (Leipzig: Winter) ◀
- Yarbus A L, 1967 *Eye Movements and Vision* translated by B Haigh (New York: Plenum Press) ◀
- Young L R, Henn V, Scherberger H (Eds), 2001 *Fundamentals of the Theory of Movement Perception by Dr. Ernst Mach* (New York: Kluwer/Plenum) ◀
- Zemon V, 2002 "Floyd Ratliff" *Proceedings of the American Philosophical Society* **146** 395–401 ◀



Nick Wade received his degree in psychology from the University of Edinburgh and his PhD from Monash University, Australia. This was followed by a postdoctoral fellowship from the Alexander von Humboldt Stiftung, at Max-Planck-Institute for Behavioural Physiology, Germany. His subsequent academic career has been at Dundee University, where he is now Emeritus Professor. His research interests are in the history of vision research, binocular and motion perception, and the interplay between visual science and art.