

PART

one

***Physiology of the
Sensorimotor
Cooperation of
the Eyes***

General Introduction

The Eyes as a Sensorimotor Unit

The two human eyes with their adnexa and nervous system connections form an indivisible entity. This fact must always be kept in mind, but for the purpose of study a distinction between the sensory and the motor systems is necessary.

Light stimuli, having gone through the changes imposed on them by the refractive media, reach the peripheral organ of vision, the retina, and produce physical and chemical alterations in the retinal receptors. In turn, these alterations provoke in the retinal neurons physicochemical and electrical changes that are transmitted as impulses to the central nervous system. Eventually, visual sensations of form, spatial relationships, and color appear in our consciousness. This sequence of events may be called the *sensory* aspect of the visual process. The events in the sensory part of the visual system also precipitate a chain of responses in the *motor* system of the eyes, in the central and peripheral nervous arrangements, and in the inner and outer muscles of the eyes.

In this unitary sensorimotor system, the sensory system transmits and elaborates the information received about the outside world. The motor system has no independent significance and is entirely in the service of the sensory system, by which it is largely governed. Understanding of this system is essential for the interpretation of the neuromuscular anomalies of the eyes.

The Tasks of the Motor System

The tasks of the motor system are (1) to enlarge the field of view by transforming the field of vision into the field of fixation, (2) to bring the image of the object of attention onto the fovea and keep it there, and (3) to position the two eyes in such a way that they are properly aligned at all times, thereby ensuring the maintenance of single binocular vision.

Nature and Control of Ocular Movements

Voluntary and Involuntary Eye Movements

In agreement with a time-honored classification, a distinction is made between voluntary and involuntary eye movements. *Voluntary* simply implies that the movements are “willed” by the individual, presumably as a result of a chain of impulses that originate in the cortex. *Involuntary* eye movements are not willed by the individual and, indeed, occur without awareness. They are elicited mainly by stimuli arising from outside the body, for example, visual or auditory, or those arising from within the body, for example, vestibular. The former are referred to as *exteroceptive*, the latter as *interoceptive* stimuli.

When the illuminance of the retina changes, the pupil of the eye constricts or dilates. When we

tilt our head to one shoulder, the eyes make a parallel movement around their anteroposterior axes, so the vertical meridians of the retinas turn in the direction opposite that of the head. The eyes attempt to right themselves. Both these motor reactions are highly useful *unconditioned reflexes*. The central nervous system structures that mediate these reflexes are subcortical. The individual is not aware they are taking place.

When a light stimulus reaches the retinal periphery, the eye turns and causes the stimulus to impinge on the area of highest resolving power, the fovea. If a binocularly fixated object approaches the eyes, the visual axes converge to maintain fixation. If for some reason the proper alignment of the visual axes has been lost, corrective fusional movements occur and restore binocular fixation. All these movements are highly useful, and most of them are also reflexive, but there is a significant difference between them and reflex movements.

If a person is lost in thought or concentrating on an object of regard, another object approaching from one side may not be noticed—at times with regrettable results. One can voluntarily stop convergence or voluntarily overconverge. In inattentive states, one may fail to make fusional movements. All these movements, then, though basically reflexive, require the cooperation of the cerebral cortex, in particular a state of visual attention. Hofmann and Bielschowsky,⁸ who published their classic study on fusional movements in 1900, clearly noted the reflex nature of these movements, but were also aware that they did not come about without the concurrence of attention. They designated the fusional movements as *psycho-optical reflexes*. At the time Hofmann and Bielschowsky published their paper, Pavlov had just begun his work on conditioned reflexes, and his findings were not yet published. Today, reflex movements that require cooperation of the cerebral cortex are designated as *conditioned reflexes*.

In summary, all eye movements, insofar as they are not voluntary, are unconditioned or conditioned reflexes performed in the service of the sensory system of the eyes, specifically in the interest of clear, distinct vision and of binocular fixation.

Cybernetic Control of the Eye Movements

The concept of reflex activity, with the neuron as the unit of the anatomical and physiologic organi-

zation of the nervous system, for a long time has been the cornerstone of neurophysiology and neurology and, consequently, also that of the sensorimotor system of vision. Chavasse¹ introduced an extreme reflexologic view into the analysis of neuromuscular anomalies of the eyes. He extended the concept of unconditioned reflexes, in the manner of Pavlov's teaching on the higher nervous activity, to include the sensory visual responses. Chavasse's views are discussed in detail in later chapters.

Control of the eye movements thus was interpreted as resulting from exteroceptive and proprioceptive stimulations. More recently, a new way of thinking and a new vocabulary have been developing. Cybernetics and information theory, together with spectacular advances in electronic technology, have brought about a revolution that could not help have an influence on the interpretation of biological phenomena. The terminology of the engineer has taken on a strangely biological cast, and the terminology of the biologist is increasingly borrowing terms from the engineer. "Closed loops," "open loops," "feedback," and "servomechanisms" are words heard today as commonly from biologists as from engineers.

The information received from the retina may be designated as retinal error signal (the difference between the desired and received placement of the image) or as *outflow* feedback. Signals sent out from tension sensors in the extraocular muscles would then represent an *inflow* (proprioceptive) feedback. Inflow feedback is the common mechanism provided for in skeletal muscles, for example, the muscles of the limbs. Whether inflow from the extraocular muscles plays a role in oculomotor control or space perception is discussed in Chapter 2.

Ludvigh,¹² one of the first to propose a cybernetic model for eye movements, stated that it is tempting to hypothesize that the retina provides the necessary feedback, since the visual environment is ordinarily heterogeneous; therefore, movements of the eyes bring about changes in the retinal and neural pattern even in the absence of any interoceptive sense. Ludvigh pointed out, however, that control of the eye movements cannot be based on retinal feedback alone.¹² The temporal relations are such that entire large excursions of several degrees, so-called saccadic movements, may be initiated and completed by the eyes before there is time for any inflow or outflow

feedback to become effective. This reasoning may not apply to the much slower fusional movements.

According to Ludvigh's hypothesis¹² a definite innervation sequence always follows when the stimulus has a specific extrafoveal position. This is an important concept well described by Hofmann,⁷ who spoke of a *motor value* of the retinal elements proportional to the distance of the stimulated element from the fovea, whose retinomotor value is equal to zero (see Retinomotor Values in Chapter 2).

The cybernetic scheme proposed by Ludvigh¹² is a qualitative one. Later authors^{2, 5, 15-17} have worked out quantitative models for oculomotor control. It is not useful to discuss them in this book; interested readers are referred to the original publications.

Apparent Movement of the Environment

When the eyes make a saccadic movement, the image of the environment sweeps across the retina, yet no movement is perceived. This phenomenon has been explained by von Holst and Mittelstaedt,⁹ Ludvigh,¹¹ and others as follows.

The control system (the "space representation center" of Ludvigh¹²) is informed of the conjugate innervation sent to the extraocular muscles. If the movement is accurately performed, the information from retinal feedback coincides with the information about the conjugate innervation, and no movement is perceived; but if the two disagree, an apparent movement of the visual environment results.

This can be shown by a simple experiment: close the left eye and push your right eye nasalward with your finger. Images will now sweep across the retina, but since the control center knows of no active innervation to the right medial rectus muscle, the environment appears to make a jump to the right. Likewise, if an extraocular muscle (e.g., the right lateral rectus muscle) is paralyzed, an innervation impulse to abduct that eye will not be executed at all or, if any abduction occurs, the eye will not abduct fully. The control center is informed of the innervation, but the absence of the proper retinal feedback again causes an apparent movement of the environment to the right. This phenomenon is the basis of *past-pointing* in paralytic strabismus, which is discussed further in Chapter 20.

Empiricism and Nativism

Historically, there were two opposing schools of thought with regard to the origin and development of normal binocular vision and spatial orientation. One maintained that humans are born without binocularity or spatial orientation and that binocularity and spatial orientation are learned functions acquired by trial and error through experience and assisted by all the other senses, especially the kinesthetic sense. This is the theory of *empiricism*: that binocular vision depends on ontogenetic development. The other school held that binocular vision and spatial orientation are not learned functions but are given to humans with the anatomico-physiologic organization of his visual system, which is innate. This is the *nativistic* teaching: that binocular vision is acquired phylogenetically rather than ontogenetically.

The principal proponents of these two schools were Hering and Helmholtz who—with very little experimental evidence on either side—battled each other fiercely during the second half of the nineteenth century. The intensity of this battle is understandable, because it is not restricted to the question of the development of binocular vision; indeed it is a battle between two attitudes toward life and existence.

One may ask why philosophic ponderings on empiricism and nativism should be found in a book on strabismus. Surprising as it may seem, they are of basic importance in the management of strabismus since the prognosis and the attitude toward timing of treatment depend on this view. If one believes that binocular vision is a learned skill and if a functional cure is sought, one will have to operate very early in a child's life. Another ophthalmologist, more nativistically inclined, may believe that, given a normal sensorimotor anlage, early surgery is not absolutely essential, just as it is of no functional use if the anlage is not there.

There is no doubt that the anlage for normal binocular vision is present at birth. No evidence exists, for instance, that sensory fusion or stereopsis are "learned" processes any more than the perception of color—as distinct from color naming—is a learned process. Certain motor skills of the eyes are learned and improvable, as are all motor skills. The situation may be compared with that of a musician. "Innate" musical talent is necessary, but to be a pianist or violinist the motor skills of fingers and arms must be learned and continually reinforced through practice.

Animal research during the past three decades has actually provided support for both the nativistic and the empiricist schools of thought. The most direct evidence for the nativistic view came from the epochal work of Hubel and Wiesel,¹⁰ who showed with microelectrode recordings that visually inexperienced kittens have striate neurons with normal orientation sensitivity and a considerable number of neurons that are responsive to stimulation from either eye. In fact, electrophysiologic data from these kittens were strikingly similar to those obtained from adult cats. The same degree of complex functional differentiation of the visual cortex is present in visually immature baby monkeys.¹⁸ These findings support a nativistic view, according to which many connections responsible for the highly organized behavior of the striate cortex must be present at birth or within a few days of it. On the other hand, we have also learned from animal experiments that *the normal postnatal development of the visual system depends on normal visual experience* and that this development can be adversely modified by abnormal visual input. For instance, environmental factors are highly effective in tuning the spatial orientation of cortical neurons.⁶ Only brief disruptions of binocularity, produced by suturing the lid of one eye in a monkey¹⁴ or by creating artificial strabismus,³ suffice to decimate or even abolish binocular neurons in the striate cortex and thus the ability to see stereoscopically.⁴ Thus, normal visual experience is essential to preserve visual functions already present at birth and to promote their further development. The contradiction between empiricism and nativism, with all its philosophical and social implications, may well be only an apparent one as far as the visual system is concerned.¹³

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