MOVEMENTS OF THE EYES

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Preface

It is not hard to see why there has recently been such an upsurge of interest in the systems controlling eye movements. The more we find out about the way in which our eyes seek out and capture objects of interest in the visual world, the more remarkable does its seemingly effortless precision and sophistication appear. At the same time—and this is perhaps why it is increasingly attracting the attention of neurophysiologists—it functions at a level of complexity somewhere between the banality of the spinal reflex and the inscrutability of the voluntary act. One may therefore hope that an understanding of how the eyes are controlled may help us when we seek to understand more complicated motor systems: and indeed it is now becoming apparent that many of what were formerly thought to be unique properties of the eye movement control system have direct parallels even in a system as complex as the control of the hand.

This book has been planned with three classes of reader in mind. First, the medical student who wishes to know rather more about the subject—one that has considerable importance as an aid to neurological diagnosis—than is available to him in more general textbooks. Second, the scientifically oriented physiology or psychology student who is interested in a field in which the application of techniques of systems analysis to neurophysiology has proved particularly fruitful; and lastly but perhaps chiefly, to the research worker in this field who, like the author himself, may well have felt a need for an up-to-date and not wholly clinical reference book that can also be used as a teaching text.

It is divided into three parts, in an attempt to reflect the clear distinction that ought to be made with physiological systems between *performance, structure,* and the notional *models* that are supposed to link structure to performance, and performance to function. Here, part 1 is intended as a description of the phenomena of eye movements, part 2 as an account of the anatomy of the system (including the mechanical properties of the eye ball itself), while part 3 attempts to relate this anatomy to the control mechanisms, and to assess the contribution of eye movements to visual function. Appendices to the text provide a review of techniques for measuring eye movements, and an introduction to linear systems analysis which it is hoped will enable the nonmathematician to follow the mathematical arguments presented in the text.

R H S Carpenter
Gonville and Caius, Cambridge
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In memoriam
D E C

Part 1

Function

Contents

1

The use of eye movements

"The muscles were of necessitie provided and given to the eye, that so it might move on every side: for if the eye stoode fast, and immoveable, we should be constrained to turne our head and necke (being all of one peece) for to see: but by these muscles it now moveth it selfe with such swiftnes and nimblenes, without stirring of the head, as is almost incredible..." [1]

Not all creatures with eyes are able to move them. But—if we ignore winks, *oeillades* and other frivolous tasks—those that do, do so in order to see better. In this first chapter, the intention is to examine very briefly the general relation between vision and eye movements—a topic discussed in more detail in chapter 11—and the ways in which the requirements of sight determine the major classes of eye movement. In subsequent chapters, these various classes are discussed in turn: but for the moment only the most general considerations will be presented. For a more complete account of the teleology of eye movements than space permits here, see Walls (1942).

1.1 Consequences of velocity blur

For a stationary object, the fineness of the detail that can just be resolved is almost entirely a function of such 'physical' factors as the size of the eye, the quality of its optics, the spacing of the receptors, and the degree to which the central pathways from them overlap in their connections. But as soon as the image of the object starts to move across the retina quite different factors come into play. The light falling on any particular receptor is now no longer constant, but fluctuates as different parts of the image pass over its receptive area. The fidelity of the pattern of activity in the receptors to the pattern of light and shade in the original image at any moment will be a function not just of the physical factors mentioned earlier, but also of how good the receptors are at *following* these fluctuations. It turns out that they are in fact rather poor at doing so. Electrical responses in the retina to brief visual stimulation under the most favourable conditions typically show a time course of the order of tens of milliseconds, and flickering lights cannot be seen as such when the frequency of their flicker is more than some 60–80 Hz. The consequent degradation of visual acuity is quite striking: from appropriate published data (for example Robson, 1966; Green and Campbell, 1965) one may calculate that a target movement as slow as $1^\circ\ s^{-1}$—that is, in which any point on the target will take nearly three minutes to cross the visual field —has roughly the same effect on resolution as three diopters of myopia!

Whether for this reason, or simply because of the difficulty of designing a visual system that will analyse and recognise shapes that move as well as

[1] The quotations at the head of each chapter are from Andreas Laurentius (1599).

those that are still, it seems that the first kind of eye movements that evolved were those designed, paradoxically, not to move the eye at all but to hold it still—still, that is, relative to the frame of reference provided by the outside world (see, for example, Walls, 1962). This means that the animal must sense the movement of the head relative to the outside world, and move the eyes in an equal and opposite direction to compensate. Now, since the eyes are only capable of rotation, and cannot displace themselves significantly with respect to the head, it follows that such a mechanism will only provide complete stabilisation against rotations of the head; if the head undergoes translation, no rotation of the eyes can possibly compensate for movements of the retinal images of objects lying at *all* distances from the eyes (figure 1.1).

This may not matter much for animals like man with eyes that face in their normal direction of progress, but for animals with side-pointing eyes—most birds, for example—who are interested in near objects as well as far, it may lead to inconvenience. The only satisfactory solution is to stabilise not the eye but the *head*, which is capable of translation as well as rotation. The result is the slightly comical gait of such birds as chickens, pigeons, ducks, etc, in which the body walks on while the head is temporarily left behind, to be jerked forward again at the next step (figure 1.2) (Dunlap and Mowrer, 1931). But for creatures with heavy heads and short necks this is not a feasible solution, and an animal like the rabbit responds to linear accelerations of the head with rotations of the eyes that are approximately such as to stabilise the horizon (section 2.2). We shall see that in man responses of the eyes solely due to translation of the head have all but disappeared.

There are two essentially different ways in which image-stabilising or *holding* movements of this type can be produced. The most obvious way is simply to use the visual signal itself: we know that one of the kinds of

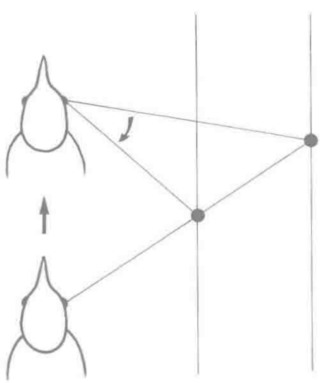

Figure 1.1. Forward movement of an animal with side-pointing eyes leads to different retinal shifts for objects at different distances.

information extracted at an early stage of visual processing is the velocity and direction of 'retinal slip'—movement of the retinal image relative to the retina—and it is easy to imagine how such a signal might be used in a negative feedback system to move the eyes in such a way as always to keep the slip velocity as near zero as possible. Such a mechanism would compensate not only for movement of the head, but also for displacements of the visual objects themselves in the outside world. Movements of this sort are well-known throughout the animal kingdom, having surprisingly similar response characteristics in creatures as different as the crab (Horridge, 1966) and man: similar mechanisms control the head movements of insects (Land, 1969; 1973). Generic names for these responses include *optokinesis* and *smooth pursuit*: they form the subject of chapter 3.

Important as this mechanism is, it has one severe drawback, inherent in all purely visual systems: it is very slow. It takes a fifth of a second or

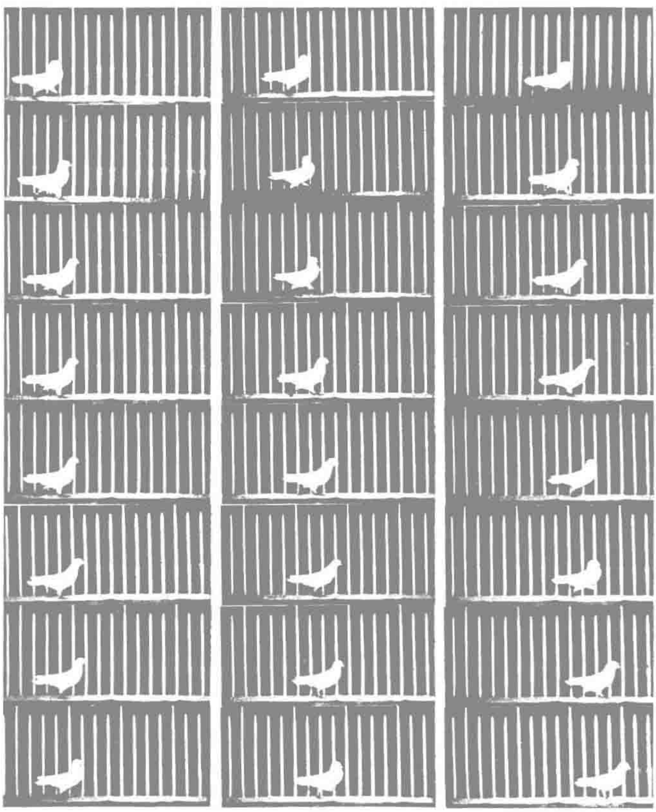

Figure 1.2. Sequential frames ($32\ s^{-1}$) of a film of a pigeon walking, showing 'nystagmus' of the head (reprinted from Dunlap and Mowrer, 1931).