A technical eye inspired by biology

It was Erasmus Darwin (1731–1802), the grandfather of Charles Darwin, who first wrote about visual vertigo in his Zoonomia, or, The Laws of Organic Life in 1794: ‘many people, when they arrive at 50 or 60 years of age, are affected with slight vertigo; which is generally but wrongly ascribed to indigestion, but in reality arises from a beginning defect of their sight ... these people do not see objects so distinctly as formerly, and by exerting their eyes more than usual they perceive the apparent motions of objects, and confound them with the real motions of them; and therefore cannot accurately balance themselves so as easily to preserve their perpendicularity by them’. Historically, it is remarkable that this description of visual vertigo and its consequences for postural balance date back to a time when vestibular function was not even understood, nearly a century before the publication of Mach’s (1875) Fundamentals of the Theory of Motion Perception (Brandt, 1991). Darwin’s Zoonomia is a mine of information on early concepts of sensorimotor control of eye movements and multisenory interactions, for example his understanding of height vertigo, which is still appealing: ‘Anyone, who stands alone on the top of a high tower, if he has not been accustomed to balance himself by objects placed at such distances and with such inclinations, begins to stagger, and endeavours to recover himself by his muscular feelings. During this time the apparent motion of objects at a distance below him is very great and the impressions of this apparent motion continue a little time after he has experienced them; and he is persuaded to incline the contrary way to counteract their effects; and either immediately falls, or applying his hands to the building, uses his muscular feeling to preserve his perpendicular attitude, contrary to the erroneous persuasions of the eyes’.

The book by Nicholas J. Wade and Benjamin W. Tatler—The Moving Tablet of the Eye—provides a fascinating and invaluable survey of the origins of modern eye movement research. As the authors state, there are numerous histories of optics and ophthalmology, but only a very few about eye movements. In the rare instances when they have been assayed historically, it has been in terms of their malfunction rather than normal operation. The title of their book is taken from the poem The Temple of Nature by Erasmus Darwin, who attributed considerable theoretical importance to eye movements. Using a candle flame as light source, he examined them experimentally by means of after-images, as did William Charles Wells (1757–1817). Changes in position of the after-image on a wall or screen reflect saccadic or pursuit eye movements. The book reveals in an educational and also entertaining way many fascinating aspects not only of ancient and modern eye measurement devices but also of visual perceptual mechanisms and illusions, and the history of eye movement terminology. The term after-image (‘Nachbild’) was used by Purkinje (1823) and was taken up by Fechner (1838) in his more detailed study of eye movements. Wade and Tatler also provide us with a rich source of portraits of influential scientists, scientific drawings and photographs of experimental setups, apparatuses and recordings.

All such historical presentations of ocular motor science tend to make evident the proximity of biology and technology, and how they interact. This is perhaps best seen in Ruete’s ophthalmotrope. An illustration of it made by Helmholtz appears in the book, and recently we found a wooden model of this device in the archives of a German Department of Ophthalmology (Fig. 1).

The current research on eye movement control now concentrates on this special relationship between biology and technology, a development that David R. Robinson with his engineering approach to neuroscience revolutionized (Robinson, 1981). Albert Fuchs praised Robinson’s merits for the ocular motor community, noting that he coined such familiar descriptors as ‘local feedback loop’ and ‘burst generator’. He said that the forces driving the eyes act on the ‘eye movement plant’. He modelled these forces in saccades as a ‘pulse and step’ and later described dysmetric saccades as resulting from ‘pulse-step mismatch’. The pulse and step were kept balanced by the ‘cerebellar repair shop’. Finally, of course, there is his legendary term for velocity-to-position conversion, the ‘oculomotor integrator’, which maintains...
eccentric eye position after a movement, has a finite 'time constant' and therefore is considered to be 'leaky' (Fuchs et al., 1993).

Nowadays it is obvious that the problems of sensorimotor control of biological systems are related to the control of technical systems. Indeed, the quantitative analysis of a biological system is not possible without first constructing a simple algorithmic model. A model can provide important insights into the structure of a system, and it does increase our understanding of the system itself. Modelling can also reveal the logical errors of simple clinical concepts. Moreover, to be able to simulate the complete or incomplete failure of a single element or an entire pathway permits us to pose direct clinical questions: questions about syndromes not yet observed, about the localization of the damage, and the mechanisms involved (Brandt, 2001).

Let us take the vestibulo-ocular reflex as an example. A basic model of the vestibulo-ocular reflex consists of measurable quantities of system input (e.g. a head velocity), which influence system components that communicate with each other and are also directly and reciprocally coupled. System output is again defined as measurable quantities (e.g. eye position). In a model in which the input is a head turn and the output eye movements, the vestibulo-ocular reflex drives the eyes to move in the opposite direction of the turning head. This keeps the gaze on the target stable. Static models describe the vestibular ocular reflex by means of mathematical matrices, whereas dynamic models use elements of linear system theory, such as high and low pass filters.

Another approach uses neuronal networks with non-linear features of model neurons and their connections. By means of such networks, the relationship between the system elements can be weighted according to their importance and adjusted to take learning processes into account. This was accomplished in a basic version of a 3D mathematical sensorimotor feed-forward model that elucidated otolithic control of binocular static eye position (Glasauer et al., 1999). Model input was defined as gravitational acceleration relative to the head (Fig. 2). The utricles represented coordinate transformations from head coordinates into utricular coordinates. The vestibular nuclei were assumed to transform these utricular coordinates into eye muscle coordinates and to scale the afferent information. The oculomotor nuclei weighted the information from parallel pathways like the medial longitudinal fascicle and the brachium conjunctivum. The eye muscles simply added pooled agonist and antagonist motoneuron activity. The box 'eye' contained the transformation from eye muscle coordinates back into head coordinates. Model output was defined as eye position relative to the head and was given as rotational vectors.

The mathematical model is depicted in Fig. 2. It can accurately simulate 3D ocular deviations of patients who have unilateral utricular loss, complete vestibular nerve failure and lesions of the vestibular nuclei or the pathways for graviception in the brainstem. To find an explanation of the mechanism underlying central positional nystagmus in neurological patients with lesions of the posterior fossa, we first had to implement the saccadic burst generator, the neural velocity to eye position integrator, including the experimentally demonstrated leakage in the torsional component, and the otolith-dependent neural control of Listing’s plane as well (Glasauer et al., 2001). The model showed for the first time that lesions of assumed otolith input from the cerebellum to the burst generator or the neural integrator result in central positional nystagmus.

David Robinson’s engineering concepts of eye movement control made the construction of such models possible as well as the demonstration of the elements, quantitative analysis and localization of eye movement control in animals and humans (Crawford, 1994; Fukushima and Kaneko, 1995). The structure, pathways and functions of eye movements are now better understood than any other biological sensorimotor system.

The book by Nicholas Wade and Benjamin Tatler contains a chapter on remote eye movement recording devices and head-mounted portable eye trackers. Such portable trackers allow monitoring of eye movements and visual exploratory behaviour in real-world activities outside the laboratory. We were inspired to combine such technical devices with the biological vestibulo-ocular reflex, which has evolved and been optimized over millions of years. We developed a new camera system for surgeons that looks where the eyes look.

This device uses voluntary and reflexive eye movements that are registered in 3D by video-oculography and then computed online as signals to drive the camera servo motors in three planes: yaw, pitch and roll (Fig. 3). Its primary objective is to allow freely mobile users to aim the optical axis of a head-mounted camera system at the target at which they are voluntarily looking in the visual field, while the ocular reflexes stabilize any image shaking by naturally counter-rolling for ‘gaze-in-space’ of the camera during head and
visual scene movements and during locomotion (Schneider et al., 2005; Brandt et al., 2006). Thus, surgeons using this camera can move their head and eyes during image acquisition without having to worry about image-shaking artefacts, and at the same time continuously document an operation. To prevent perception of apparent motion of the visual scene (oscillopsia) during rapid eye and camera movements, an artificial saccadic suppression mechanism can be incorporated, which is triggered by saccade onset. This artificial motion suppression can be achieved by repeating (‘freezing’) the last frame acquired before saccade onset for the duration of the camera saccade. In addition, the vergence angle of the eyes delivers valuable information for a possible autofocus functionality, since this angle directly depends on the distance of the eyes from the observed object.

Another exciting aspect of the book The Moving Tablet of the Eye is that it does not describe the work of the individual scientist in isolation but in the context of interacting ideas and findings of groups of scientists who collaborate, such as Wells and Darwin, Purkinje and Flourens or Mach, Breuer, and Crum Brown. Fortunately, the book was not conceived as an encyclopaedia, but some readers will still miss one name or the other, for example Johannes Ohm (1928), who invented the technique of ‘Hebelnystagmographie’ in 1913 and which he used meticulously to measure eye movements as a practising ophthalmologist, especially the nystagmus of miners (‘Augenzittern’). I myself also regretted the absence of my highly esteemed teacher Richard Jung, who made electronystagmography an integral part of clinical routine (Jung and Mittermaier, 1939). Another name missing is that of Gordon Holmes who focussed on vision, but also...
contributed significantly to our understanding of eye movements, stereopsis and oculars (Phillips, 1979). His interest in dynamic spatial orientation was mainly visual and oculomotor, as witnessed by the quite typical title of one of his late lectures, given as the John Mallet Purser lecture in 1936: ‘Looking and seeing: movements and fixation of the eyes’. Finally, as a neurologist, I cannot conclude without mentioning the work of John Leigh and David Zee as presented in their unrivalled textbook, ‘The Neurology of Eye Movements’.

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