COGNITIVE Neuroscience *of* ATTENTION

A Developmental Perspective

Edited by

John E. Richards

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Preface

The 1980s saw a new paradigm emerge in psychology—the field of cognitive neuroscience. Cognitive neuroscience has the premise that it is necessary to understand brain and neural systems in the study of cognition. Starting with animal and neuropsychological experiments, the field has emerged to using neuroimaging techniques (PET, MRI, fMRI, EEG/ERP, MEG), controlled invasive animal and human work, and experimental psychology using models of neuroscience to guide its work. One aspect of this work has been a developmental approach to cognitive neuroscience—"developmental cognitive neuroscience." The developmental approach asserts that changes in brain structure and function underlie much of cognitive development. Theories and experiments in cognitive development must rely on an understanding of neural development. Developmental research may provide a "model preparation" that aids work in cognitive neuroscience. The onset and development of specific neural–behavioral systems may tease apart the roles of separate systems in cognitive neuroscience models.

Attention has long been of interest to psychologists. William James saw it as an important field for psychological research, and it has always played a role in explanations of behavior. Cognitive psychologists, and cognitive developmental psychologists, have studied attention as a foundational area. It was only natural that in the very beginnings of cognitive neuroscience an understanding of the role of neural systems in attention was of interest. Early cognitive neuroscience studies of attention using primates and neuropsychological models have now been enhanced with neuroimaging models. The role of brain *changes* in attention *development* is a natural extension of work in this field. Techniques from neuropsychology, neuroimaging, and neuroscience-based experimental psychology are now being applied to the study of developmental changes in attention.

Which brings us to the current book. Developmental research in young infants, in children, and in the life span provides an important complement to work with adults in the understanding of attention. Many neural systems are immature, or nonfunctional, in the young infant. The lack of these systems, corresponding behavioral characteristics, and the developmental onset of the neural and behavioral systems, provides some information about how these neural systems are expressed in intact adults. Similarly, the changes in brain systems in the elderly (e.g., correlates of Alzheimer's) and changes in attention in the elderly may be considered in a similar light. This volume provides several models of the neural bases of attention, and details how developmental research on these topics leads to a fuller understanding of the cognitive neuroscience of attention. This book provides a contemporary summary of work in this area and a systematic background for further study of attention development from a cognitive neuroscience perspective.

Part I of the book deals with the neural basis of eye movements, and how attention development may be characterized based on an understanding of development in those neural systems. Part II explores the overt and covert orienting of attention, attention directed to objects and to spatial locations, and the relation of attention development and brain development to more general issues in cognitive development. Part III contains chapters on the neural basis of attention development as related to memory, possible neural relation to individual differences in infant attention and cognition, and a life-span approach to studying attention development. Each section includes an invited "summary and commentary" chapter that highlights some of the issues raised.

The part sections are suggestions for coordinating chapters, but are not meant to be absolute boundaries. For example, many of the concepts involved in the covert shift of attention found in the second section have their basis in the neural systems controlling eye movements discussed in Part I. Thus, the chapters by Rafal, and Hood, Atkinson, and Braddick, borrow heavily on concepts introduced in the chapters by Schiller, and Maurer and Lewis; in the third section the chapter by Enns, Brodeur, and Trick on life-span changes in covert attention relies on concepts presented in Parts I and II. Similarly, the development of the object concept depends on delayed recognition memory presumed by Bell in the second section to be based on development in the frontal lobes, and thus is related to recognition memory development presented by Nelson and Dukette, and related to individual differences in infant cognition discussed by Colombo and Janowsky, the latter chapters being found in Part III. I hope that the reader benefits from the perspectives in all of the chapters when looking for information on attention development.

Preparation of the book began with a conference in May 1995. Nine of the authors, and about 50 attendees, met on a beautiful spring weekend at the University of South Carolina. The conference included formal presentations and workshops in which the neural basis of attention development was discussed. The chapters represent part of the formal presentations, which have been greatly expanded in scope. Some other chapters, and summary and commentaries, were added to expand the book over a broader range of developmental issues.

We have attempted to present an "integrated" approach across chapters within sections, as well as across sections. Rather than a series of separate chapters, many of the chapters specifically build on elements of the others. Within each section there is reference to other chapters in the section; authors refer to chapters in other sections as well. There are common experimental designs intended to address similar questions, common theoretical issues, and common sets of research data that are discussed. The summary and commentary chapters highlight some of the common issues and themes.

The Internet aided greatly in the preparation of the book. Most of the chapters were transmitted from author to editor by e-mail attachments. I was able to use word processors to read multiple formats, print and deliver copies in a similar printed format, and so forth. Many of the authors also transmitted graphics via e-mail for the figures. I developed a World-Wide-Web site that was accessible to each of the authors. As the chapters came in they were put in "html" and zipped formats. Each author could access what the others had written, develop integrated chapters based on that access, and update their own work accordingly. Most of the authors visited the Web site at least once, and many did several times. I believe that this resulted in tighter chapter integration than would have been possible by delivering 14 hard copy chapters among 25 authors. This also allowed me to transmit everything to the publisher in a common format on electronic media. The computer revolution has allowed such work. I highly recommend its usage for such an edited book.

ACKNOWLEDGMENTS

I would like to acknowledge support of this book from several sources. The College of Liberal Arts at the University of South Carolina, directed by Dean Lester Lefton, provided the funding for the conference that provided the impetus for this work. Dr. Lefton's generous allocation of money for this conference was crucial for starting this process. The Department of Psychology, chaired by Dr. Keith Davis, also provided financial support for the conference, and helped support the many details that go into preparation of a book of this kind. I was supported by a Research Scientist Development Award from the National Institute of Mental Health that gave me the extra time to do this book in a timely fashion. And finally, I received generous emotional support and patience from my family, who graciously accepted my long hours and conference trips with little complaint.

John E. Richards

Contents

Part I

ATTENTION AND EYE MOVEMENTS

Chapter 1

The Neural Control of Visually Guided Eye Movements

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Along with the eyes, Nature has created a system to move them about efficiently. The eyes of many species have become specialized in that they contain a small central region in the retina, the fovea, where the photoreceptors are tightly packed which consequently yields high acuity perception. Therefore, to be able to analyze an object in the visual scene in fine detail, the center of gaze has to be directed to it. In addition, when either the object or the person is in motion, it is desirable to maintain the center of gaze on the object. These requirements have produced two distinct systems of conjugate eye movements: the saccadic and the smooth pursuit. The function of the saccadic system is to acquire visual objects for central viewing; the function of the smooth pursuit system is to maintain objects on the fovea while either the object or the person is in motion.

Our eyes are on the move most of the time during our waking hours. We make about 3 saccadic eye movements per second, some 170,000 a day and about 5 billion in an average life time. During the intervening fixations, each of which lasts 200–500 ms, the eyes are stationary in the orbit only when neither the head nor the object viewed is in motion. If there is motion, the object remains on the fovea by virtue of the fact that the eyes engage in smooth-pursuit tracking.

The neural systems involved in the control of visually guided eye movements, the topic of this presentation, are numerous and complex yet are tremendously robust. Seldom does one hear about individuals complaining at the end of the day of having made those 170,000 saccades and endless pursuit eye movements.

That these two types of eye movements, the saccadic and the smooth pursuit, are governed at higher levels by different neural systems has been known for a long time. When the velocity of an object to be tracked is gradually increased, a sudden break in performance occurs when tracking breaks down; the eye can no longer keep up with the moving object. When this happens, the saccadic system kicks in and moves the eyes to catch up with the object. Thus there is a clear velocity discontinuum between tracking and saccadic eye movements. The two systems also have dramatically different latency responses for the initiation of smooth pursuit and saccadic eye movements. This has first been shown by Rashbass (1961) who used what is now called a step-ramp paradigm. Following fixation of a spot on a homogeneous background, it is turned off and at the same time another spot appears somewhere in the periphery, which is then ramped at various velocities. The task of the subject is to make a saccade to the target and to track it. An example of this is shown in Fig. 1.1. The data in this case were collected from a monkey (Schiller & Logothetis, 1987). Examination of the eye traces shows something quite remarkable: The eyes begin to track the peripheral spot with a latency of 75 to 100 ms in this case, and do so *before* the saccade is initiated to it with a latency of 125 to 150 ms. In fact, it has been shown, that when a large portion of the visual field is set in motion, pursuit movements can be initiated in less time than 50 ms provided the stimuli have high contrast (Miles, Kawano, & Optican, 1986). High contrast assures rapid conduction velocities through the retina.

These observations have established, therefore, at the behavioral level, that there are different neural mechanisms involved in the control of saccadic and pursuit eye movements. In what follows I first discuss the various neural systems of saccadic eye-movement generation. Both the sensory and motor aspects of eye-movement production are considered. In the last section we take a brief look at the neural systems involved in pursuit eye movement.

BRAINSTEM CONTROL OF EYE MOVEMENTS

Each eye is moved around in the orbit using six extraocular muscles. Four of these are the recti muscles, the medial, lateral, superior, and inferior. Each opponent pair may be thought of as moving the eyes along two prime axes, the horizontal and the vertical. Diagonal eye movements are brought about by the combined action of the four recti muscles. The remaining two muscles, the superior and inferior obliques, participate mostly in inducing rotatory motion, the kind of motion that comes into play when the head is tilted. One of the important functions of the oblique muscles is to counter rotate the eyes so as to keep them stable with respect to the world.

The eye and its musculature have several features that make them the delight of engineers. The eye is a nearly perfectly balanced ball that is

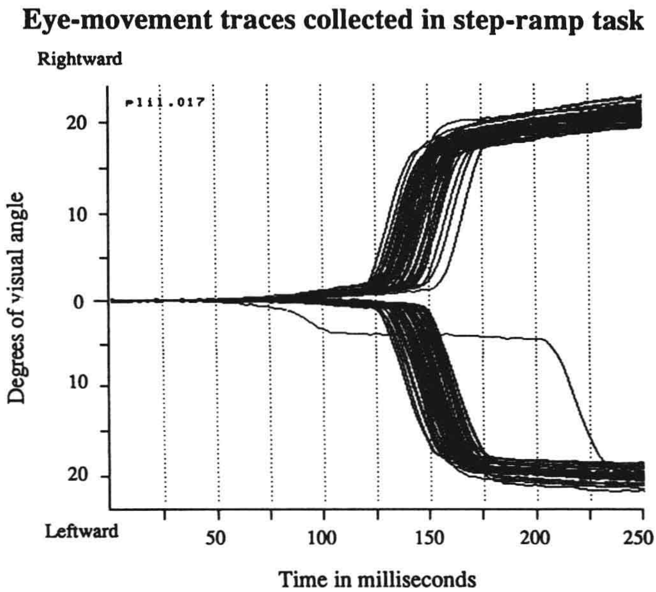

FIG. 1.1. Horizontal eye-movement traces obtained while a monkey performs on a step-ramp task. Following fixation of a central spot it is doused; at the same time a similar spot appears either to the right or the left of fixation at an 18° eccentricity and is moved peripherally along the horizontal axis at 20 deg/sec. Eye-movement trace collection began when the target was turned on in the periphery. The shorter latencies involved in activating the pursuit system are made evident by the fact that pursuit eye movements for the moving target actually begin before the monkey acquires it for foveal viewing with a saccade. Pursuit eye movements in this situation begin between 75 and 100 ms, whereas saccades are initiated between 125 and 150 ms. Adapted from Schiller and Logothetis (1987).

nicely viscous damped in its orbit. Unlike other muscle systems, it was not necessary to design the extraocular muscles to carry loads. The fibers of each muscle are not segmented: they run the entire length of the muscle. These facts make the analysis of eye motion readily amenable to study.

Three sets of cranial nuclei contain the neurons that innervate the six extraocular muscles of each eye through the third, fourth, and sixth cranial nerves: the oculomotor nuclei whose neurons innervate all the muscles except for the lateral rectus and the superior oblique, the trochlear nucleus whose neurons innervate the superior oblique, and the abducens nucleus whose neurons innervate the lateral rectus.

Figure 1.2 shows the response properties of a single cell in the oculomotor nucleus whose axon innervates the inferior rectus (Schiller, 1970). Shown are the action potentials for the cell over time and the monkey's eye movements in the vertical plane. The upper set of traces were collected

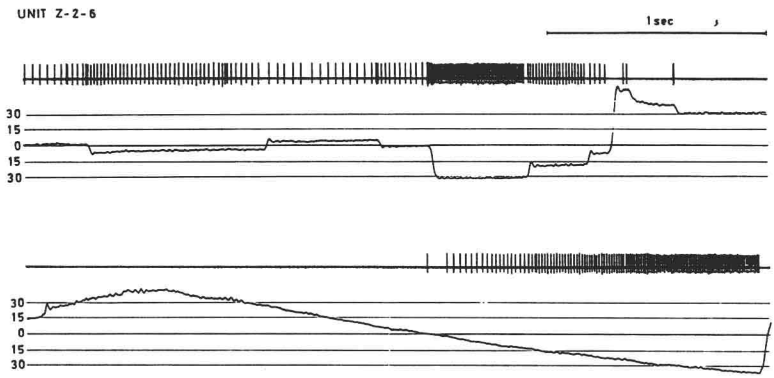

FIG. 1.2. Action potentials obtained from a single cell in the oculomotor nucleus that innervates the inferior rectus muscle. The activity of the neuron is shown along with vertical eye-movement traces. The upper set of records show neuronal activity while spontaneous eye movements are made and consist of saccadic eye movements with intervening fixations. The lower set of traces show neuronal activity during smooth-pursuit eye movement obtained by moving an object downward in front of the monkey. The rate of maintained activity of the neuron is linearly proportional to the angular displacement of the eye. Saccadic eye movements are associated with high-frequency bursts, the durations of which are proportional to saccade size. From Schiller (1970).

while the monkey looked around in the laboratory with his head restrained. Under such conditions the animal made saccadic eye movements with intervening fixations. The lower set of traces were collected while an object was moved downward in front of the monkey.

I emphasize three points about this figure. The first is that the rate of maintained activity exhibited by this neuron is proportional to the degree of downward deviation of the eye in orbit. The higher the activity the more acetylcholine is released at the terminals and consequently the more the inferior rectus contracts. It has been shown that there is a linear relationship between the degree of angular deviation of the eye and the rate of activity in neurons that form the final common path to the eye muscles. The second point is that the neuron discharges with a high frequency burst during the execution of downward saccadic eye movements; the size of the saccade is proportional to the duration of this high frequency burst. Upward saccades seen in the figure are associated with a pause of activity during which it is safe to assume that the neurons innervating the superior rectus discharge with high frequencies. The third point is that the neuron discharges in association with pursuit eye movements in a similar proportional fashion as was revealed when the monkey was fixating various objects in the stationary visual scene. This can be seen in the lower set of traces of Fig. 1.2.

I should note here one more interesting fact about the records shown in Fig. 1.2. Immediately after the execution of a saccadic eye movement brought about by a high-frequency neuronal burst, only a minimal overshoot can be seen. This is not accomplished by some sort of counteractivity in neurons innervating the antagonist muscle. If that were the case one would see in this record a brief burst immediately after the completion of an upward saccade. The remarkable ability of the eye to stop on a dime, so to speak, seems to be due simply to the excellent viscous damping achieved in tenon's capsule within which the eye resides.

Eye movements can be artificially induced by electrically stimulating many different sites in the brain. The upper portion of Fig. 1.3 shows what happens when the abducens nucleus is stimulated electrically through a microelectrode. As the duration of the high-frequency burst is increased, the size of the saccade produced gets progressively larger as might be expected on the basis of what I had just described for natural neuronal discharges.

On the basis of these observations it appears that at the level of the oculomotor complex in the brainstem, where the neurons reside whose axons innervate the extraocular muscles, the saccadic and smooth-pursuit eye movements are executed by the same set of neurons. The coding operation seen here may be termed a rate/duration code: the higher the maintained rate, the greater the angular deviation of the eye in orbit; the longer the duration of the high frequency burst seen in these neurons, the larger the saccade produced (Robinson, 1975; Schiller, 1970).

Right above the nuclei innervating the extraocular muscles there is a complement of neurons in the brain stem in which the various components of the neuronal responses associated with eye movements can be seen separately. Several classes of neurons have been identified (Fuchs, Kaneko, & Scudder, 1985). These include the following types: burst neurons that discharge in high-frequency bursts during saccadic eye movements but otherwise remain silent, omnipause neurons that fire at a constant rate but pause whenever a saccade is made, and tonic neurons whose discharge rate is proportional to angular deviation of the eye in orbit but do not have bursts or pauses associated with saccadic eye movements. It is assumed that the activity of these and several other classes of neurons drives the cells in the oculomotor, trochlear, and abducens nuclei to produce the desired saccadic and smooth pursuit eye movements.

THE SUPERIOR COLLICULUS AND SACCADIC EYE MOVEMENTS

In considering the role of the superior colliculus in eye-movement control it should first be pointed out that this structure is one that has undergone tremendous changes in the course of evolution. In more primitive animals