



Idiosyncratic characteristics of saccadic eye movements when viewing different visual environments

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Abstract

Eye position was recorded in different viewing conditions to assess whether the temporal and spatial characteristics of saccadic eye movements in different individuals are idiosyncratic. Our aim was to determine the degree to which oculomotor control is based on endogenous factors. A total of 15 naive subjects viewed five visual environments: (1) The absence of visual stimulation (i.e. a dark room); (2) a repetitive visual environment (i.e. simple textured patterns); (3) a complex natural scene; (4) a visual search task; and (5) reading text. Although differences in visual environment had significant effects on eye movements, idiosyncrasies were also apparent. For example, the mean fixation duration and size of an individual's saccadic eye movements when passively viewing a complex natural scene covaried significantly with those same parameters in the absence of visual stimulation and in a repetitive visual environment. In contrast, an individual's spatio-temporal characteristics of eye movements during active tasks such as reading text or visual search covaried together, but did not correlate with the pattern of eye movements in normal viewing reveal an endogenous influence on oculomotor control. The independent covariance of eye movements during different visual tasks shows that saccadic eye movements during active tasks like reading or visual search differ from those engaged during the passive inspection of visual scene. © 1999 Elsevier Science Ltd. All rights reserved.

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1. Introduction

The way we look at the world, whether in the observation of natural scenes or in cognitive tasks such as reading, shows that visual information is acquired in episodes bounded by saccadic eye movements (Dodge, 1903; Buswell, 1935). The importance of such movements is based on the fact that, although some information from a scene can be deduced from a single glance (Potter, 1976; Biederman, Mezzanotte & Rabinowitz, 1982), more detailed analysis and identification requires additional fixations (Loftus, 1972; Kowler & Steinman, 1977; Parker, 1978; Schlingensiepen, Campbell, Legge & Walker, 1986). Despite the important role saccadic eye movements play in visual exploration, little is

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entification requires Kowler & Steinman, Campbell Legge longer fixation durations are associated with more difficult words (Zola, 1984; Balota, Pollatsek & Rayner, 1985; Pollatsek, Rayner & Balota, 1986). However,

difficult words (Zola, 1984; Balota, Pollatsek & Rayner, 1985; Pollatsek, Rayner & Balota, 1986). However, saccadic eye movements show a variety of stereotypic patterns, from the constrained type during reading (Taylor, 1965) to those used to view scenes (Yarbus, 1967; Noton & Stark, 1971). This implies that intrinsic oculomotor activity (independent of the ongoing processing demands of the visual scene) may also be im-

known about how their spatio-temporal characteristics

A popular explanation for variation in the size and

frequency of saccadic eye movements is that they result

from shifts in attention between specific objects in the

scene (Just & Carpenter, 1980; Morrison, 1984; Rayner

& Pollatsek, 1992). Eye movements when reading text,

for example, can be influenced by the syntax of the

sentence (Carpenter & Just, 1983; Rayner & Pollatsek,

1987), and the linguistic characteristics of a word;

are determined in natural viewing.

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portant (O'Regan, 1990). Indeed, the temporal characteristics of eye movements observed when reading normal text has been shown to be very similar to scanning text in which the complexity of the written information is markedly reduced (Vitu, O'Regan, Inhoff & Topolski, 1995).

The aim of the present study was to determine the extent to which the temporal and spatial characteristics of saccadic eye movements are influenced by endogenous factors. Accordingly, eye position was recorded in a variety of viewing conditions: the absence of visual stimulation (i.e. the dark), viewing a repetitive visual environment (simple patterns), inspecting a complex natural scene, during a visual search task and reading text. If endogenous factors are involved in the generation of saccadic eye movements, we would predict that an individual's average fixation duration and saccade size should covary across tasks. The results show that, although changes in the visual environment affect eye movements, idiosyncratic patterns were also evident; thus, revealing an additional endogenous influence on oculomotor control.

2. Methods

We solicited volunteers between 20 and 30 years of age (students, faculty and staff from Duke University) who did not require corrective lenses and had no history of ophthalmological disease. Subjects were screened using a Snellen letter chart, and the first 15 subjects with normal color vision and a Snellen ratio of 1 or greater at viewing distances of both 6 and 3 m were enrolled in the study.

2.1. Eye movements

An infrared eve-tracking system (Model 210, Applied Science Laboratories, Bedford, MA) interfaced with a computer via an A/D converter (Indec Systems, Inc.) was used to monitor eye position by recording changes in the reflectance of an infrared beam from the limbus (horizontal movements) and the lower lid (vertical movements). This device measures horizontal and vertical eye position over a range of approximately $+15^{\circ}$, with an accuracy of greater than 0.25°. Prior to each recording session, the eye tracking system was calibrated by having subjects make repeated eye movements over a measured grid. If the recorded x, yco-ordinates of the eye tracking signal corresponded to the dimensions of the grid, we proceeded to record the subjects' responses. The output of the eye position signal was collected at 100 Hz and analysed using a software program specifically written for this purpose. The software computed horizontal and vertical eye displacement signal as a function of time to determine eye velocity. Saccadic eye movements were then automatically detected on the basis of their spatio-temporal characteristics. The threshold for detecting a saccadic eye movement was an eye displacement greater than 0.2° at a velocity of not less than 20 deg/s (Zuber, Stark & Cook, 1965). Although these criteria preclude detection of small saccadic eye movements (i.e. microsaccades), the fact that none of the visual tasks involved a specific instruction to fixate means that they would constitute only a small proportion of the total number of saccadic eye movements (Cunitz & Steinman, 1969; Steinman, Haddad, Skavenski & Wyman, 1973).



Fig. 1. Graph showing (A) the mean fixation duration and (B) the mean saccade size of 15 naive observers in five different viewing conditions. Note the decrease in fixation duration and the increase in saccade size with increased complexity of the visual scene and with the increased cognitive demand of the task. An ANOVA shows a significant effect of viewing condition on both fixation duration and saccade size (P < 0.0001). Significant differences were apparent between the following contexts: Fixation duration–dark versus scenes, visual search, reading (P < 0.0001); simple patterns versus scenes, visual search, reading (P < 0.0001); scenes versus visual search, reading (P < 0.0001); simple patterns, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, reading (P < 0.005); simple patterns versus scenes, visual search, re

A) Fixation Duration (s)



B) Saccade Size (°)



Fig. 2. Three dimensional graphs showing the relationship between (A) fixation duration and (B) saccade size when viewing natural scenes, simple pattern and in darkness. A significant correlation is apparent between all visual environments as reflected by their tendency to follow the principal diagonal. Thus individuals who make longer fixations in the dark make longer fixations when viewing a natural scene or simple patterns. Similarly, subjects who make larger saccades in the dark make larger saccades when viewing scenes or patterns.

2.2. Stimulus presentation

All stimuli were generated on a computer with the software package MacLaboratory for Psychology Research 3.0 (D.L. Chute, Drexel University) and were viewed on a 20", high resolution, color monitor (Apple G28J-A) using an adjustable chin rest and forehead bar to stabilise the head at a viewing distance of 0.3 m. With the exception of the trials in darkness, testing was carried out in a room in which the computer monitor was the only source of illumination, and all viewing was binocular.

Eye movements were recorded in five different stimulus environments: (i) Darkness; (ii) viewing simple textured patterns; (iii) observing a complex natural scene; (iv) during a visual search task; and (v) reading text. For the dark condition, subjects were placed in lighttight room and instructed to keep their eyes open, their head still and direct their gaze forward. The simple textured patterns included five different patterns (70° wide and 60° tall) variously composed of different combinations of dots, squares or lines. The only instruction in this task was to keep your direction of gaze on the screen. Five photographs (60° wide and 42° tall) of picturesque scenes (Out on the Porch Calendar, 1995, Algonquin Books, Chapel Hill, NC) were selected for natural viewing. Subjects were told that they were not obliged to look at everything in the scene, but to try and act as though viewing the scene in real life. For the search task, subjects were instructed to seek a specific icon (Waldo) in the children's book 'The Great Waldo Search'. These images (44° wide and 54° tall) were ideal, because they provide a single readily recognisable target in a background of decoys and distracters. Although subjects were under the impression that all images used contained the icon, it was present in only five. Eye movements were only recorded when viewing images that did not contain Waldo. For the reading task, extracts were taken from a biochemistry textbook, an autobiography, two psychology books, a children's novel, and a history book. The visual angle of each letter was 4° wide and 4° tall. Subjects were asked questions about each simple text to assess comprehension.

2.3. Statistical analysis

Each visual environment (with the exception of the dark) contained five different images. The presentation of consecutive images in each environment was subject paced with each image being presented for 20 s. Eye movements in the dark were recorded continuously in 100 s trials. In each of the three sessions, eye movements were recorded while subjects viewed all the visual environments. Mean fixation duration and saccade size were determined from the three sessions, with the resul-

tant number of saccades analysed for each individual ranging from approximately 500 in the dark to about 1500 when reading. To assess the effect of different viewing environments, an analysis of variance was performed. Finally, the covariance of saccadic eye movements in individuals across different visual environments was determined using Pearson productmoment correlations and principal components analysis (StatView 4.1; Abacus Concepts, Berkeley, CA).

3. Results

3.1. Effect of different visual environments on the temporal and spatial characteristics of saccadic eye movements

The frequency and size of saccadic eye movements are clearly influenced by the characteristics of the visual scene and the nature of the visual task (Fig. 1). Active tasks such as visual search or reading text tended to generate shorter fixation durations and larger eye movements than did passive viewing of natural scenes or simple patterns. These results concur with previous reports showing that an increase in cognitive demand results in a more efficient oculomotor strategy (Huey, 1900; Kowler, Pizlo, Zhu, Erkelens, Steinman & Collewijn, 1992; Epelboim, Steinman, Kowler, Edwards, Pizlo, Erkelens et al., 1995). Differences in the visual environment also affected the spatial and temporal characteristics of saccades. For example, passive viewing of a complex natural scene caused a decrease in fixation duration and an increase in saccade size compared with viewing repetitive simple patterns or in the absence of visual stimulation.

The presence of eye movements in the dark shows that the absence of patterned visual stimulation does not prevent saccadic eye movements (see also Cornsweet, 1956; Skavenski & Steinman, 1970), and thus demonstrates an endogenous drive to move the eyes. The similarity between eye movements in the dark and viewing simple patterns also shows that visual stimulation in the absence of complexity is not sufficient to change the default pattern of saccadic eye movements. Indeed, these results are consistent with the idea that when subjects are not required to perform any particular visual task the presence of saccadic eye movements reflects an over-learned motor habit (Steinman et al., 1973).

3.2. Idiosyncratic differences in the temporal and spatial characteristics of saccadic eye movements

Marked interindividual differences in mean fixation duration and saccade size were apparent in all visual contexts. In the dark, the mean fixation duration varied from about 0.3-1.4 s, whereas mean saccade size ranged from $1.2-6.0^{\circ}$ (Fig. 2). Similar variation was apparent when viewing a natural scene, where mean fixation duration and saccade size varied between 0.2-0.4 s and $3.2-7.0^{\circ}$, respectively in different individuals. To determine whether this variation was consistent in individuals across different visual environments, we performed a correlation analysis (Table 1). Mean fixa-

Table 1

Matrix showing the Pearson product-moment correlations between (a) mean fixation duration; and (b) saccade size in 15 subjects exposed to five viewing conditions

	Dark	Simple patterns	Natural scenes	Visual search	Reading
<i>(a)</i>					
Dark	_				
Simple patterns	0.58	_			
	(<i>P</i> <0.05)				
Scenes	0.72	0.58	_		
	(<i>P</i> <0.005)	(P < 0.05)			
Visual search	-0.2	-0.24	0.22	_	
	(P = 0.9)	(P = 0.4)	(P = 0.4)		
Reading	-0.13	-0.21	0.15	0.52	_
-	(P = 0.7)	(P = 0.4)	(P = 0.6)	(P<0.05)	
<i>(b)</i>					
Dark	_				
Simple patterns	0.73	_			
	(P<0.005)				
Scenes	0.61	0.59	_		
	(<i>P</i> <0.05)	(P < 0.05)			
Visual search	0.01	0.11	0.28	_	
	(P = 0.9)	(P = 0.7)	(P = 0.4)		
Reading	-0.48	-0.6	-0.22	0.48	
-	(P < 0.1)	(<i>P</i> <0.05)	(P = 0.5)	(P < 0.1)	





B) Saccade Size (°)



Fig. 3. Scatterplots showing the correlation between (A) fixation duration and (B) saccade size when reading or doing a visual search task. Correlations between these visual environments were apparent for both eye movement parameters.

tion duration and mean saccade size viewing a complex natural scene covaried significantly with these measures when viewing a simple pattern or in the dark. A correlation was also apparent for both fixation duration and saccade size during visual search and reading, but not when viewing other visual environments (Fig. 3). The idiosyncratic nature of the oculomotor activity is further demonstrated by the fact that fixation duration and saccade size varied independently; thus, an individual's mean fixation duration did not predict mean saccade size.

Because correlation analysis can only indicate the covariance of two variables, we also performed princi-

pal components analysis to assess covariance across all environments (Table 2). This analysis shows that most of the variance in fixation duration and saccade size in the dark, viewing simple patterns and inspecting a complex scene can be explained by one factor, whereas a second factor explained the majority of the variance in the search and reading tasks. An individual's eye movements in the absence of visual stimulation (or in a repetitive visual environment), therefore, predicts the pattern observed when viewing a complex natural scene, whereas an individual's pattern of saccades during reading correlated with the pattern found in visual search.

4. Discussion

The main result from this study is that individuals have idiosyncratic temporal and spatial patterns of eye movements. The size and frequency of an individual's saccadic eye movements when viewing a complex natural scene covaried significantly with those same parameters in the dark or viewing simple patterns. In contrast, mean fixation duration and saccade size when reading text correlated with corresponding measures during visual search, but not when viewing a complex natural scene, simple patterns or the dark. These results suggest that oculomotor control of saccadic eye movements during active visual tasks like reading or visual search differs from that engaged during passive inspection of visual scenes.

Saccadic eye movements are thought to be controlled cortically by two parallel pathways. Changes in gaze related to remembered, anticipated or learned behavior, appear to be controlled mainly through a frontal lobe pathway that acts through the superior colliculus, whereas reorienting eye movements to novel visual stimuli appear to be the concern of a pathway emanating from posterior parietal cortex (for review see Leigh & Zee, 1991). Although connections between frontal and parietal cortex preclude a strict separation of function, it is attractive to speculate that the dichotomy in correlations between eye movements during active and passive viewing results from the differential control of these two neural pathways.

The demonstration of idiosyncrasies in the size and frequency of saccadic eye movements is comparable to studies showing individuals adopt characteristic scanpaths when looking at familiar scenes, figures and objects (Noton & Stark, 1971; Zhou et al., 1993). Indeed, it has been proposed that these spatial patterns of eye movements are important for visual learning and recognition. Are the idiosyncratic temporal patterns of eye movements we report also important for visual perception? A number of studies suggest that it is the programming and execution of eye movements, rather

Principal components analysis for the variation in (a) mean fixation duration; and (b) saccade size in 15 subjects studied^a

	Dark	Simple patterns	Natural scenes	Visual search	Reading
(<i>a</i>)					
Factor 1	0.88	0.85	0.85	-0.08	-0.19
Factor 2	-0.08	-0.19	0.39	0.84	0.85
(<i>b</i>)					
Factor 1	0.89	0.90	0.75	-0.01	-0.68
Factor 2	0.05	0.08	0.43	0.93	0.63

^a The values represent the correlation factors. Independent analysis of fixation duration and saccade size shows that one factor explains the majority of the variance between individuals for the dark, simple pattern and natural scene conditions, whereas another factor explains the majority of the variance in the visual search and reading tasks. These results imply different oculomotor centres saccadic eye movements during active and passive viewing.

than the processing of visual stimuli, that is the limiting factor in image acquisition. Reading speed, for example, increases when text is presented serially without the need to make eye movements (Juola, Ward & McNamara, 1982; Rubin & Turano, 1991), and recognition of objects or patterns presented tachistoscopically can occur at intervals as low as 50 ms (Sperling, Budiansky, Spivak & Johnson, 1971; Loftus, 1981). However, other studies, using visual masking paradigms, have shown the ability to identify an object is severely impaired if followed within a few hundred ms by another object (Duncan, Ward & Shapiro, 1994; Husain, Shapiro, Martin & Kennard, 1997). These results demonstrate that the dwell time of visual attention is similar to an average fixation duration. This suggests that idiosyncratic differences in oculomotor behaviour may reflect intrinsic temporal differences between individuals in their processing of visual stimuli.

The concept of sensory information acting on an endogenous pattern of motor activity (cf. Lashley, 1951) is evident in other active exploratory behaviours such as the palpations made during tactile discriminations (Darian-Smith, 1984), the whisking movements of rodent vibrissae for somatic sensation (Chapin, 1987; Carvell & Simmons, 1990, 1995) and the sniffing movements used for odour detection (Macrides, Eichenbaum & Forbes, 1982). Interestingly, the periodic activity of some of these peripheral sensor and effector organs has been related to intrinsic neuronal oscillations. The µrhythm, for example, which is recorded over rolandic regions of the brain has been associated with limb movements and tactile stimulation (Gastaut, 1952; Chatrian, Petersen & Lazarte, 1959; Nicolelis, Baccala, Lin & Chapin, 1995). A similar relationship is apparent in the olfactory system, where bouts of exploratory sniffing are phase locked to the theta-rhythm (Macrides et al., 1982; Vanderwolf, 1992). The interaction between motor behaviour and sensory processing in other systems implies a similar relationship exists for oculomotor behaviour. Interestingly, patterns of eye movements have been related to both the occipital α -rhythm (Mulholland, 1972; Wertheim, 1974), and to λ waves recorded over parieto-occipital cortex (Chatrian, 1976; Fourment, Calvet & Bancaud, 1976; Jousmaski, Hamalainen & Hari, 1997).

In conclusion, we have demonstrated idiosyncratic spatial and temporal patterns of saccadic eye movements in normal viewing. This reveals a significant endogenous influence on oculomotor control. The independent covariance of eye movements during different visual tasks shows that eye movements during active visual tasks like reading or visual search differ from those employed during the passive inspection of visual scenes.

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References

- Biederman, I., Mezzanotte, R. J., & Rabinowitz, J. C. (1982). Scene Perception: detecting and judging objects undergoing violation. *Cognitive Psychology*, 14, 143–177.
- Balota, D. A., Pollatsek, A., & Rayner, K. (1985). The interaction of contextual constraints and parafoveal visual information in reading. *Cognitive Psychology*, 17, 364–390.
- Buswell, G. T. (1935). *How people look at pictures*. Chicago: Chicago University.
- Carpenter, P. A., & Just, M. A. (1983). What your eyes do while your mind is reading. In K. Rayner, *Eye movements in reading: perceptual and language processes* (pp. 275–307). New York: Academic.
- Carvell, G. E., & Simmons, D. J. (1990). Biometric analyses of vibrissal tactile discrimination in the rat. *Journal of Neuroscience*, 10, 2638–2648.

- Carvell, G. E., & Simmons, D. J. (1995). Task and subject related differences in sensorimotor behavior during active touch. Somatosensory and Motor Research, 12, 1–9.
- Chapin, J. K. (1987). Modulation of cutaneous sensory transmission during movement: possible mechanism and biological significance. In S. P. Wise, *Higher brain functions: recent explorations of the brain's emergent properties* (pp. 181–209). New York: Wiley and Sons.
- Chatrian, G. (1976). The lambda waves. In A. Remond, *Handbook of electroencephalography and clinical neurophysiology*, vol. 6A (pp. 123–149). Amsterdam: Elsevier.
- Chatrian, G., Petersen, M., & Lazarte, J. (1959). The blocking of the rolandic wicket rhythm and some central changes related to movement. *Electroencephlalography and Clinical Neurophysiology*, 11, 497–510.
- Cornsweet, T. N. (1956). Determination of the stimuli for involuntary drifts and saccadic eye movements. *Journal of the Optical Society of America*, 46, 987–993.
- Cunitz, R. J., & Steinman, R. M. (1969). Comparison of saccadic eye movements during fixation and reading. *Vision Research*, 9, 683– 693.
- Darian-Smith, I. (1984). The sense of touch: performance and peripheral neural processes. In I. Darian-Smith, *Handbook of physiology I: the nervous system*. In: Sensory processes, vol. III (pp. 739–787). New York: American Physiological Society.
- Duncan, J., Ward, R., & Shapiro, K. (1994). Direct measurement of attentional dwell time in human vision. *Nature*, 369, 313–315.
- Dodge, R. (1903). Five types of eye movement in the horizontal meridian plane of the field of regard. *American Journal of Physiol*ogy, 8, 307–329.
- Epelboim, J., Steinman, R. M., Kowler, E., Edwards, M., Pizlo, Z., Erkelens, C. J., & Collewijn, H. (1995). The function of visual search and memory in sequential looking tasks. *Vision Research*, 35, 3401–3422.
- Fourment, A., Calvet, A. F., & Bancaud, J. (1976). Electrocorticography of waves associated with eye movements in man during wakefulness. *Electroencephalography and Clinical Neurophysiol*ogy, 40, 457–469.
- Gastaut, H. (1952). Etude electrocorticographique de la reativitie des rhythmes rolandiques. *Review du Neurogie*, 87, 176–182.
- Huey, E. B. (1900). On the psychology and physiology of reading. *The American Journal of Psychology*, 11, 283-302.
- Husain, M., Shapiro, K., Martin, J., & Kennard, C. (1997). Abnormal temporal dynamics of visual attention in spatial neglect patients. *Nature*, 385, 154–156.
- Jousmaski, V., Hamalainen, M., & Hari, R. (1997). Magnetic source imaging during a visually guided task. *Neuroreport*, 7, 2961–2964.
- Juola, J. F., Ward, N. J., & McNamara, T. (1982). Visual search and reading of rapid, serial presentation of letter strings, words and text. *Journal of Experimental Psychology: General*, 111, 208–227.
- Just, M. A., & Carpenter, P. A. (1980). A theory of reading: from eye fixations to comprehension. *Psychological Review*, 87, 329–354.
- Kowler, E., & Steinman, R. M. (1977). The role of saccades in counting. *Vision Research*, 17, 95–108.
- Kowler, E., Pizlo, Z., Zhu, G., Erkelens, C. J., Steinman, R. M., & Collewijn, H. (1992). Coordination of head and eyes during the performance of natural (and unnatural) visual tasks. In A. Berthoz, P. P. Vidal, & W. Graf, *The head-neck sensory motor* system (pp. 419–426). Oxford: Oxford University.
- Lashley, K. S. (1951). The problem of serial order in behavior. In W. A. Jeffress, *Cerebral mechanisms in behavior: the Hixon symposium* (pp. 112–136). New York: Wiley.
- Leigh, R. J., & Zee, D. S. (1991). The neurology of eye movements. Philadelphia: FA Davis.
- Loftus, G. R. (1972). Eye fixations and recognition memory for pictures. *Cognitive Psychology*, *3*, 525–551.

- Loftus, G. R. (1981). Tachistoscopic simulations of eye fixations on pictures. Journal of Experimental Psychology: Human Learning and Memory, 7, 369–376.
- Macrides, F., Eichenbaum, H. B., & Forbes, W. B. (1982). Temporal relationship between sniffing and the limbic rhythm during odor discrimination reversal learning. *Journal of Neuroscience*, 12, 1705–1717.
- Morrison, R. E. (1984). Manipulation of stimulus onset delay in reading: evidence for parallel programming of saccades. *Journal of Experimental Psychology: Human Perception and Performance*, 10, 667–682.
- Mulholland, T. B. (1972). Occipital alpha revisted. *Psychological Bulletin*, 78, 176–182.
- Nicolelis, M. A. L., Baccala, L. A., Lin, R. C., & Chapin, J. K. (1995). Sensorimotor encoding by synchronous neural ensemble activity at multiple levels of the somatosensory system. *Science*, 268, 1353–1358.
- Noton, D., & Stark, D. (1971). Scan paths in eye movements during pattern recognition. *Science*, *171*, 308–311.
- O'Regan, J. K. (1990). Eye movements and reading. In E. Kowler, Eye movements and their role in visual and cognitive processes (pp. 395–453). New York: Elsevier.
- Parker, R. E. (1978). Picture processing during recognition. Journal of Experimental Psychology: Human Perception and Performance, 4, 284–293.
- Pollatsek, A., Rayner, K., & Balota, D. A. (1986). Inferences about eye movement control from the perceptual span in reading. *Peception and Psychophysics*, 40, 123–130.
- Potter, M. C. (1976). Short-term conceptual memory for pictures. Journal of Experimental Psychology: Human Learning and Memory, 2, 509–522.
- Rayner, K., & Pollatsek, A. (1987). Eye movements in reading: a tutorial review. In K. Rayner, *Eye movements in reading: perceptual and language processes* (pp. 327–362). New York: Academic.
- Rayner, K., & Pollatsek, A. (1992). Eye movements and scene perception. *Canadian Journal of Psychology*, 46, 342–376.
- Rubin, G. S., & Turano, K. (1991). Reading without saccadic eye movements. Vision Research, 32, 895–902.
- Schlingensiepen, K.-H., Campbell, F. W., Legge, G. E., & Walker, T. D. (1986). The importance of eye movements in the analysis of simple patterns. *Vision Research*, 7, 1111–1117.
- Skavenski, A. A., & Steinman, R. M. (1970). Control of eye position in the dark. *Vision Research*, 10, 193–202.
- Sperling, G., Budiansky, J., Spivak, J. G., & Johnson, M. C. (1971). Extremely rapid visual search: the maximum rate of scanning letters for the presence of a numeral. *Science*, 174, 307–311.
- Steinman, R. M., Haddad, G. M., Skavenski, A. A., & Wyman, D. (1973). Miniature eye movement. *Science*, 181, 810–819.
- Taylor, S. E. (1965). Eye movements in reading: fact and fallacy. American Educational Research Journal, 2, 187–202.
- Vanderwolf, C. H. (1992). Hippocampal activity, olfaction, and sniffing: an olfactory input to the dentate gyrus. *Brain Research*, 593, 197–208.
- Vitu, F., O'Regan, J. K., Inhoff, A. W., & Topolski, R. (1995). Mindless reading: eye-movement characteristics are similar in scanning letter strings and reading texts. *Perception and Psychophysics*, 57, 352–364.
- Wertheim, A. H. (1974). Oculomotor control and the occipital alpha activity: a review and a hypothesis. *Acta Psychologica Amsterdam*, 38, 235–256.
- Yarbus, A. (1967). Eye movements and vision. New York: Plenum.
- Zhou, G., Ezumi, K., & Stark, L. W. (1993). Efficiency of search patterns. Comput. Biol. Med., 23, 511–524.
- Zola, D. (1984). Redundancy and word perception during reading. Perception and Psychophysics, 36, 277–284.
- Zuber, B. L., Stark, L., & Cook, G. (1965). Micro-saccades and the velocity-amplitude relationship for saccadic eye movements. *Sci*ence, 150, 1459–1460.