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Eye movements: The past 25 years

Eileen Kowler

Department of Psychology, Rutgers University, Piscataway, NJ 08854

Abstract

This article reviews the past 25 of research on eye movements (1986–2011). Emphasis is on three oculomotor behaviors: gaze control, smooth pursuit and saccades, and on their interactions with vision. Focus over the past 25 years has remained on the fundamental and classical questions: What are the mechanisms that keep gaze stable with either stationary or moving targets? How does the motion of the image on the retina affect vision? Where do we look – and why – when performing a complex task? How can the world appear clear and stable despite continual movements of the eyes? The past 25 years of investigation of these questions has seen progress and transformations at all levels due to new approaches (behavioral, neural and theoretical) aimed at studying how eye movements cope with real-world visual and cognitive demands. The work has led to a better understanding of how prediction, learning and attention work with sensory signals to contribute to the effective operation of eye movements in visually rich environments.

K: Our charge is this: The last 25 years of eye movement research (1986–2010) in 25 journal pages.

A: 25 years, 25 pages. Can't be done. Too vast, too many topics, too many approaches, too many things to consider: the behavior, the brain, connections to vision and to cognition. The measurements, the methods.

B: And don't forget there's no consensus. No consensus on anything.

A: I disagree.

B: Who's the audience for this?

K: Good question. In principle, everyone. Eye movements are the first step in seeing, stabilizing retinal images against displacements caused by movements of the head, and taking the fovea from place to place to find interesting things to look at. Yet, eye movements are the last step too, because if there's one thing that the last 25 years has taught us, it's that eye movements are not "evoked" by sensory error signals – such as motion on the retina, or a displacement of a detail some distance from the fovea. They are a response to a representation of the visual world. And, not a just representation of the objects or the visual scene, but also information about plans, goals, interests, and probable sources of rewards or useful information. Even expectations about future events.

B: There could be quite a payoff. If we actually understand things well enough to predict the pattern of movements in any given condition or task, we might be able

Contact information: Eileen Kowler, Department of Psychology, 152 Frelinghuysen Road, Rutgers University, Piscataway, NJ 08854, kowler@rci.rutgers.edu.

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to figure out what happens along the whole neural path, from the retinal signal, up through higher visual areas, over to frontal cortex, and back down to the brainstem, with all kinds of interactions within and across levels. We could use eye movements as a clue to what someone is perceiving or thinking about, or what they can and can't remember, when they do some complicated task.

A: Wait a second. What do you mean by “complicated task”? What kind of task? Reading or visual search? How about knitting or driving?

K: Yes, those are all good examples.

A: No way; never will happen. Can't be done.

K: Enough pessimism. We need to consider what's been accomplished. We'll start with gaze control. Then, we'll take on smooth pursuit, and finally, we'll deal with saccades.

A: Just three topics?

K: Let's just read the text, and then we'll have some commentary at the end.

A: Fine, but I'm commenting whenever I feel like it.

1. Gaze control

1.1. Maintained fixation: Head stable and head free

It would seem that one of the easiest things you can ask a human to do with the eye is to look at a stationary target. This behavior – “maintained fixation” – was studied in earnest beginning in the 1950's by visual scientists who were interested in finding out about the motion of the image on the retina that accompanied visual judgments under conditions typical of psychophysical laboratory investigations. This meant sparse, well-controlled, visual stimuli: small, simple targets – points or thin lines, for example – viewed in darkness by experienced, committed observers making concerted efforts to fixate carefully while their heads were rigidly stabilized by a bitebar.

These early recordings of eye movements during fixation were made with the contact lens optical lever – an ingenious device, custom-built by the investigators, which was capable of recording eye movements down to seconds of arc by detecting the position of a narrow beam of light reflected off a mirror mounted on a tightly-fitting scleral contact lens. The early studies revealed the classical fixation pattern: slow oscillations of the eye, interrupted periodically (at most, 2 or 3 times per second) by saccades (“microsaccades”) whose sizes rarely exceed 12–15' and which occurred simultaneously in both eyes (for review see Collewijn & Kowler, 2008; Steinman, Haddad, Skavenski & Wyman, 1973). Figure 1a shows examples of the eye movements during fixation. In a recent novel addition to the approaches to the study of fixation, Putnam et al. (2005) recorded the position of the retinal image by means of adaptive optics, and confirmed the excellent stability of the line of sight (Fig. 1b).

Within the past 25 years, a number of reviews of the literature on fixational eye movements have appeared, showing the extent to which this behavior continues to be a focus of active interest (Collewijn & Kowler, 2008; Martinez-Conde et al., 2002, 2009; Rolfs, 2009; Kowler, 1990, 1991; Steinman & Levinson, 1990; Steinman, 2003). These reviews include and extend several of the themes first developed and presented in Steinman et al. (1973). For example, microsaccades are not the primary means of maintaining stable fixation. Saccade rates can be reduced by simple voluntary effort and stable fixation maintained exclusively by slow eye movements – slow control. Slow control acts to maintain stable fixation mainly by controlling the velocity of the retinal image, rather than by correcting offset errors in

fixation position (Epelboim & Kowler, 1993). Microsaccades, meanwhile, do not possess the characteristics of an involuntary reflex, or a special class of eye movements, but rather have the same basic properties as their larger, unambiguously volitional, counterparts.

The classical view of maintained fixation, going back to the original contact lens optical lever studies, was altered when studies appeared that described fixation under more natural conditions, without the constraint to maintain stable head position. These studies of fixation while the head was free to move were done with a version of the magnetic field search coil method that made it possible to record eye movements accurately ($1'$) in freely moving observers, without contamination by effects of head translation. Eye movements were studied during fixation (Steinman & Collewijn, 1980, Ferman, Collewijn, Jansen & Van den Berg, 1987), or during a variety of visual or visuomotor tasks (Epelboim et al., 1995, 1997; Epelboim, 1998; Kowler et al., 1992; Steinman, Menezes & Herst, 2006). When head movements were permitted, the oculomotor systems responsible for compensating for head motions did not do a perfect job. The imperfect compensation resulted in average retinal image speeds ranging from about $\frac{1}{2}$ to 4 or 5 deg/s, depending on the extent of head movements (Skavenski et al., 1979; Steinman & Collewijn, 1980; Ferman et al., 1987) (Fig. 1c).

In addition to the higher retinal image speeds, the pattern of saccades during fixation was found to change as well. Saccades dropped out of the fixation pattern during deliberate head oscillation, when, interestingly, image velocities and the variability of eye position also increased (see Fig. 1c).

The retinal image speeds of .5 to 5 deg/s, found during active head motions, are 2 to 20 times faster than average retinal speeds when the head is held stable. These values represent the retinal image motion that the visual system typically confronts during the performance of natural tasks when the head is free to move. Image motion under natural conditions will vary depending on how much the head is moving, and on the effectiveness of compensation (compensation levels can vary over wide ranges; Collewijn, 1989a,b; Epelboim et al., 1995). This means that, in principle, the oculomotor system can adjust retinal image motion to levels that would be optimal for any given task. Much of the discussion of eye movements of fixation over the past 25 years has involved questions about the significance for vision of the retinal image motion produced by eye movements.

1.2. The role of retinal image motion in vision

Image motion on the retina is crucial for vision. Too much motion impairs vision (Burr & Ross, 1982). Too little motion is a problem as well. In the extreme, stabilizing the retinal image (by using the recorded eye movement signal to control motion of the stimulus) causes objects to fade from view within seconds. Increasing the velocity of image motion to values that are faster than those typically found during fixation when the head is held in place results in improved visibility (for review, see Collewijn & Kowler, 2008). Retinal image motion also affects visual acuity. Visual acuity for moving targets is robust to increases in image motion up to about 2 deg/s, with the effects of motion dependent on factors such as retinal eccentricity, contrast, spatial configuration and the presence of flankers (Carney, Silverstein, Klein, 1995; Murphy, 1978; Westheimer & McKee, 1975; Morgan & Benton, 1989; Macredo, Crossland & Rubin, 2008; Chung, Levi & Bedell, 1996). Image motion produced as a consequence of uncompensated head rotations can have smaller effects on contrast sensitivity than equivalent image motion created by moving the stimulus itself (Steinman et al., 1985). Steinman & Levinson (1990) provide a historical review and analysis of the role of image motion in maintaining high quality vision.

The classical studies on vision with stabilized images found that retinal image motion was more beneficial to the visibility of low spatial frequency patterns than high spatial frequency patterns. Recent results by Rucci et al. (2007) challenge this long-held view. Rucci et al. tested contrast sensitivity for retinally-stabilized and unstabilized tilted gratings with spatial frequencies of either 4 or 11 cycles/deg. The gratings were shown with superimposed fields of visual noise, with high frequency noise superimposed on the 4 cycle/deg grating, and low frequency noise on the 11 cycle/deg grating. The method was a departure from prior studies of the effects of image motion in that testing was restricted to relatively brief intervals following a large saccade. This was done by having subjects make a saccade to a cued location, and, after the eye landed, presenting the grating for 1 second, either stabilized or unstabilized. Under these conditions Rucci et al. (2007) found that only the higher spatial frequency grating benefited from allowing image motion. Performance for the lower frequency grating (orientation judgments, as well as contrast sensitivity) was unaffected by stabilization. Rucci et al. concluded that the relatively modest retinal image motions occurring during the brief one-second presentation of the grating did not produce enough local variation in contrast to make much difference to the encoding of low spatial frequencies, but was sufficient to allow the high spatial frequency pattern to stand out from the low frequency superimposed noise. They interpreted these findings as showing that retinal image motion produced by eye movements can act as a filter to enhance the visibility of fine visual details within the typical visual environment, which is dominated by low spatial frequency information.

Rucci et al.'s (2007) results illustrate how image motion can benefit vision. This is a fortunate outcome because image motion is inevitable in normal viewing. In a classic paper Walls (1962) pointed out that the main reason we have eye movements is not to move the image, but to stabilize gaze against the effects of head motion. We do not need eye movements for the purpose of generating image motion – we need them to ensure that image motion does not get out of hand.

1.3. Microsaccades

The past few years has also seen considerable interest in saccades during fixation. Saccades occur intermittently during maintained fixation, in some cases as often as two or three times per second, and in some individuals or tasks as infrequently as one every several seconds.

The classical studies of maintained fixation reported the sizes of saccades rarely exceed 12–15 minutes of arc (microsaccades). Studies over the past 10 years have reported considerably larger saccades during fixation, with amplitudes out to half degree or more (Møller, Larsen, Tygsen, & Sjølie, 2002; Engbert & Kliegl, 2003). Many factors could be responsible for the larger saccades, including increased head motions due to use of head rests rather than bitebars (Møller et al., 2002), use of illuminated rather than dark rooms, and the use of instrumentation with higher noise levels than the optical lever (see Collewyn & Kowler, 2008, for more discussion). In addition, there is inherent ambiguity in the instruction to “fixate” that could lead to differences in subjective estimates of the acceptable zone of fixation.

The issue of the sizes of saccades during fixation is raised because, although saccades up to 1 degree in may occur during fixation (Engbert & Kliegl, 2004; Martinez-Conde et al., 2009), there has never been any need to find a special functional role for saccades larger than about 15'–20': shifts of gaze of that size or larger are needed because of the decline of visual resolution with eccentricity. Thus, to avoid ambiguity, I'll reserve the term microsaccade to refer to saccades smaller than 15 min arc.

The past 25 years has seen the development of a variety of approaches, both psychophysical and neurophysiological, to understand the origin and role of microsaccades.

1.3.1. Perceptual causes and consequences of small saccades

Microsaccades search and scan micro-displays: One possible function for microsaccades is to bring the line of sight to a succession of locations of interest, functioning as a search or scan pattern, analogous to the function of larger saccades (Steinman et al., 1973). When this idea was tested with tasks such as counting, or threading a needle, microsaccades were either not made too often, or did not improve performance (Winterson & Collewijn, 1976; Bridgeman & Palca, 1980; Kowler & Steinman, 1979). On the other hand, saccades just a bit larger than the classical microsaccade bound, $>15\text{--}20$ minutes of arc, can improve performance of visual tasks, such as counting (Kowler & Steinman, 1977), letter recognition (Kowler & Anton, 1987), or visual search (Schlingensiepen et al., 1986). Recently, Ko, Polletti & Rucci (2010) re-examined the utility of microsaccades ($<15\text{--}20'$) by studying saccadic patterns during a new version of the needle threading task. They found saccades less than $20'$ were used to look back and forth between thread and needle. This pattern suggests that microsaccades can have a useful function during active visual tasks, analogous to that of larger saccades in larger visual arrays (see 3.8 for discussion of larger saccades during active tasks).

Saccades can revive faded extrafoveal images: Retinal transients can revive the visibility of fading, low contrast extra-foveal stimuli under circumstances where the retinal image motions produced by slow or smooth eye movements is insufficient (Clark & Belcher, 1962). In line with these observations, Martinez-Conde et al. (2006) found higher rates of saccades, and larger saccades (about $20'$), during periods when an eccentric (3–9 deg) medium contrast small grating was visible than when it had faded. Troncoso et al. (2008) made similar observations in testing the perceptual filling-in of a small disc at 12 deg eccentricity surrounded by an equi-luminant array of dots (saccades were on average .4 deg). These results demonstrate a role for saccadic retinal transients out of the classical micro-range under conditions (e.g., minimal head motion) where the image motions created by smooth or slow eye movements were unlikely to be sufficient to maintain visibility of the extrafoveal (3–12 deg eccentric) targets.

Fading of foveal images has not been reported during prolonged periods of fixation, with or without microsaccades. Study of vision with stabilized images and imposed retinal image motions of various kinds found that any image motion is better than none, but have not revealed a special role for microsaccades or saccade-like image transients in maintaining the visibility of foveal images (reviewed in Steinman & Levinson, 1990; Collewijn & Kowler, 2008; see also Poletti & Rucci, 2010).

Microsaccades affect the perceptual oscillation between rivalrous patterns: Van Dam and Van Ee (2005, 2006a,b) found that transient changes in retinal stimulation, including those produced by microsaccades, while viewing binocularly rivalrous stimuli (gratings of different orientation), affected which eye dominated the percept. Comparable retinal changes produced by moving the stimulus in the absence of saccades also affected perceptual dominance, showing that the retinal change, not the saccadic command, was critical. For other types of perceptual rivalries, such as binocularly viewed forms that could be perceived at one of two different slants, saccades (regardless of size) were not associated with the occurrence of the perceptual flips.

Saccades during fixation may reflect the direction of a shift of attention: Interest in the connection between saccades during fixation and shifts of attention has been fueled by the

prospect of using small saccades as overt indicators of otherwise hidden attention shifts (see also 3.3), a boon for laboratory experiments that study attention to peripheral targets during maintained fixation. In support of the idea that microsaccades signal larger shifts of attention Hafed & Clark (2002) found that peripheral cues produced a significantly higher proportion of small saccades in the direction of the cue (or in the direction of an imperative stimulus), although the occurrence of saccades overall was not high (25%). They also found that performance was better in trials containing small saccades made in the direction of the target, supporting the view that the small saccades reflected the attention shifts. Engbert & Kleigl (2003) obtained comparable results. Horowitz et al. (2007), however, did not find a relationship between saccadic direction and performance when saccadic direction was pitted against an attentional cue. The question of what conditions would and would not be expected to produce links between small saccades and attention continues to be debated (e.g., Laubrock, Kliegl, Rolfs & Engbert, 2010).

1.3.2. Neural causes and consequences of small saccades—Two new sets of neurophysiological investigations shed light on both the generation of microsaccades, and their significance for vision.

Microsaccades are generated by activity in the superior colliculus: Hafed, Goffart & Krauzlis (2009) performed a pioneering study of the neural origin of microsaccades. They studied responses of neurons in the deep layers of the rostral pole of the superior colliculus, an area that had been associated with the maintenance of fixation and inhibition of large saccades (Munoz & Wurtz, 1993). Previously, Hafed et al. (2008) found that inactivation of the rostral region could produce systematic offsets in the preferred locus of fixation. Hafed et al. (2009) found single neurons that fired before microsaccades, with neurons selective as to preferred direction and size. The neurons responded before or during saccades as small as 3 min arc – a microsaccade by anyone’s definition. Some neurons also responded before or during saccades as large as 5 degrees. The neural activity associated with the saccades persisted in darkness.

Hafed et al. (2009) proposed a model of microsaccade generation based on the idea that the function of the neurons in the rostral pole is to ensure accurate fixation. These neurons could do so, they suggested, by ‘monitoring’ the mean activity level encoded by the neural population in the colliculus relative to a representation of the selected locus of fixation. Changes in the mean activity level of the population, which could be caused by any number of factors, then would evoke a microsaccade. While this model would seem to revive the original position-correcting-reflex model of microsaccade generation proposed by Cornsweet (1956), and challenged by subsequent work (Nachmias, 1959; 1961; Steinman et al., 1973), Hafed et al. did not talk about fixation reflexes. Instead, they emphasized that by placing the control center in the colliculus, all sorts of higher level influences, from attention shifts to voluntary or task-based strategies (e.g., Basso & Wurtz, 1998; McPeck & Keller, 2004; Krauzlis, Liston & Carello, 2004; Kustov & Robinson, 1996) could bias the population activity, and in so doing increase the probability of microsaccades. It is useful to note that in this model, microsaccades could also be evoked by noisy fluctuations in the neural population mean.

Saccades and microsaccades modulate neural firing in V1 and V4: The past 25 years of oculomotor research saw the emergence of a new, and technically challenging, endeavor, namely, the study of the response of visual neurons to the retinal image changes and motor commands produced by eye movements. This extends and develops the original findings of Wurtz (1969), who showed that neurons in V1 respond equivalently to image motion whether produced by saccades or by a rapid translation of the stimulus across the retina. Interest in recent years has turned to the neural effects associated with the smaller eye

movements of fixation. Leopold & Logothetis (1998) reported that neurons in V1 responded with either suppressed (37%) or enhanced activity (17%) following saccades as small as 10', while V4 always showed enhancement. They speculated that these effects might mean that the saccade-linked signals could enhance temporal synchronization of visual activity. Martinez-Conde, Macknick & Hubel (2000) reported bursts in V1 following somewhat larger saccades, up to 2 degrees.

Snodderly, Kagan & Gur (2001), on the other hand, found a more complex pattern: post-saccadic bursts in some cells, and sustained activity during the fixation pauses between saccades in others. Kagan, Gur & Snodderly (2008) confirmed and then extended these findings in two ways. First, they found that the responses of the saccade-linked burst cells could also be produced by high speed retinal image motion, even in the absence of saccades. Second, they found neurons that were sensitive to saccades in the dark, responding with a brief decrease, then an increase, in activity following the occurrence of a saccade (Rajkai, Lakatos, Chen, Pincze, Karmos & Schroeder, 2008, reported comparable patterns of activity in V1 following large saccades made in darkness). Taken together, these results show eye movement related modulation of neural activity with a variety of different patterns: post-saccadic enhancements, post-saccadic suppression, and drift-based modulations.

Using a somewhat different approach, Bosman, Womelsdorf, Desimone & Fries (2009) studied neural effects linked to saccades that occurred during intervals of fixation while the monkey was engaged in a task requiring attention to an eccentric grating pattern. They found that saccades during fixation (the population ranged in size from a few minutes of arc to 1 deg) modified the temporal synchronization of neural activity in V1 and V4, in support of the proposal by Leopold & Logothetis (1998) (see above). Bosman et al. (2009) were particularly interested in evidence that the saccades modified the power of the local field potential in the 40–60 Hz frequency band (i.e., gamma-band synchronization), which had previously been associated with modulations in the strength of attention (Womelsdorf et al., 2006). Bosman et al. (2009) found that for an interval of about 200 ms following the saccades, the strength of the gamma-band synchronization decreased, and this decrease was associated with slightly slower responses in the psychophysical task. Thus, the effect of the microsaccades, if any, was to slightly impair task performance. It is early (as Bosman et al. note) to fully evaluate the functional significance of these findings. Do they represent evidence for neural saccadic suppression? Are the effects of the saccades on neural activity due to the image motion or to corollary discharge signals? Would the contribution of the saccades to neural synchronization be the same had the image motion during intervals between saccades been faster and thus more representative of the moderate or high velocity motions found in active tasks?

1.4. Summary

Eye movements during fixation result from activity of the visual and vestibular compensatory systems that function to keep gaze relatively stable in the face of movements of the head. The past 25 years has seen renewed interest in the eye movements during fixation and their effects on vision.

The interest in the effects of eye movements of fixation on vision has centered around the role of retinal image motion. There continues to be broad agreement (going back to the original studies of vision with stabilized images) that retinal image motion during maintained fixation is critical for vision: too much image motion degrades resolution, and too little motion can lead to image fading. In natural situations, where the head is free to move, retinal image motion is provided by head movements, and thus the main task for compensatory eye movements is to prevent retinal motion from becoming too fast to allow clear vision. Adjustments in retinal image velocities to values that are appropriate (neither

too fast nor too slow) for the task at hand can be carried out by changing the degree of compensation for the head motion. Small saccades, and microsaccades in particular (<12'–15'), whose neural origin, at least in the superior colliculus, is now known, are not the ideal generators of visually-useful image motions.

The past 25 years has also seen renewed interest in the role of microsaccades and other small saccades during fixation, including their role in perceptual tasks and their links to attention. Recent work suggests that microsaccades may be useful in tasks where gaze shifts between closely spaced details are required, analogous to the role of large saccades within larger visual arrays.

Investigations of the effects of eye movements on visual neurons are beginning to reveal correlations between saccadic movements, as well as smooth eye oscillations, on neural firing. Some of these correlations are due to the image motion itself, and some to signals originating from the eye movement commands. These techniques, combined with new psychophysical investigations, may be able to address two central questions that were raised, but not resolved, over the past 25 years: (1) Do saccades, or saccade-like motions, have special significance for visibility that cannot be matched or exceeded by slow or smooth eye movements? (2) How do the high-velocity smooth image motions, of the sort found in freely-moving observers, affect visual function in different representative visual tasks?

2. Smooth pursuit

Smooth pursuit refers to smooth tracking of selected, and typically foveal, targets. Strictly speaking, smooth pursuit is not under voluntary control in that it is not possible to initiate smooth pursuit across a stationary environment, or to completely suppress pursuit in an environment consisting of only moving targets.

The approach to smooth pursuit has changed dramatically over the past 25 years. During the 1960's and into the 1970's there were active debates about whether to view pursuit as a sensorimotor reflex, initiated and maintained solely by the motion of the target across the retina, or to emphasize the role of processes such as selective attention and expectations. Pursuit is now seen as an active response, configured on the basis of a host of available cues and signals, including motion, selective attention, cognitive expectations, and past experience.

2.1. Motion

A long standing question in the study of smooth pursuit has been whether the motion signals needed to sustain pursuit are based on the motion of the target across the retina ("retinal slip"), or, alternatively, a higher level representation that is closer to the motion that is perceived. Initial efforts to address this question consisted of novel demonstrations that pursuit could be obtained with stimuli that generated strong percepts of motion without corresponding motion of a stimulus across the retina (e.g., Yasui & Young, 1975; Cushman et al., 1984; Van den Berg, 1988; Van den Berg & Collewyn, 1987; Wyatt & Pola, 1979, 1989; Steinbach, 1976; Ringach et al., 1996). These findings supported the view that a common sensory signal serves both smooth pursuit and motion perception, a view later reinforced by discoveries that motion signals from the same area of the brain, visual area MT, could provide input for both perceived motion and smooth pursuit (Newsome & Pare, 1988; Komatsu & Wurtz, 1989; Groh, Born & Newsome, 1997). The past 25 years saw a refinement of these efforts that took advantage of the increasing sophistication of our understanding of motion processing.

Beutter & Stone (1998, 2000), for example, found that the direction of pursuit of moving patterns was influenced by the shape of the surrounding aperture, showing that pursuit (like perception) can recover the motion of the inferred object and is not constrained to follow the motion of the local elements. Masson & Stone (2002) continued the exploration of pursuit of “local” (image) vs. “global” (object) motion by studying pursuit of tilted diamonds (See Fig. 2). The first 100 ms or so of pursuit depended on the local cues, with the direction of pursuit determined by the vector average of the motion directions of the 4 edges of the shapes. After that, pursuit followed the motion of the whole object, paralleling the percepts with these stimuli. They concluded that the motion signals contributing to sustained pursuit depended on an “object-motion pathway” (see also Wallace, Stone & Masson, 2005).

Other studies contributed to the case that perception and pursuit share common representations of motion. For example: Smooth pursuit (like perception) can be driven by both motion aftereffects (Braun, Pracejus & Gegenfurtner, 2006), and second-order motion (Hawken & Gegenfurtner, 2001). Pursuit and perceptual judgments are both insensitive to accelerating motion (Watamaniuk & Heinen, 2003), both are about equally sensitive to information about the likely direction of upcoming motion (Krauzlis & Adler, 2001), and both can integrate information over large regions across the retina (Heinen & Watamaniuk, 1998; Osborne & Lisberger, 2009). The impairments of pursuit produced by brief blanking of a moving target are reduced by cues that create the perceptual impression of a target moving behind an occluder (Churchland, Chou & Lisberger, 2003).

Other approaches to comparing pursuit and perceived motion focused on signal/noise properties. Kowler & McKee (1987) found that the sensitivity of pursuit to small differences in target velocity was poor soon after the onset of target motion, but once steady state eye velocities were achieved (about 600 ms after motion onset) pursuit could reliably discriminate differences in velocity of about 7–8%. These values are comparable to perceptual discrimination when the same motions were presented briefly (200 ms). Stone & Krauzlis (2003) found that thresholds for the discrimination of motion direction for perception and pursuit were quite similar. Gegenfurtner, Xing, Scott & Hawken (2003) also found comparable discrimination thresholds (speed discrimination) for pursuit and perception, but low trial-by-trial correlations. They concluded that pursuit and perception have similar levels of precision, but were affected by different sources of noise, perhaps originating from processes subsequent to initial motion encoding (see also Krauzlis & Adler, 2001). The case for differences in the processing streams for pursuit and perception was recently strengthened by the findings of Tavassoli & Ringach (2010), who found that the response of pursuit to a brief perturbation of target motion was better than the perceptual discrimination of the same motion perturbation.

Poor discrimination of velocity during the early portions of pursuit was confirmed by Rasche & Gegenfurtner (2009), who argued that reports of somewhat better discrimination during early portions of pursuit in monkey (Osborne, Hohl, Bialek & Lisberger, 2007) were likely due to differences in species or to training. An interesting aspect of finding poor discrimination early in pursuit was that it coincided with an interval where pursuit was also very sensitive to expectations and learning (section 2.4), with higher pursuit velocities associated with experience tracking higher velocity target motions in the recent past (Kowler & McKee, 1987; Carl & Gellman, 1987).

Another similarity between pursuit and perception is that both depend on selective attention.

2.2. Smooth pursuit and attention

At any given moment the visual scene contains a host of moving elements. These are produced by a remarkable variety of natural or machine-produced sources: flying birds,

running squirrels, moving people, objects that we manipulate and move from place to place, or the objects that move across computer displays. Even in a stationary environment our own head or body motions will generate complex patterns of retinal image motion of stationary objects in ways that depend on the geometric relationships between our pattern of motion and the direction and distance of each object. In the context of all the motion, the pursuit system must make a choice.

Classical studies (Ter Braak & Buis, 1970) showed that in the presence of two different large, interleaved patterns of moving stripes, the eye could pursue whichever was selected. The effectiveness of this choice – selective attention – in determining the stimulus for smooth eye movements was documented in subsequent studies, with agreement that there was little influence of the motion that was not selected (i.e., not attended), provided that stimulus factors, such as retinal eccentricity and contrast, were equivalent (Dodge & Fox, 1928; Murphy et al., 1975; Kowler et al., 1984; Collewijn & Tamminga, 1984, 1986). More recent studies have shown that the influence of the background (or other non-targets) on pursuit depended on factors including the velocity of motion, the relative velocities of the background and the pursuit target (background motion in the same direction of the target tended to help, while motion opposite to the pursuit target tended to hurt), and when, with respect to the onset of pursuit, the background (non-target) motion occurred (e.g., Masson, Proteau & Mestre, 1995; Lindner & Ilg, 2006; Nieman & Hoffman, 1997; Ferrera & Lisberger, 1995; and Spering & Gegenfurtner, 2007, who provide a detailed review of past findings).

Recent work has sought to understand the mechanisms that carry out the selection with emphasis on the following three questions:

2.2.1 How do pursuit and saccades work together to select targets?—Shared selection of the target for saccades and pursuit is an effective way of dealing with environments containing multiple targets because only one decision (which one of these should I look at?) is needed. We rely on a saccade to bring a selected moving target to the fovea, when pursuit can then take over to keep the target there. Evidence favors a close coupling between the control of selection for pursuit and saccades.

Krauzlis & Dill (2002) found that the same neurons in the superior colliculus responded prior to the selection of a target, regardless of whether the selection was carried out by a saccade or pursuit. Stimulating these same neurons at levels below those that would produce saccades could bias the choice of the target for pursuit (Carello & Krauzlis, 2004). Gardner & Lisberger (2001, 2002) made a strong case for a common selective mechanism, finding that in the presence of a pair of moving targets, pursuit showed stronger selectivity after a saccade was made to one of the targets, regardless of whether the saccade resulted from the monkey's free choice or from electrical stimulation. They argued for a process of attentional selection of the pursuit target that could be directed by the generation of the saccadic command. However, there are also examples where the order is reversed. Liston & Krauzlis (2003) positioned bands of moving noise fields above and below fixation. Selection of one of the moving bands was prompted by a perceptual discrimination task, namely, look from the center to a higher contrast probe stimulus that had been presented briefly before the moving fields. Pursuit showed evidence of selection before the saccade, even occasionally following the wrong target, but later changing direction to correct the error shortly before the saccade (see also Krauzlis et al., 1999).

Anyone hoping for a simple resolution to the question of which type of eye movement, pursuit or saccade, reflects the selection first will find little comfort in the results of Erkelens (2006). He presented a series of moving targets in different locations, each moving for about

1 second in a random direction. In one condition, the moving targets appeared one at a time. In another condition a new moving target appeared before the current target was removed. In either situation, subjects had to hop around the display, looking at and pursuing whatever appeared. In the case where targets appeared one at a time, pursuit latencies (125 ms) were considerably shorter than saccadic latencies (229 ms). But when there was some temporal overlap, pursuit and saccadic latencies were both about 250 ms, and highly correlated across the segments. Erkelens (2006) explained this pattern of results by proposing a two-stage process in which the preparation of pursuit and saccades starts at the same time (initiated by the same shift of attention), with the execution of each controlled by a separate system.

2.2.2. Do pursuit and perception share common attentional systems?—The role of perceptual attention in the selection of the target for pursuit has been demonstrated by experiments that required pursuit of one target and perceptual judgments about another. Khurana & Kowler (1987) found that identification judgments about the pursued target were more accurate than those made about the non-targets (their experiments controlled for effects of retinal velocity), and that diverting attention to the non-target also led to reductions in pursuit velocity. Lovejoy, Fowler & Krauzlis (2009) found that attention during pursuit focused on the target, and less on objects that moved in the same pattern, but were located either in front of or behind the target.

There are asymmetries between the effect of attention on pursuit and perception in that it is possible to move some attention away from the pursued target and improve judgments about the non-target with little effect on pursuit (Khurana & Kowler, 1987). Asymmetric effects of attention are not unusual in dual-task experiments that involve concurrent perceptual tasks, and their presence typically signals that the two tasks are not making equivalent demands on processing resources (Sperling & Doshier, 1986). Kerzel, Born & Suoto (2009) reported an asymmetry in the other direction, that is, larger effects of attention on pursuit than on the perceptual judgment. In their experiment the judgments were made about briefly flashed targets, rather than moving targets.

One implication of the asymmetries is that attention is not acting at a single locus for either perception or pursuit. For example, sensory motion signals representing the “unselected” targets during pursuit may be available to support perceptual judgments, and be subject to further filtering or attenuation at any number of subsequent levels prior to the formulation of the final pursuit motor command.

2.3.3. Can selection fail to be effective?—Selecting the target for pursuit takes time, just like any shift of attention from one location to another (Reeves & Sperling, 1986; Weichselgartner & Sperling, 1995). If two potential pursuit targets begin moving simultaneously, before cues about which to track are presented or can be processed, pursuit may reflect the average of the available motions (Keller & Khan, 1986; Lisberger & Ferrera, 1997; Recanzone & Wurtz, 1999). Cues that signal which target is to be tracked, including its location and direction of motion, diminish the averaging and the effects of distractors on pursuit (Adler, Bala & Krauzlis, 2002; Krauzlis et al., 1999; Ferrera & Lisberger, 1995; Garbutt & Lisberger, 2006). Sperling, Gegenfurtner & Kerzel (2006), as part of a comprehensive study of the effects of distractors on pursuit, found that a distractor can produce a brief pursuit response opposite to its direction of motion, and attributed these effects to inhibitory signals (perhaps connected to attention) generated as part of attempts to ignore the distractors.

2.4. Anticipatory smooth eye movements and ‘predictive tracking’

The past 25 years has also seen a new understanding of the role played by prediction in smooth pursuit. The first clear evidence for prediction during pursuit came from studies of tracking of repetitive motions (for example, a target moving back and forth following a sinusoidal pattern), in which the eye was shown to reverse direction in time with, and sometimes shortly before, the target (Dodge et al., 1930; Westheimer, 1954). Predictive tracking got more attention in the 1960’s as part of attempts to develop linear systems models of smooth pursuit. Prediction was attributed to special circuitry that came into play only for periodic motions, allowing the pursuit system to learn, and then generate, the repetitive oculomotor patterns (Dallos & Jones, 1963; also, Barnes & Asselman, 1991).

Smooth pursuit, however, can also be initiated before the motion of the target begins. Such anticipatory smooth eye movements were studied in detail beginning in the 1970’s and found to occur before various types of expected target motions (Kowler & Steinman, 1979a,b; 1981; Boman & Hotson, 1988, 1992; 1988; Kao & Morrow, 1994; Heinen & Liu, 1997; Barnes & Schmid, 2002). Anticipatory smooth eye movements were also observed when the direction or the time of the expected motion was not completely predictable, with the properties of the eye movements depending on the past history of target motions (Kowler et al., 1984; Heinen, Badler & Ting, 2005; Badler & Heinen, 2006; Kowler & McKee, 1987; Collins & Barnes, 2009; deHemptinne, Nozaradian, Duvivier, Lefevre & Missal, 2007). The presence of anticipatory smooth eye movements with random motions shows that, in contrast to the assumptions contained in the earliest models of “predictive tracking” in the 1960’s, prediction does not switch in and out of the processing stream, but is available as an ever-present feature of smooth pursuit.

A: I know we’re not supposed to comment yet, but I have to say, this all seems like a lot of complication. Why should the pursuit system need to predict?

B: To make up for processing delays; why else? It’s a safe bet that most of the motions we encounter will be fairly predictable. Totally random motions are rare, unless you’re encountering things like an insect trying to evade capture. With anticipatory responses we avoid the large pursuit errors that would be caused by delays. Small errors shouldn’t be much of a problem.

A: That’s all fine, but something seems to be missing. Are the processing delays associated with pursuit really so long? Latencies are only about 100 ms, and pursuit dynamics are fast in response to random perturbations to the motion introduced while pursuit is already underway. Many showed this: Tavassoli & Ringach in 2009; Osborne & Lisberger in 2009; Schwartz & Lisberger in 1994; and Churchland & Lisberger in 2002. So why bother with anticipation? Maybe there’s another reason.

K: We’re getting ahead of ourselves. There have been two main approaches to anticipatory smooth eye movements, one emphasizing a role for learning, and the other for symbolic cues.

2.4.1. Learning—Fig. 3 taken from Kao & Morrow (1994), shows the results of learning to track a pattern of motion. A subject tracked the same 40 deg/s constant velocity motion for 20 trials, and then, unexpectedly, the velocity shifted to 5 deg/s. Yet the eye continued to produce fast pursuit for another two cycles. Some of this learning can be a matter of adjustments of pursuit gain (Kahlon & Lisberger, 1996), but gain adjustments alone do not account for cases where changes in direction are learned (Leung & Kettner, 1997; Medina, Carey & Lisberger, 2005).

Barnes & Schmid (2002) proposed that learning the pursuit trajectories involve “the short-term storage of premotor drive information and its subsequent reproduction as an anticipatory estimate...under the control of a separate timing mechanism” (p. 323; also Barnes & Collins, 2008a,b). The search for a neural mechanism to control the learning has focused on the cerebellum, a structure that may have the capacity to store and generate pursuit trajectories, along with the associated temporal and spatial cues (Kettner et al., 1997; Suh & Kettner, 2000; Medina & Lisberger, 2008; 2009). (See Zee & Walker (2003) for detailed review of the role of the cerebellum in pursuit, and Cerminara, Apps & Marple-Horvat, 2009, for evidence that cerebellum can encode trajectories of target motion.)

2.4.2. Cognitive expectations and symbolic cues—Anticipatory smooth eye movements, which occur just before pursuit gets underway, could also be a product of learning, particularly given their dependence on the past history of target motions (e.g., Kowler et al., 1984). However, humans (primates, more generally) can also make use of symbolic cues to signal the future path of the moving target. Fig. 4 shows anticipatory smooth eye movements in response to symbolic cues (Kowler, 1989). The target was a disc heading down an inverted-Y shaped tube, where the future path of the disc was indicated by the barrier blocking one of the arms of the Y. Auditory cues (“right” vs. “left”) were tested as well. Both types of cues led to anticipatory smooth eye movements, overriding (but not abolishing) the influence of the immediately prior trials (sequential dependencies). Jarrett & Barnes (2002, 2005), Eggert, Ladda & Straube (2009) and Ladda, Eggert, Glasauer & Straube (2007) also found anticipatory smooth eye movements in response to various types of symbolic cues that disclosed the direction or velocity of future target motion. Burke & Barnes (2008) showed that observing a target in motion (but not actively tracking it) was able to contribute to the expectations that enhanced subsequent pursuit of the same motion presented after a delay, although active tracking produced stronger effects.

2.4.3. The neural basis of anticipatory smooth eye movements—One of the more intriguing developments over the past 25 years has been the proposal that anticipatory smooth eye movements found before the onset of pursuit are a different phenomenon from the ‘predictive tracking’ or learning (see above) observed when pursuit is already underway. Heinen (1995) found that directionally-selective neurons in supplementary eye field (SEF, a portion of the dorsomedial frontal cortex, DMFC) were active during the initiation of pursuit of constant velocity motions. Although the SEF is associated with preparation of saccades (Stuphorn, Brown & Schall, 2010), Heinen (1995) proposed that the SEF could have a special function in the initiation of pursuit, and in anticipatory pursuit:

“Another possibility is that the DMFC is part of a separate motion processing/pursuit path that originates in early visual areas (V1/V2) and goes through parietal areas to the FEF and DMFC...The purpose of such an extra ‘loop’ on the classic pursuit pathway might be to facilitate the initiation or control of eye movements that would otherwise depend solely on retinal slip... The DMFC could facilitate smooth pursuit, even in cases where no anticipation or prediction occurs, by issuing a preparatory or motor set signal. In other words, the DMFC might be involved in telling the eyes ‘when’ to move to boost performance ...beyond that which would occur due to simple anatomical latency constraints” (p 360–1).

Subsequent work lent support to the proposal that the cortex (SEF, in particular) is providing an alternative pathway that is solely concerned with the initiation of pursuit, including anticipatory pursuit. Heinen & Lu (1997) found greater SEF activity when the timing of expected motion was predictable. De Hemptinne, Lefèvre & Missal (2008), using color cues to signal the direction of upcoming motion, found that the directionally selective responses in SEF began shortly before the initiation of the anticipatory response. Missal & Heinen

(2001, 2004) showed that stimulation of SEF produces smooth eye responses, but only if the stimulation was delivered shortly (about 175 ms) before the motion, and only when motion was expected. Stimulation was not effective during maintained fixation or during maintained pursuit, evidence that supports a special role for SEF in anticipatory smooth eye movements. In more recent work, neurons in SEF have been found that represent various aspects of the decisions made in preparation for pursuit, including the significance of cues signaling whether an upcoming target motion should be pursued or ignored (Yang, Hwang, Ford & Heinen, 2010; Shichinohe et al., 2009).

2.5. Summary

All of these developments that point to the involvement of cues, signals, plans, attention and expectations in the preparation of pursuit are beginning to blur the classical line between pursuit and saccades.

It may go a little too far to equate anticipatory pursuit with saccades. But the evidence indicates that some aspects of saccades and anticipatory smooth eye movements share neural areas, and, by implication, the same processing steps: shared environmental cues, shared decisions, shared target selection, and shared expectations of future events and future plans, all in the interests of fostering coordinated behavior. Anticipatory smooth eye movements, like saccades, are eye movement that occur at moments of transition. In most of the lab studies, the transition is the initiation of pursuit. But in real life, transitions from one object to another are mediated by saccades and shifts of attention. Saccades and the initiation of pursuit are closely linked.

This overlap between pursuit and saccades was the main argument in Krauzlis's (2004) review of the pursuit pathways, which considered the role of motion signals and attention as well (see also Krauzlis & Stone, 1999), and concluded by saying:

“As an alternative to the traditional view of pursuit and saccades as distinct oculomotor subsystems, the control of pursuit and saccades might be viewed as different outcomes resulting from a single cascade of sensory-motor functions. From this viewpoint, the several obvious differences between pursuit and saccades illustrate the variety of outcomes that are possible with these layers of control, rather than indicate the presence of independent systems of control...”

One obvious difference, namely, saccades are voluntary and pursuit seems not to be, was explained by the following:

“...our capacity to represent motion information in the absence of extant sensory signals appears to be much more limited than our ability to abstractly represent spatial information. This limitation of our imaginations, rather than differences in overall organization, may explain why pursuit appears to be less voluntary than saccades” (Krauzlis, 2004, p 599).

A. This still doesn't explain why we have predictive, anticipatory eye movements.

K. Prediction in the brain is ubiquitous. We can't avoid it. Motor preparation is based on predicting and preparing for the consequences of actions. Perceptual judgments made under uncertainty are influenced by expectations and probabilities. Smooth pursuit is one part of a bigger picture.

A. But there are limits. We can't initiate pursuit without motion of a target.

B. Sure we can – expected motion will do it.

A. Just the initiation of pursuit? What about maintaining pursuit?

K. Maintaining is another matter. Once you've gotten up to speed, the retinal velocities are fairly low, and as we saw already, the system can quickly generate responses to unexpected perturbations once pursuit is underway.. The difficult part, as with anything, isn't maintaining the behavior; it's the major transitions: stationary to moving, right to left, slow to fast. Use what you have: cues, past history, attention, all of it, to boost the ability to cope with change.

A. And so we shouldn't think of the pursuit as an isolated system?

B. Collewijn in 1989 made analogous arguments with respect to the vestibulo-ocular response.

A. Where does that leave saccades? Saccades have all sorts of functions related to vision that don't seem to overlap with pursuit.

3. Saccades

Saccadic eye movements are the rapid shifts of the line of sight made to bring the fovea – the center of best vision – from one selected location to another. Saccades are useful and efficient ways to sample the visual environment, allowing the important work of vision to be done during the periods of relative retinal stability and, consequently, high visual acuity, that occur between successive saccades. Saccades are the characteristic mode of exploratory movements across a wide range of species and types of visual systems (see Land, 1999).

Knowledge about the planning and generation of saccades has ballooned over the past 25 years. Investigators have largely abandoned the once-popular paradigm of studying saccades made to track the abrupt jumps of a single point of light moving in darkness. The past 25 years has seen novel explorations of the saccadic patterns during tasks designed to capture the demands and complexities of vision in real life, comprising anything from search of natural scenes to walking down hallways or devising geometric proofs. This review can only discuss a small portion of the news of the last quarter century, and will focus (and even here incompletely) on a few topics that seem most relevant to the connections between eye movements and vision.

3.1. Where we look when we view pictures

In 1985 Koch & Ullman proposed the notion of a “saliency map”. The saliency map was defined as a “global measure of conspicuity” derived from the local contrast of features such as luminance, orientation, color, and motion (for a precursor, see Engel, 1974). The saliency map was believed to be computed at early visual levels (V1, plausibly), prior to the identification of individual objects, even prior to segmentation of figure from ground. The notion of a saliency map became one of the most influential constructs over the past 25 years, even while undergoing revisions and developments in how it may be computed (e.g., Itti & Koch, 2001; Bruce & Tsotsos, 2009). Koch & Ullman (1985) linked the saliency map to the distribution of attention – and, consequently, eye fixations – across a scene. The higher the computed physical salience, the more likely a given location would be attended (or fixated).

The original proponents of the idea that a saliency map could serve as a precise quantitative predictor of scanning eye movement patterns made no bones about what was useful, and then what was missing, in this deliberately bottom-up approach. Here is what was useful, from Koch & Ullman (1985, p. 221): “Formulating the operation of selective attention in terms of these mechanisms [physical salience] rather than the language of higher cognitive concepts, has the advantage that specific predictions concerning the anatomy and electrophysiology of the specialized cortical regions involved in attention can be derived”. And, what was missing: “Although such a simple computational architecture might

accurately describe how attention is deployed within the first few hundreds of milliseconds after the presentation of a new scene, it is obvious that a more complete model of attentional control must include top-down, volitional biasing influences as well. The computational challenge, then, lies in the integration of bottom-up and top-down cues, such as to provide coherent control signals for the focus of attention, and in the interplay between attentional orientating and scene or object recognition.” (Itti & Koch (2001, p 7).

The incorporation of at least some top-down influences into a single saliency map would appear to be a feasible goal, given the current understanding of the effects of attention and learning on perception. Many of the perceptual effects of either voluntary attention or perceptual learning result from modulation of the effective feature contrast or signal/noise ratios across the image by means of operations likely to occur at early visual levels (Doshier & Lu, 2000; Gould, Wolfgang & Smith, 2007; Pestilli, Ling & Carrasco, 2009; Li, Polat, Makous & Bevalier, 2009; Lu, Liu & Doshier, 2010; Reynolds, Pasternak & Desimone, 2000; Motter, 1993). Thus, incorporating top-down cues does not necessarily require sacrificing the computational precision of the original saliency map models, or even altering the basic structure of the approach (e.g., Naavalpakkam & Itti, 2005).

Neurophysiological studies also supported the feasibility of incorporating top down cues into saliency maps. These studies found patterns of activity linked to voluntary attention or to saccadic planning in cortical areas such as LIP or FEF (Bisley & Goldberg, 2003; Thompson, Bichot & Sato, 2005; Quian Quiroga, Snyder, Batista, Cui & Andersen, 2006; Snyder, Batista & Andersen, 2000). Many argued that top-down influences on attention, and on saccades as well, were so important that the term saliency map, which originated from analysis of physical characteristics, should be replaced by a different label, for example, ‘priority map’, to emphasize that the map includes information about the locations of useful and task-relevant information (Gottlieb & Balan, 2010; Gottlieb, Balan, Oristaglio & Schneider, 2009; Serences & Yantis, 2006; Fecteau & Munoz, 2006).

A key question for understanding the planning of saccadic eye movements has been whether the notion of a saliency map, with or without top down signals, allows us to understand the spatial patterns of saccades during the inspection of visual scenes. Predicting patterns of saccades requires significant additions to the original saliency map models in order to specify how a map of the visual field can be converted into a succession of saccadic goals. Two assumptions have been crucial. First, to choose each saccadic goal, gaze is assumed to be attracted to one region, for example, the region with the momentarily highest strength (“winner take all”). Second, to prevent the line of sight from constantly revisiting the same locations, salient locations are assumed to lose strength for some period of time after being fixated (“inhibition of return”) (Itti & Koch, 2001). These assumptions may be important for predicting patterns of saccades, but are not needed for predicting perceptual recognition because attention can be distributed across a scene to multiple locations during saccade-free episodes of fixation (Bahcall & Kowler, 1999; Palmer, Verghese & Pavel, 2000).

In apparent support of the suitability of these two assumptions (winner-take-all and inhibition of return), studies have shown that spatial patterns of eye movements during inspection of scenes agreed, in general, with computed salience levels (Fig. 5). Gaze positions tended to cluster at locations with high levels of physical salience (high feature contrast) (Parkhurst, Law & Neibur, 2002; DeCarlo & Santella, 2002). Predictions of gaze locations improved when the effect of retinal eccentricity on contrast sensitivity and spatial resolution was added to the model (Peters, Iyer, Itti & Koch, 2005). Saliency has also been able to predict aspects of scan patterns with dynamic images (movies) (Tseng, Carmi, Cameron, Munoz & Itti, 2009; Le Meur, Le Callet & Barba, 2007).

Despite the apparent success of these attempts, significant questions remain about how best to deal with top-down contributions. Many studies challenged the idea that a map that begins by specifying physical salience is the best way to provide a meaningful account of saccadic scanning patterns. Studies demonstrated that factors other than physical salience were far more important for determining patterns of eye movements made to inspect scenes. Some of these factors were observed during studies of simple scene inspection, and others in studies that imposed a task or goal (search, for example) to motivate scanning. Examples of factors that influenced eye movements (either adding to or overriding effects of computed physical salience) include: the overall layout of the scene and visual contextual cues about the likely location of key objects (Torralba, Oliva, Castelhana & Henderson, 2006; Neider & Zelinsky, 2005; Eckstein, Drescher & Shimozaki, 2006; Intraub, Hoffman, Wetherhold, Stoebs, 2006); decisions to focus attention on particular features (Pomplun, 2006); representations of objects (rather than just their component features) (Einhäuser, Spain & Perona, 2008; Baddeley & Tatler, 2006); goals and purposes of the task being performed (Turano et al., 2003; Pelz & Canosa, 2001; Einhäuser, Rutishauser & Koch, 2008; Foulsham & Underwood, 2007; Malcolm & Henderson, 2010; Rothkopf, Hayhoe, 2007); and the probability of obtaining a reward for successful task performance (Navalpakkam, Koch & Perona, 2009).

The question raised by this diverse set of perceptual and task-driven influences on eye movements is whether it is more productive in the long run to continue the attempt to predict scanning patterns on the basis of a computed saliency map, with various perceptual and top-down factors incorporated, or whether such a map, complex as it eventually would be, is the most useful way to capture saccadic strategies, or the neural control processes that underlie the saccadic decisions. Answering this question will require a comparison of saliency (or priority) maps with alternative approaches. One alternative approach is described below.

3.2. Visibility models

Predicting eye movement patterns on the basis of a salience map, with or without top down factors included, is based on the view that the main motivation behind saccades is to take the line of sight to a region that already stands out from the neighboring surround. Alternatively, *visibility models* do not make this assumption. These models begin by acknowledging that the purpose of saccades is not to take the line of sight to what can already be seen, but rather to improve the visibility and clarity of eccentric details that cannot be resolved adequately from the current fixation position. These approaches, in contrast to saliency maps, are not interested in what might attract the line of sight, but rather begin by asking what saccades contribute to task performance.

Najemnik & Geisler (2005) provide a convincing example of what these alternative approaches, based on visibility, can reveal about saccades. They studied saccadic patterns during visual search for a small grating patch hidden in visual noise. They found that search patterns, including the number of saccades required to find the target, as well as aspects of the spatial distribution of landing locations, could be predicted by an ideal searcher model in which each saccade was directed to the location that would yield the highest probability of finding the target. The ideal searcher was limited by visual capacities that were set to match those of the human, in particular, the drop-off in contrast sensitivity with eccentricity. Thus, the strategy can be seen as one of sending the line of sight to locations that maximized search performance (proportion correct) by considering, before each saccade, the effect of the eye's next landing position on the visibility of all locations throughout the visual field. Najemnik & Geisler (2009) showed that the same performance could be achieved by a related, but simpler, computational strategy than the one implemented in their original model, thus potentially capturing the strategy used by human searchers in a biologically plausible framework.

A similar approach is found in Legge, Klitz & Tjan's (1997) ideal observer model of reading, in which the landing positions of each successive saccade were chosen so as to maximize the probability of recognizing each successive word in a line of text. This model was able to predict the spatial distributions of saccadic landing positions during reading (Legge, Hooven, Klitz, Stephen Mansfield & Tjan, 2002; for related discussions of landing positions of saccades during reading, see Epelboim, Booth, Ashkenazy, Taleghani, Steinman 1997; Engbert, Longtin, & Kliegl, 2002; Schnitzer & Kowler, 2006). Renninger, Verghese & Coughlan (2007) analyzed eye movements during a shape recognition task and found that choices of where to look could be predicted by the fall off in orientation acuity with eccentricity, combined with a local strategy of looking at the most informative portions of the shape. Motter & Belky (1998a,b) and Motter & Simoni (2007) predicted eye movement patterns during a search through densely packed arrays on the basis of the reduction in spatial resolution with eccentricity, and the visual effects of crowding.

Other approaches were quite different, but kept to the theme that improving visibility was of primary importance in selecting where to look. Tatler (2007) attributed tendencies to keep gaze near the center of a scene to the adoption of an 'optimal viewing position' from which large portions of the scene could be identified from a single locus (see also O'Regan, 1990, for development and application of this concept to eye movements during reading). Steinman, Pizlo, Forofonova & Epelboim (2003) studied gaze shifts during a pointing task in which the visibility of the targets was directly manipulated by having subjects wear contact lenses that degraded acuity. They found that the variability of the landing positions of saccades depended on visual acuity. However, rather than poor acuity (blurred targets) resulting in poorer saccadic performance, the results showed the opposite pattern. Conditions with high acuity resulted in the largest gaze errors, while experimental manipulations that reduced acuity resulted in the line of sight landing close to the target. Steinman et al. (2003) argued that these patterns represented an optimal strategy of looking only as close to targets as needed to support the task. This conclusion incorporates that assumption that "work" or effort is needed to look accurately at a target. This effort could be the allocation of resources (e.g., attention) to the chosen saccadic goal (see 3.3).

The models of saccadic scanning strategies described in sections 3.1 and 3.2 begin from fundamentally different assumptions about the motivation behind saccadic planning. Saliency-based approaches (3.1) hold that we look at places because they stand out from the background, while visibility approaches (3.2) begin by assuming we look at places that will lead to successful task performance. By beginning with the assumption that saccades are made so as to best accomplish the task goals, visibility approaches avoid having to devise ways of incorporating top-down factors into models of saccadic performance. Top down factors are already incorporated, given the assumption that saccadic planning seeks to maximize task performance. This is not to say that identifying the various top-down factors contributing to task performance will be an easy matter. For complex tasks, it surely will not. However, visibility models provide the structure within which their contribution can be understood.

Neither of these two approaches to understanding patterns of saccades made an explicit distinction between saccadic eye movements and perceptual attention. The link between attention and saccades is discussed below.

3.3. Saccades and attention

Attention is important for the control of saccades, just as it was for smooth pursuit (Section 2.2.2). When visual arrays contain many possible targets, saccades, if they are to be accurate, require a selective filter to define or designate the target and attenuate signals from everything else.

3.3.1. Dual-task studies of saccades and perceptual attention—The connection between saccades and perceptual attention has been explored in experiments that used dual-task psychophysical methods, in which perceptual judgments are made during the latency interval of saccades. Finding that judgments are more accurate for perceptual targets located near the saccadic goal than for targets located elsewhere would support the existence of a common selective filter controlling both perceptual attention and saccades.

Kowler, Andersen, Doshier & Blaser (1995) found evidence for a common filter in dual task studies of perceptual judgments and saccades. Their results in the form of Attentional Operating Characteristics (AOC's; see Sperling & Doshier, 1986) are shown in Fig. 7a. The AOC's show that as more emphasis was placed on the perceptual task, saccadic latencies increased. Saccadic and perceptual performance (when the targets for each were in different locations) never reached the 'independence point', which defines expected performance if the tasks can be done without mutual interference. Similar results were observed for saccadic landing positions, which became less precise the more attention was devoted to the perceptual target. The tradeoff between the saccadic and perceptual tasks, with performance falling short of the independence point, is a signature pattern that characterizes processes that share resources.

But attention does not have to be glued to the saccadic goal. Perceptual performance at locations other than the saccadic goal can be improved with by only modest increases in latency (about 20%) (Fig. 7a and also Gersch et al., 2008; Wilder et al., 2009). Thus, achieving a pattern of accurate and timely saccades may not require all that much attenuation of signals at non-goal locations. This also means that some perceptual tasks (those with modest demands on attention) will not show strong tradeoffs with saccades. Similar considerations applied to the effects of attention on smooth pursuit (Section 2.2.2).

Using various dual-task experimental paradigms, a number of studies have found superior performance at the goal of the saccade relative to other locations (Hoffman & Subramaniam, 1995; Deubel & Schneider, 1996; Deubel, 2008; Van der Stigchel & Theeuwes, 2005; McPeck, Maljkovic & Nakayama, 1999; Godijn & Theeuwes, 2003; Baldauf & Deubel, 2008; Gersch, Kowler & Doshier, 2004; Gersch, Kowler, Schnitzer & Doshier, 2008, 2009), including tasks where the saccadic goals were not dictated by the experimenters, and saccades were motivated by a "real" task (counting) (Wilder et al., 2009). Comparable attentional effects are found before arm movements (Baldauf & Deubel, 2006), however, in some cases multiple goals of arm movements can be attended without cost (Jonikaitis & Deubel, 2010). Montagnini & Castet (2007) recently found that perceptual performance at non-saccadic goal locations could be improved without cost to saccades under conditions that may have facilitated sharing of resources between the locations: the perceptual target (a tilted grating among vertically-oriented gratings) was located opposite to the saccadic target on the majority of the trials, and the presentation of the perceptual target coincided with the cue disclosing the location of the saccadic goal.

3.3.2. Attention and saccadic sequences—The links between attention and saccades have a different character when perceptual cues mark the saccadic path during the performance of a sequence of saccades Gersch et al. (2008, 2009) found that when a color cue marks the path, attention could be distributed along the cued path, even at locations previously fixated, without interfering with the performance of the saccadic sequence (for example, Fig. 7b). (These effects were superimposed on a "top-down" mediated shift of attention to the goal of the next saccade.) The distribution of attention along the color-cued path implies that multiple mechanisms of attention are at work during saccadic sequences, with "feature-based" attention (Melcher, Papatthomas & Vidnyanszky, 2005; Sàenz, Bura as & Boynton, 2003) operating independently of the planning of saccades. Feature-based

attention can facilitate perceptual analyses across the display without disrupting ongoing saccadic performance.

Finding that features can draw attention independently of saccades during the performance of saccadic sequences brings us back to the question of whether saccades are drawn to perceptually salient regions (3.1). Perceptual salience can provide visual cues that allow potential saccadic targets to stand out, but salience plays no direct role in saccadic programming. The generation of the saccades requires an additional level of processing: a top-down decision, or an intention (Snyder, Batista & Andersen, 2000). These top-down saccadic decisions can then have perceptual consequences, as shown by the various dual task studies described above, due to (for example) connections between areas responsible for saccadic planning and visual areas such as V4 (e.g., Moore & Armstrong, 2003).

3.3.3. Attention and “center-of-gravity” saccades—Attention defines the effective saccadic target and attenuates signals from non-targets. An example of the importance of attention in defining the saccadic target comes from the so-called “center of gravity” saccades, which have been the subject of investigations going back to Coren & Hoenig (1972) and Findlay (1982). Center-of-gravity saccades occur when targets are surrounded by non-targets, and the saccades, instead of landing at the designated target, land in the midst of the whole configuration. Center-of-gravity saccades were originally seen as unavoidable errors, a sign of the operation of a special reflexive “averaging” subsystem (why else would otherwise cooperative subjects fail to look at the target?), but more recent work has shifted the responsibility for averaging to the operation of a selective filter that was not given either the time, or the visual cues, to find the target before the saccade was launched. This shift in view was prompted by findings that saccades became more accurate (less influence of the surrounding non-targets) when more time was allowed for target selection to occur (Ottes, Van Gisbergen & Eggermont, 1985; Cöeffé & O’Regan, 1987; Cohen, Schnitzer, Gersch, Singh & Kowler, 2007), or when cues or instructions were given to signal where the saccade should land (He & Kowler, 1989, 1991; Findlay & Blythe, 2009). These considerations show that center-of-gravity saccades are no different from any saccade: they direct the line of sight to the attended region.

Once the selected target region is defined, saccadic landing positions can be determined by the spatial pooling of signals (Kowler & Blaser, 1995; McGowan et al., 1998). Spatial pooling may underlie the ability to aim the line of sight to spatially-extended objects or shapes without having to invest effort in selecting a particular endpoint (Melcher & Kowler, 1999; Vishwanath & Kowler, 2003; Guez, Marchal, Le Gargasson, Grall & O’Regan, 1994). Saccades, on average, land near the center of target shapes, but landing positions other than the center can be adopted depending on visual characteristics of the target, the distribution of attention, or the goals of the tasks (He & Kowler, 1991; Vishwanath & Kowler, 2003; 2004; Brouwer, Franz & Gegenfurtner, 2009; Johansson et al., 2001; Findlay & Brown, 2006; Cohen et al., 2007).

3.3.4. Saccades and perceptual attention: summary—There is a productive and mutually beneficial relationship between saccades and perceptual attention. Perceptual attention can be distributed across a scene or display without evoking any saccades, contributing to the selection of useful places to look. The saccadic decision itself is accompanied by a shift of attention to the selected goal, and such shifts of attention have measurable perceptual consequences. Pre-saccadic attention, however, can be distributed over a spatially-extended region and need not pinpoint a precise landing location (the landing location can be determined via spatial averaging.) The pre-saccadic shifts of attention, and their perceptual effects, are difficult if not impossible to avoid: it is not possible to decide to look at one target while simultaneously and successfully shifting

complete perceptual attention to another. Nevertheless, either a relatively small delay in the launching of the saccade, or the presence of feature cues, can significantly expand the reach of attention prior to saccades. The perceptual effects of pre-saccadic shifts of attention during active scanning tasks may result from connections between neural regions connected to saccadic planning (frontal eye field, for example) and neurons in the visual system.

3.4. Saccadic reaction times

Hanes & Schall (1996) asked a very fundamental question about neural basis of saccadic planning: What accounts for the variability of saccadic reaction time? Is it a change in the rate at which activity levels increase, or, alternatively, in the threshold activity level needed to launch the saccade? To distinguish these two possibilities, Hanes & Schall (1996) studied the activity of FEF neurons during the interval preceding a saccade made to a peripheral target. They found that the time taken for activity levels to reach threshold was correlated with reaction time: the faster the rate of rise of activity, the shorter the saccadic reaction time. This influential paper was followed by many that applied stochastic models to the study of the neural basis of saccadic decisions (see, for example, Schall, 2004; Gold & Shadlen, 2007; Sugrue, Corrado & Newsome, 2004).

At about the same time Carpenter and Williams (1995) were asking similar questions about saccadic reaction times observed in behavioral experiments. They developed a model to account for saccadic performance in various choice reaction time situations in which a saccade is made to one of two available targets. In their model, termed “LATER” (Linear approach to threshold with ergodic rate), a decision signal was assumed to grow from a given starting level to a threshold level at a variable rate. The model predicted that changes in the rate of growth of the signal, and changes in the threshold level, would have different effects on the shape of the reaction time distribution. Analyses of distributions of saccadic reaction times in various experiments supported the predictions. Reddi, Assress & Carpenter (2003), for example, showed that changes in the discriminability of the sensory signals led to changes in the distribution of saccadic latencies that were consistent with modulations in the rate of growth of the decision signal, whereas changes in speed/accuracy criteria produced modulations in saccadic latency consistent with the expected changes in the threshold. The LATER model has been applied to different types of saccadic tasks in order to capture processing events leading up to the generation of saccades (see, for example, Oswal, Ogden & Carpenter, 2007; Sharika, Ramakrishnan & Murthy, 2008; Harwood, Madelain, Wallman & Krauzlis, 2008. See Beintema, van Loon & van den Berg, 2005; Palmer, Huk & Shadlen, 2005; and Ludwig, 2009; for discussions of alternatives). Saccadic reaction time can also be affected by the brief flash of distractors far from the location of the saccadic target (the “remote distractor effect”, e.g., Walker, Deubel, Schneider & Findlay, 1997; Bompas & Sumner, 2009).

3.5. Concurrent preparation of pairs of saccades

McPeck, Skavenski & Nakayama (2000) found some unusual saccadic behavior in an unusual situation. They asked their observers to saccade to an ‘oddball’ target, for example, a red circle presented along with two green ones. The color of the oddball changed randomly between red and green across trials, and as a result, biases (expectancies) about the color of the target in upcoming trials developed as a function of prior trial sequences. Although often observed for location cues (Falmagne et al., 1975; Kowler et al., 1984), sequential dependencies can occur for color cues, as well in the context of visual search (Maljkovic & Nakayama, 1994). McPeck et al. (2000) found that following a sequence of trials in which the color of the target remained the same, a trial in which the target was the opposite color led to a saccade that went to the incorrect color followed quickly, with vanishingly small reaction time, by a corrective saccade (see Fig. 8).

Pairs of saccades separated by short latencies had been observed previously in various tasks, including visual search (Viviani & Swenson, 1982) and “double-step” tracking, where a target jumps to a pair of locations in rapid sequence (Becker & Jurgens, 1979). Becker & Jurgens (1979) and McPeck et al. (2000) proposed that under certain circumstances pairs of saccades could be prepared in parallel (or, concurrently), with plans for the first saccade running slightly ahead in time of the second (also, Theeuwes, Kramer, Han, Irwin & Zelinsky, 1999). In support of concurrent programming, McPeck & Keller (2002) showed that some visuo-movement neurons in superior colliculus would fire if the goal of the second saccade fell in the neuron’s receptive field even before the execution of the first saccade. Concurrent planning, accompanied by a signal that keeps track of eye position across the saccadic pair (Sommer & Wurtz, 2002) may also be a means of implementing rapid saccadic corrections during performance of saccadic sequences (Wu et al., 2009; Ramakrishnan et al., 2010).

These brief intersaccadic pauses between concurrently planned saccades are not the same as ‘express saccades’, which refer to short-latency saccades that occur when the fixation target is removed prior to appearance of the saccadic goal (Fischer & Ramsperger, 1984, 1986), or following extensive practice and learning (Sparks, Rohrer & Zhang, 2000). Express saccades have been the basis of much discussion during the past 25 years. Some have attributed express saccades to a separate neural system (Schiller, Sandell & Maunsell, 1987), while others, observing that the short-latencies occur on only a portion of trials, have attributed express saccades to strategies of pre-programming based on guesses about upcoming target locations (Kowler, 1990; Paré & Munoz, 1996; Carpenter, 2001; for a related approach see Edelman, Kristjánsson and Nakayama, 2007).

Some studies have recently challenged the idea that concurrent programming of a sequence of two saccades can be accounted for solely by setting up a race between two visual targets for the control of the eye. These studies did not question the basic idea of concurrent planning, but instead provided evidence for the existence of a separate “countermanding stage” or “stop signal” which, if activated soon enough, could either cancel, truncate or modify the initial saccade and facilitate execution of the second saccade (e.g., Asrress & Carpenter, 2001; Camalier, Gotler, Murthy, Thompson, Logan, Palmeri & Schall, 2007; Colonius, Özyurt & Arndt, 2001).

Examples from a variety of tasks suggest that concurrent planning is a useful option during search or scanning. In a study of visual search using brief (half second) presentations and only two possible target locations, Araujo, Kowler & Pavel (2001) found that a vivid cue signaling the likely location of the target was typically not used when planning the saccade, even though taking the cue into account would almost always have led to near perfect performance (identifying the orientation of the target) at apparently little cost (only an additional 50 ms in saccadic latency). This shows a reluctance to delay a given saccade until the best landing location can be determined. The cue, though, was not totally ignored. The hastily planned initial saccades were followed – often with latencies < 100 ms – by second saccades to the more probable location. Although this was a futile strategy (since the stimuli had been removed before the second saccade arrived), it shows that the planning of the optimal saccade (the one that took advantage of the cue) started before the initial (but useless) saccade. The ability to plan a pair of saccades concurrently, and carry out the sequence quickly, facilitates such heedless strategies because the processes needed to initiate the second saccade need not await completion of the first. Thus, for saccades, the cost in time of mistakes is small.

Further evidence in support of concurrent planning comes from the results of a search task studied by Caspi, Buetter & Eckstein (2004). They had subjects search for a bright Gaussian

blob presented along with dimmer distractor blobs in a display where blob intensity continually varied over time. Using a reverse correlation method they found that the plans for the second saccade in the trial were based on visual information collected during the interval preceding the first saccade.

There is also evidence for concurrent planning of pairs of saccades during free scanning of scenes. Philips & Segraves (2010) studied cells in frontal eye field of monkeys scanning photographs. The typical response was for the cell to fire when the target of the next saccade fell in its response field. However, they also found many cells that fired two targets ahead. The “two target ahead” activity, when observed, was typically found during the latter portion of intersaccadic pauses, implying that the planning of a saccade does not always need to wait for the prior saccade to land at a target.

Concurrent, or parallel, planning of saccades facilitates scanning strategies that favor speed over accuracy. Planning rapid sequences of saccades, and then quickly correcting as needed, may be a more efficient use of time and resources than trying to plan each saccade as carefully and accurately as possible (Cöeffé & O’Regan, 1987; Araujo et al., 2001; Hooge & Erkelens, 1996, 1998, 1999; Wu et al., 2010; Kowler & Pavel, 2007).

3.6. Perceiving a clear and stable world across saccades

Saccadic displacements of the retina, in foveate animals like ourselves, are indispensable for vision, but they also exact a significant cost: The perceptual system must have a way to cope with the continual changes in the position of the retinal image produced by saccades. Our own experience tells us that this effort is a great success. Perceptual experience is seamless despite saccades, and the world appears clear and stable. The chaos on the retina does not reach awareness, nor does it seem to impair our ability to perceive the objects around us, or to keep track of their locations, or to remember the contents of a scene as we look around.

The question of how perceptual mechanisms cope with saccades is so old, difficult, multi-faceted and central to the operations of the visual system that it has broken down into a variety of separate issues, each with its own literatures and sets of controversies. Only a small part of the theories, results and debates over the past 25 years can be reviewed below. For other recent reviews, each with a different emphasis, see Skavenski (1990), Ross, Morrone & Burr (2001), Berman & Colby (2009), Melcher & Colby (2008), Bridgeman (2007), Pola (2004, 2007) and Wurtz (2008).

3.6.1. Perceptual and motor localization around the time of saccades—Classical treatments of perceptual localization credit the ability to perceive the world as stable in the face of the continual retinal displacements produced by saccades to the operation of a ‘corollary discharge’ signal that records the size and direction of intended, planned, saccades. This signal allows the projected retinal displacements due to saccades to be effectively discounted, and attributed to eye rotations rather than to the motion of the environment. Corollary discharge signals, along with visual masking, also inhibit perception during saccades (“saccadic suppression”), contributing to the ability to perceptually connect pre-saccadic and post-saccadic views of the environment (e.g., Burr & Morrone, 1994; Diamond, Ross & Morrone, 2000; Campbell & Wurtz, 1978; Bremer, Kubischik, Hoffman & Krekelberg, 2009). This review will focus on perceptual localization around the time of saccades. There have also been related lines of work on the perception of location and motion during smooth pursuit eye movements (for example, Brenner, Smeets & Van den Berg, 2001; Kerzel, Pilar, Ziegler & Brenner, 2006; Turano & Massof, 2001; Freeman, Champion & Warren, 2010; Bedell, Tong & Aydin, 2010) and on the perception of location and depth during vergence eye movements (e.g., Erkelens & Van Ee, 1998; Zhang, Cantor & Schor, 2010).

If corollary discharge signals were accurate, precise and timely, errors in localization would be no larger than during episodes of saccade-free fixation. When experiments were done to measure localization by means of motor responses – pointing at targets, for example – with nothing visible except the single target to be localized, errors were equivalent to those during steady fixation (Hansen & Skavenski, 1977; Burr, Morrone & Ross, 2001). These results demonstrate that an accurate and timely corollary discharge signal can be accessed by motor programming systems (see also Sommer & Wurtz, 2002). Neurons in parietal cortex, whose activity is modulated on the basis of eye position (Andersen, Essick & Siegel, 1985), or that encode signals in a head-centered map (e.g., Duhamel, Bremmer, BenHamed & Graf, 1997), may contribute to the accurate guidance of the arm when the target location in the retina is displaced due to saccades (Andersen, Snyder, Bradley & Xing, 1997).

These results hold for motor localization. Perceptual localization is another matter. Psychophysical measurements of where targets appear to be require the use of a perceptual reference signal to act as a point of comparison. If the reference is present along with the flashed target, the task becomes one of relative perceptual localization, and for relative localization, corollary discharge signals might not be necessary or relevant. Thus, localization around or during saccades should be equivalent to localization during fixation. On the other hand, if the reference is presented before or after the flashed target, simultaneous relative location cues are avoided, but visual memory becomes a factor. The more time that goes by between the presentation of the flash and the collection of the perceptual report, the more important visual memory becomes. Either way, if the objective is to assess the role of corollary discharge in perceptual localization, the road is not an easy one. It is necessary to contend with the effects of visual references, or the quality and nature of visual memory as it decays or transforms over time, or both.

Studies by Matin and colleagues going back to the 1960's measured the perceived location of targets flashed around the time of saccades relative to visual references present before saccades. These studies revealed large errors in perceptual localization for targets flashed beginning about 200 ms before saccadic onset and continuing 200 ms after saccadic offset (e.g., Matin & Pearce, 1965). The perceptual errors were consistent with use of a corollary discharge signal that was slow to reach the perceptual system. Matin (1974) argued that the impression of a stable perceptual world across saccades did not require corollary discharge, but instead was the result of the visual system relying on signals encoding relative location, which should not change during saccades, combined with the effects of visual masking (saccadic suppression) to remove the smeared image during saccades. In more recent work, consistent with this theme of visual processes dominating non-visual (extraretinal) signals, Matin & Li (1994) have shown that the geometric properties of the visual background can influence the perceived position of the eye in the orbit (see also Li & Matin, 2005a,b).

But relative perceptual localization is not immune to effects of saccades (Cai, Pouget, Schlag-Rey & Schlag, 1997; Ross, Morrone & Burr, 1997). Ross et al. (1997), for example, measured the perceived position of a briefly-flashed target (a vertical line presented during large horizontal saccades) with respect to a visual reference (a horizontal “ruler”) presented after the saccade. They found that targets flashed briefly, sometime during the interval between about 50 ms before the saccade until 50 ms after the saccade, were seen as displaced toward the saccadic target. The displacements affected targets located on either side of the saccadic goal, thus the phenomenon was termed ‘visual compression’. The perceptual displacements that characterized compression were large: 10 deg in size, for 20 deg saccades. Later, Lappe, Awater & Krekelberg (2000) showed that visual compression required the presence of the visual reference (the “ruler”) after the saccade. When the reference was removed, and targets were flashed in darkness, with their locations indicated by means of a movable cursor, compression was reduced and targets were seen as displaced

in the direction of the saccade, similar to the pattern originally found by Matin and colleagues (summarized above).

Related patterns of mislocalization were reported by Deubel, Schneider & Bridgeman (1996) and Deubel, Bridgeman & Schneider (1998), who studied the perceived displacement of targets that jumped before or after saccades. Intra-saccadic jumps are typically difficult to detect, however, Deubel et al. (1996, 1998) showed that blanking the target during the jump made it possible to detect the jump and identify its direction accurately (see also Dassonville, Schlag & Schlag-Rey, 1995). Deubel et al. (1998) proposed that under typical circumstances, where details are not blanked during saccades, perceptual stability relies on the implicit assumption made by the visual system that a selected visual reference – typically, the saccadic target – remains stationary during the saccade (see also Lennie & Sidwell, 1978; Matin; Maij, Brenner, Li, Cornelissen & Smeets, 2010; Honda, 1999, 2005, 2006). Other visual details (such as targets flashed during or around the time of saccades) may be seen in illusory locations because their positions are encoded relative to the selected “stationary” reference.

Studies of target localization (perceptual or motor) during saccades were originally (1960’s and 1970’s) viewed as routes to evaluating the accuracy and time course of the corollary discharge signal. The accuracy or time course of the corollary discharge signal is no longer the only issue because once relative perceptual localization is shown to be affected by saccades, visual transformations must also be involved (for example, Kregelberg, Kubischik, Hoffman & Bremmer, 2003; see Brenner, Meijer & Cornelissen, 2005, and Pola, 2004, for alternative views). These visual transformations occur when the system is busy with operations we are never meant to notice, operations that presumably underlie the ability to weave together pre- and post-saccadic views of the environment into a seamless and stable representation of the visual world. One of these operations is neural remapping.

3.6.2. Remapping and the neural origin of corollary discharge signals—Neural remapping is a remarkable phenomenon. Remapping, and its broader implications for vision, has been reviewed recently by Berman & Colby (2009) and Wurtz (2008).

Remapping was discovered by Duhamel, Colby & Goldberg (1992), who found that neurons in area LIP can shift the location of their receptive fields prior to saccades by an amount and in a direction that depends on the plans for an upcoming saccade. As a result, neurons begin to respond to targets at the predicted future post-saccadic retinal location. Nakamura & Colby (2002) found that neurons in visual area V3a show predictive remapping (but not neurons in V1). Remapping across the hemifields survives transection of the cerebral commissures (although there are initial deficits) showing that multiple circuits, including subcortical networks, are involved (see Berman & Colby, 2009, for discussion). Remapping does not occur uniformly or automatically across the visual field, but is limited to selected, attended, targets (Gottlieb, Kusunoki & Goldberg, 1998). (The pre-saccadic shifts of attention to the saccadic target, which have been connected to the control of saccades, section 3.3, may play a role in signaling the locations to be remapped.) Sommer & Wurtz (2006) recently found that the corollary discharge signals encoding the saccadic commands responsible for remapping of neurons in frontal eye field originate from the superior colliculus and travel to cortical areas through the thalamus. When these pathways were inactivated, remapping was significantly and substantially reduced.

Perceptual indicators of neural remapping are beginning to be investigated (Melcher & Colby, 2008). For example, the temporal and spatial pattern of the receptive field shifts during remapping might contribute to the visual compressions and other mislocalizations found during saccades (see 3.6.1). To explore other possible perceptual consequences of

remapping, Melcher (2007, 2009) studied the transsaccadic transfer of perceptual aftereffects. He showed that tilt aftereffects have characteristics that may be accounted for by remapping. Specifically, just before the saccade the strength of the aftereffect declined at fixation (even though the test and the adapting patterns were at the same retinal location) and increased at the saccadic goal. The saccadic goal occupied a different spatial location from the adapting stimulus, one that corresponded to the future receptive field of the remapped visual neurons that were presumably stimulated by the adapting pattern. Remapping has also been studied by a variety of psychophysical paradigms that have been shown to be sensitive to information preserved across saccades (e.g., De Pisapia, Kaunitz & Melcher, 2010; Melcher & Morrone, 2003).

Remapping is often discussed in the context of processes that contribute to maintaining the percept of a stable world across saccade because it allows visual neurons to prepare for the stimuli that will fall in their future (post-saccadic) receptive fields. This means that the critical transitions between pre-saccadic and post-saccadic receptive fields can be accomplished just before and during the saccade, when saccadic suppression hides the mess and chaos. In this sense remapping is another example of a predictive oculomotor process (see also section 2.4). The predictions generated by remapping can contribute to the seamless transition between pre- and post-saccadic views of the world and allow the acquisition of visual information from the new, selected post-saccadic object to begin with minimal delay, as soon as the saccade lands.

3.7. Saccadic adaptation

Another example of a trans-saccadic phenomenon is saccadic adaptation. Saccadic adaptation is fundamental to maintaining saccadic accuracy because it allows saccades to learn from their mistakes. The phenomenon of saccadic adaptation was first studied in detail by McLaughlin (1967). He found that if a target is displaced to a new location during the saccade, the saccade will (as expected) miss the target. But after only a few trials, saccadic accuracy begins to improve to its original levels. After a period of adaptation, saccadic errors will persist for a short time in the absence of the intra-saccadic displacements. The presence of such an aftereffect is a sign that genuine sensory or motor changes had occurred. Adaptation is fundamental to maintaining saccadic accuracy (e.g., Erkelens & Hulleman, 1993; Wallman & Fuchs, 1998; Chaturvedi & Van Gisbergen, 1997) and is one of many adaptive phenomena that characterize various aspects of oculomotor control (see Berthoz & Melvill-Jones, 1985, for reviews).

Recent studies by Chen-Harris, Joiner, Ethier, Zee & Shadmehr (2008) and Ethier, Zee & Shadmehr (2008) produced important insights into the nature of the control processes that underlie saccadic adaptation. These studies compared two possible sources of adaptation: a change in the mapping between the encoded target location and the saccadic response, and a change in an internal forward model that monitors efferent signals and adjusts parameters so as to steer the saccade to the target while the saccade still in progress. Analysis of the velocity, acceleration and duration of the adapted saccades showed that both processes were engaged. In one case, however, when adaptation induced increases in saccadic amplitude (as opposed to either decreases in amplitude or changes in direction), only the change in sensory-motor mapping, not the adjustment of forward models, was involved.

What is the nature of the visual error signal that drives saccadic adaptation? It is typically assumed that the error signal is the offset of the saccadic landing position relative to the target, but studies have suggested that this is not the case. Bahcall & Kowler (2000) found that adaptation is unaffected by experimental manipulations that alter the offset error signals. For example, adaptation is unaffected by instructions to look only 75% of the way to the target, or by the use of a large circle as a saccadic target instead of the typical small point.

The one condition that did prevent adaptation, inserting a temporal delay of 400 ms before the post-saccadic target appeared, did not change the offset error, but did prevent adaptation. Based on this evidence, Bahcall & Kowler (2000) concluded that adaptation was not prompted by offset error per se, but was the result of a visual comparison process, specifically, a comparison between the position of targets on the retina after the saccade lands to the position that would be predicted on the basis of the corollary discharge signal accompanying the planned saccade. A discrepancy between actual and predicted landing locations would generate a signal akin to visual motion and could then trigger the adaptive processes. Deubel (1991) made a similar proposal based on findings of adaptation with large textured patterns. The receptive field changes accompanying neural remapping (see 3.6.2.) provides a neural basis for this visual comparison model to work.

3.7.1. Saccadic adaptation and perceptual localization—Saccadic adaptation is also accompanied by illusory visual mislocalizations. Bahcall & Kowler (1999) found that after a period of saccadic adaptation, the location of the pre-saccadic target appeared displaced by an amount that corresponded in magnitude and direction to the adaptive shift in saccade size. Awater, Burr, Lappe, Morrone & Goldberg (2005) found consistent results in that the focus of perceptual compression (3.6.1) after adaptation corresponded to the endpoint of the adapted saccade. Zimmerman & Lappe (2010), like Moidell & Bedell (1988), but different from Awater et al. (2005), found mislocalizations following a period of saccadic adaptation even during steady fixation. All of these experiments were done under different conditions, differing with respect to the presence of any visual references, the size of the saccades, the required adaptive shift, the time of any test or probe stimuli with respect to the saccade, and the time that elapsed between the flash of the target and the perceptual report. All (not surprisingly) drew different conclusions about the mechanisms responsible, some visual, some involving memory, and some involving corollary discharge signals generated at a level prior to the site of adaptation of the saccades.

Zimmerman & Lappe (2010) proposed perhaps the most radical view, namely, that saccadic adaptation induces changes to the visual representation of space. The suggestion that there are genuine visual changes following saccadic adaptation has some intriguing aspects. A fundamental idea behind attempts to understand saccadic adaptation is that saccadic adaptation is a response to errors, e.g., discrepancies between the predicted and actual post-saccadic visual locations. In natural scenes, any such errors, regardless of their source, will normally escape awareness because they occur during the intervals when saccadic suppression is in force. The errors do not escape detection by the saccadic system. The saccadic system needs these signals, which we cannot perceive, to keep itself in tune, making the necessary adjustments (at various neural levels; see Chen-Harris et al., 2008; Ethier et al., 2008) until things are once again aligned. But, if the visual maps change as well, this raises the question of how the saccadic system retrieves its error signals. Perhaps there multiple maps, some that change with adaptation, and some that do not.

3.8. Saccadic patterns in active tasks

One of the most important innovations over the past 25 years has been the development of novel means of studying eye movements during active tasks in which observers not only look around, but move around, for example: walking corridors, either real (Turano, Geruschat & Baker, 2002) or virtual (Rothkopf, Ballard & Hayhoe, 2007), driving (real roads, not simulators! Land & Lee, 1994; Kandil, Rotter & Lappe, 2009), working in the kitchen (Land, Mennie & Rutsted, 1999; Land & Hayhoe, 2001), playing cricket (Land & McLeod, 2000), washing hands (Pelz & Canosa, 2001), and assembling toys (Steinman et al., 2006).

Natural situations such as these involve binocular saccadic eye movements. Work over the past 25 years has shown that when shifting gaze between stationary targets under natural conditions, binocular saccades have both conjugate and disjunctive components, which means that changes in vergence are carried out by saccades, and not by slow eye movements (Erkelens, Van der Steen, Steinman & Collewijn, 1989; Erkelens, Steinman & Steinman, 1989; Collewijn, Erkelens & Steinman, 1995; 1997; see also Wismeijer, Erkelens, van Ee, & Wexler, 2010; Chaturvedi & Gisbergen, 1992; and Nuthmann & Kliegl, 2009; for discussion of vergence eye movements in different tasks).

Below a few of the investigations of eye movements during active tasks, and some of their implications, are discussed.

Ballard, Hayhoe & Pelz (1995) devised a novel block copying task in which a set of virtual blocks (2D images on a display) of different colors had to be assembled into a pattern that duplicated that of a model (Fig. 9). The pathways taken by the saccades showed that subjects were reluctant to rely on memory as often as might be supposed, preferring the strategy of looking back toward the model to check the color and the location of each block added to their construction. As the construction proceeded, these look-back saccades began to drop out of the pattern. Ballard et al. (1995) emphasized the wisdom of such a strategy given that memory is limited and there is no corresponding limit on the production of saccades. O'Regan (1992) made a comparable case, arguing that there was no good reason to develop a visual system that could remember lots of details since any detail that was forgotten could be easily retrieved by looking around. One thing that became apparent from this work was that it was not possible to talk about how eye movements enable effective visuomotor performance without taking into account the role of memory.

Eye movements and memory became a popular topic. At about the same time as Ballard et al.'s (1995) work and O'Regan's (1992) article, much attention was being paid to demonstrations of "change blindness". Experiments showed that changes made to prominent details of a scene often went unnoticed (Rensink, 2000; O'Regan, Rensink & Clark, 1999), indicating that only a portion of the available scene is encoded and preserved across saccades (also, O'Regan & Levy-Shoen, 1983; Irwin, Yantis & Jonides, 1983). Subsequent work showed that the ability to notice changes can be better than the original reports indicated, provided that the changes are limited to objects at fixation or at the target of saccades (Henderson & Hollingworth, 2003), or objects or features that are very relevant to the task (Droll, Hayhoe, Triesch & Sullivan, 2005). There was also evidence that memory for objects in a scene could build up over repeated views (Melcher, 2001, 2006; Melcher & Kowler, 2001), including evidence for memory build-up in newer versions of the original block-copying task (Aivar, Hayhoe, Chizk, Mruzek, 2005). Nevertheless, there are still significant attentional bottlenecks that place a limit on what can be noticed or remembered from a scene or display. Even high contrast details at or near the locus of fixation are likely to go unnoticed if they are not the immediate object of attention (Mack & Rock, 1998; Kahneman, Beatty & Pollack, 1967; Wilder et al., 2009; Droll, Gigone & Hayhoe, 2007).

Epelboim & Suppes (2001) studied eye movements, and their relation to memory, while performing a cognitive task (solving a geometry problem). They assumed that immediate memory was limited, and that the contents of viewed locations of the diagram would eventually be overwritten as new locations were examined. Epelbom & Suppes (2001) used a finite state Markov model to estimate the capacity of immediate memory from the frequency of re-fixations, and arrived at an estimate of 4–5 items – not far from the estimates derived from tests of visual memory during steady fixation (e.g., Luck & Vogel, 1997). Applying an approach like Epelboim & Suppes (2001) to different sorts of cognitive tasks could be valuable as part of attempts to use eye movements as a tool to infer

underlying and hidden cognitive strategies, something that it generally difficult to do without an explicit theory of how the eye movements contribute to the task (see Viviani, 1990, for this argument).

Natural tasks also require coordination of eye, head and arm. Epelboim, Steinman, Kowler, Pizlo, Erkelens, Collewijn & Edwards (1995) studied eye, head and arm movements while tapping a series of 5 colored rods located at randomly chosen places (Fig. 10). By the end of 10 repetitions with the same pattern, subjects had learned the positions of the rods and could perform the task very quickly. Learning was less effective when the task was made easier (or so it seemed) by requiring that subjects just look at the rods without tapping. Looking-only was done more slowly, and without the same degree of improvement found over trials for the tapping task. Epelboim et al. (1995, 1997, 1998) also found that the tapping task induced faster saccades (eye-in-head movement), faster shifts of gaze in space (due to reduced compensation for head movements), faster retinal image velocities between gaze shifts (see section 1), and larger gaze errors, than only looking. Snyder et al. (2002) reported related results for monkey. These findings indicated a prominent role for superordinate task constraints on the coordination of movements of eye and head.

Flanagan & Johansson (2003), Rotman, Troje, Johansson & Flanagan (2006), and Johansson, Wrestling, Bäckström & Flanagan (2001) continued the theme of task constraints – particularly visuomotor tasks – on eye movements. These investigators found several novel properties of the eye movements made by people performing simple actions. While performing actions, the line of sight typically arrives at the target before the arm (e.g., Ballard et al., 1995; Epelboim et al., 1995; Johansson et al., 2001; Sailer, Flanagan & Johansson, 2005; Land et al., 1999). This implies that gaze might provide a reference location to assist in guiding the arm. Johansson et al. (2001), who studied grasping movements as well as reaching, took this idea further and suggested that when the line of sight arrives at the target before the arm it allows the visual system to gather accurate information about the target. An important use of the visual information is to predict some of the expected sensori-motor consequences of the arm movements, and to facilitate the programming of rapid corrections in the event the predictions are not met. The eye movement strategy of looking ahead to the target thus provides what they called “spatiotemporal check points” for the “development, maintenance and adaptation of correlations between visual and somatosensory information (proprioceptive and tactile) and efferent copy signals [from the arm and fingers] required for predictions of motor commands in natural manipulatory tasks” (p 6931).

Facilitating the planning of movements of the arm cannot be the only explanation for why the eye leads the arm, however. Flanagan & Johansson (2003) showed that the same eye movement patterns made by people performing the actions are also made by people who are merely observing the actions (they studied actions such as block-stacking tasks, and simple reaching) (Fig. 11). Flanagan & Johansson (2003), and Rotman et al. (2006) proposed that the eye movement patterns of the observers are derived from both cognitive models (of the actions and task), as well as by analysis of the trajectory of the actor’s motions. Of course, this strategy has no obvious functional advantages for the observer, who did not have to do anything other than watch the actions of someone else. Flanagan & Johansson (2003) and Rotman et al. (2006) explained their results by linking their observation to hypotheses that saccadic motor plans can be activated simply by watching actions (Rizzolatti et al., 2001). They also suggested, however, that the eye movements of the observers were part of a built-in strategy that encourages the learning of relationship between actions and their consequences. In support of this idea, which connects eye movement planning to observations of actions, Rotman et al. (2006) showed that eye movement patterns were quite

different when the percept of an “action in progress” was prevented by allowing the observer to see the objects moved by the actor without seeing the actor himself.

The work summarized above illustrates some of the attempts to unearth the function of eye movements in real-world tasks. It is evident that this work is complex and ambitious: everything from designing the task, to making the measurements, to interpreting the data are far more challenging than more constrained lab tasks. The results have revealed that the ties between eye movements and the accompanying cognitive, motor and perceptual events are profound, raising questions about the nature of memory, the role of prediction, the contribution of learning, and the interactions of movements of eye, head and arm. As the technologies to perform these kinds of experiments evolve, along with the imaginations of the scientists, we can expect to see observations of eye movements over the next 25 years playing a leading role in any attempts to understand mind and action.

3.9. Summary

The main questions confronting attempts to understand saccadic eye movements have not changed over the past 25 (or more) years: What determines the decisions made about where to look? How are these decisions carried out? How do we maintain the percept of a clear and stable world despite the occurrence of saccades? Over the past 25 years, the approaches – experimental and theoretical – to these questions have changed so dramatically that the nature of a “typical” laboratory study of saccades is almost unrecognizable from what it was in 1986.

We have learned that many fundamental characteristics of saccades, comprising processes at various levels of preparation, seem optimally suited to supporting the performance of visual tasks. Saccades are planned so as to seek out locations containing useful information, and saccadic plans may be based on internal models that are informed about the limitations of our visual system, as well as by models of the sequence of operations needed to perform the given task. We have also learned that while the aggregate set of locations we choose to fixate appears to be optimal for a task, individual saccades will often target useless locations (and quickly correct these errors) in order to limit the time and resources devoted to saccadic planning. Mechanisms of saccadic planning facilitate such strategies by allowing multiple saccades to be planned at once, and by allowing saccades to be rapidly cancelled or re-directed as needed. Links between saccades and perceptual attention also appear flexible enough to meet the needs of both vision and saccadic control. Shifts of attention to the saccadic goal may support the integration of information across separate glances. At the same time mechanisms and options are available (use of perceptual cues or modest delay of saccades) to support a spatially- broader visual analysis a without significant disruption to saccadic plans.

We are also beginning to learn how the planning and execution of saccades is tied to the planning of movements of the head and the arm, both at a high level of decision formation, and a lower level of movement execution.

Work over the last 25 years has also converged on the notion that that the saccadic system is inherently predictive, using pre-saccadic shifts of attention and signals representing planned saccades to encode the location we are about to fixate, and to prepare visual neurons, in advance, for the post-saccadic image. These predictions may be instrumental in processes ranging from the control of saccadic accuracy (by means of adaptive saccadic adjustments) to the weaving together of discrete glances in a way that gives us the impression of a clear and stable perceptual world despite the continual displacements of the retinal image produced by saccades.

4. Epilogue

K: Now you can see why I wanted you here. I need your perspectives.

A: Really, our perspective? Now, finally, at the end? You haven't let us say much so far. So, we get to kick in something to the closing?

K: That was the plan, yes.

B: You must want some kind of summary of what stood out over the past 25 years. Here's one: The past 25 years saw a huge and welcome transformation. Oculomotor researchers left behind their dark rooms and tiny fixation points, and stopped arguing about whether saccades are reflexive or voluntary, or arguing about the gain of smooth pursuit. No more experiments to persuade pursuit or saccades to abandon reliance on prediction or learning. Prediction, learning, and attention are all crucial to the effective operation of eye movements in visually rich environments. Now eye movements are studied when observers examine objects, scenes, movies, or things that people can actually pick up and handle, just as they would in typical activities outside the lab.

A: The neuroscience of eye movements changed as well. In the last 25 years oculomotorists discovered they cared about the cortex.

K: What can we expect for the next 25 years?

B: We need to understand the effects of retinal image motion. Eye movements exert enormous control over the motion of the image on the retina by setting the characteristics of the compensatory systems or setting saccade rates. But we still don't understand how that control is used in natural vision; we don't know what is optimal for a given task.

A: I like the idea of blurring of the line between smooth pursuit and saccades. There's a lot that can be done with that.

B: I bet that in 25 years we'll be able to record activity of populations of neurons at a fine enough spatial and temporal scale that we'll be able to observe and model what the brain is doing during all these new oculomotor tasks we keep inventing.

K: You mean human brains.

B: Of course, and after that we'll make genuine inroads on new clinical fronts. Don't forget about individual differences and genetics. And, also, I want to see the robot built that samples the world using its sensors the way that humans move their eyes.

A: All that in 25 years? Could be, but consider this: People have always been curious about how the eye moves. We have long appreciated eye movements to be lawful and rule-governed, and interactive with vision and cognition. The models and rules have gotten more complex over the past 25 years, but in a sense things have gotten simpler because we know much more about what eye movements accomplish and how they work, and we have better tools (experimental and computational) to study them. There are still plenty of mysteries out there. Robots are fine, but I'm waiting for the next revelation that knocks my socks off.

K: Just what I was hoping to hear. Let's get to it.

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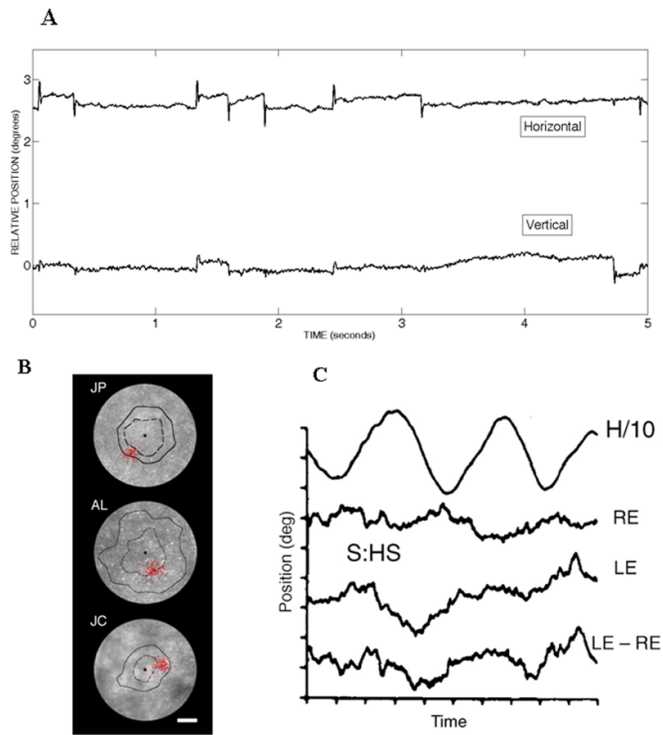


Figure 1.

(a) Eye movements during fixation of a stationary point target recorded with the Dual Purkinje Eyetracker. (b) Retinal montages of the foveal cone mosaic for three subjects. The black square represents the foveal center; the dashed black line is the isodensity contour line representing a 5% increase in cone spacing, and the solid black line is the isodensity contour line representing a 15% increase in cone spacing. Red dots are individual fixation locations. Scale bar is 50 μm . NM Putnam, HJ Hofer, N Doble, L Chen, J Carroll, DR Williams (2005) The locus of fixation and the foveal cone mosaic. *Journal of Vision*, 17: 5(7), 632–639. Figure 1. (c) Eye movements during fixation while the head is rotating. Traces show movements of head, right eye, left eye, and vergence (right eye – left eye). Image velocities were the same as the eye traces. From R. Steinman & H Collewijn (1980) Binocular retinal image motion during active head rotation. *Vision Research*, 20, 415–429; Fig. 1.

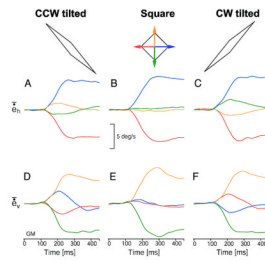


Figure 2.

Smooth pursuit of moving shapes. Mean horizontal and vertical pursuit speeds averaged over trials for 1 observer. Rightward and upward values are positive and up. Colors indicate direction of motion of the stimulus. The moving square produced either purely horizontal or purely vertical eye movements depending on the direction of motion of the square. The tilted diamonds produced a more complex response, generating pursuit along both horizontal and vertical meridians for about 100–200 ms, showing the dependence of the response on the motion vectors of the individual edges of the shape. From G.S. Masson & L.S. Stone (2002) *From following edges to pursuing objects. Journal of Neurophysiology*, 88, 2869–2873. (Fig. 1)

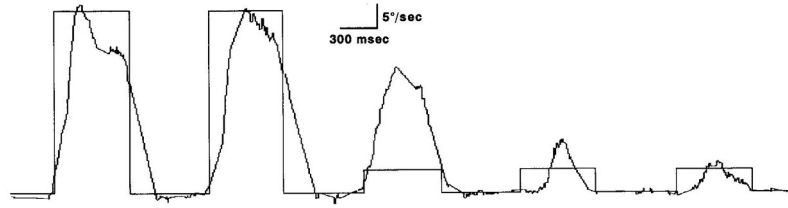


Figure 3.

Illustration of effects of learning on smooth pursuit. Subjects tracked two cycles of constant velocity (40 deg/s) motion (traces show target and eye velocity). After that, velocity decreased to 5 deg/s. Pursuit, however, continued to be influenced by the learned velocity. From G.W. Kao & M.J. Morrow (1994) The relationship of anticipatory smooth eye movement to smooth pursuit initiation. *Vision Research*, 34, 3027–3036. (Fig. 10)

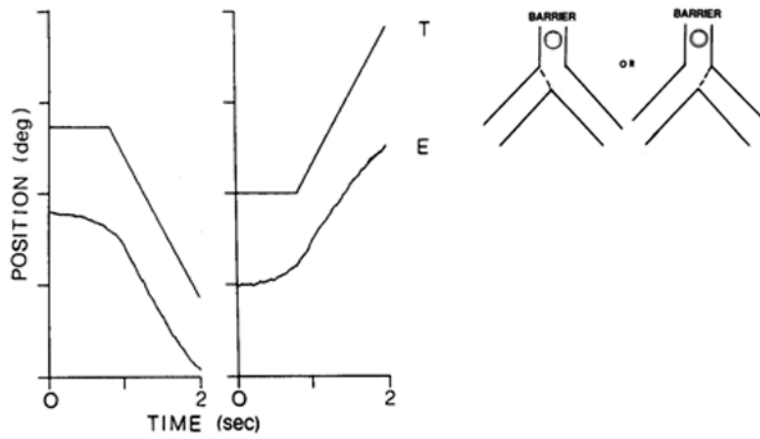


Figure 4.

Examples of anticipatory smooth eye movements, showing pursuit (lower traces) beginning before horizontal motion of the target (upper traces). Stimuli (shown on the right) were discs moving downward within a Y-shaped tube. The disc entered either the right or left arm of the Y. The horizontal path was indicated by the visual barrier that blocked the untraveled arm. From E. Kowler (1989). Cognitive expectations, not habits, determine anticipatory smooth oculomotor pursuit. *Vision Research*, 29, 1049–1057. (Figs. 1 and 2.)

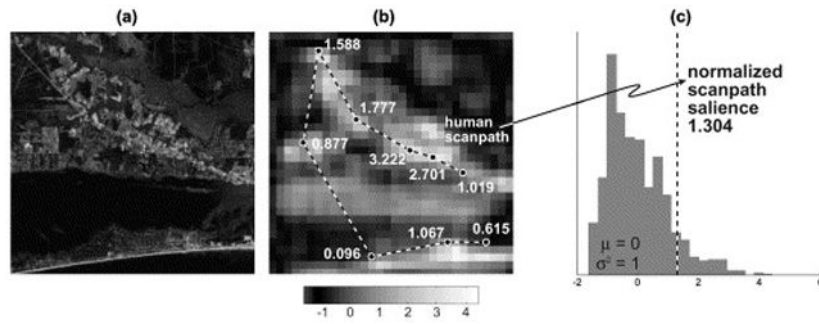


Figure 5. Illustration of a comparison of eye fixation positions (dashed lines, middle panel) with computed saliency levels (numbers next to fixation locations, middle panel) during inspection of the image shown in the left panel. The right panel shows average computed saliency values for all locations in the image. The dashed line is the average computed saliency level of the fixated locations. From R.J. Peters, A. Iyer, L. Itti & C. Koch (2005) Components of bottom-up gaze allocation in natural images. *Vision Research*, 45, 2397–2416. (fig. 7)

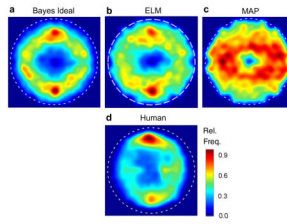


Figure 6.

Comparison of 3 model searchers to human performance. Najemnik & W. Geisler (2009). Each panel shows average spatial distribution of fixated locations. The Bayes Ideal and ELM (entropy limit minimization) visibility models generate predictions more similar to the human than the MAP searcher, whose winner-take-all strategy is closer to the predictions of saliency models (section 3.1). From J. Najemnik & W.S. Geisler (2009) Simple summation rule for optimal fixation selection in visual search. *Vision Research*, 49, 1286–1294. Fig. 4.

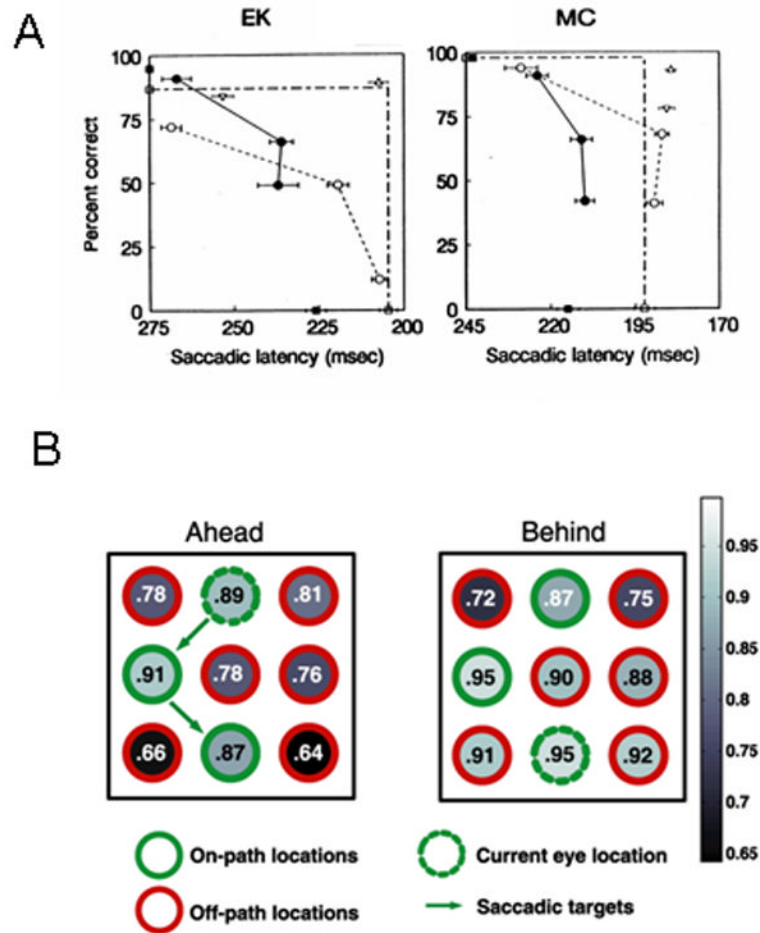


Figure 7.

(a) Attentional operating characteristics, showing performance tradeoff between saccadic and perceptual performance when making saccades to one target and reporting the identity of another. Location of the saccadic target was either constant in a block (open symbols) or cued before each trial (filled symbols). The 3 data points in each function show performance under instructions to give different relative weights to the two tasks. The intersection of the dashed lines is the independence point, showing performance expected if there are no shared resources between saccadic and perceptual tasks. From E Kowler, E. Anderson, B Doshier & E Blaser (1995) The role of attention in the programming of saccades. *Vision Research* 35, 1897–1916. (fig. 11) (b) Orientation discrimination during pauses between saccades made to look along a color cued (green) path. Only a portion of the saccadic path is shown. Current eye position is shown by the dashed circle. *Ahead*: Eye position was at the top; the remaining two green cued locations are saccadic targets. *Behind*: Eye position reached the bottom. The remaining two green locations were previously fixated. All red cued locations are outside the saccadic path. From: TM Gersch, E Kowler, B Schnitzer & B Doshier (2009) Attention during sequences of saccades along marked and memorized paths. *Vision Research*, 49, 1256–1266 (fig. 3).

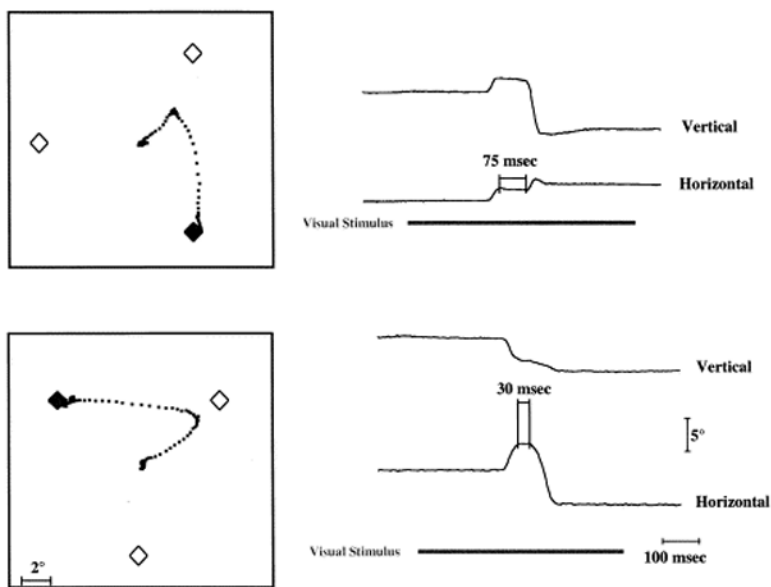


Figure 8. Evidence for concurrent planning of pairs of saccades. The sample eye traces show an incorrect saccade to a distractor followed by a second saccade to the target. From: R.M. McPeck, A.A. Skavenski & K. Nakayama (1999) Concurrent processing of saccades in visual search. *Vision Research*, 40, 2499–2516 (fig. 3)

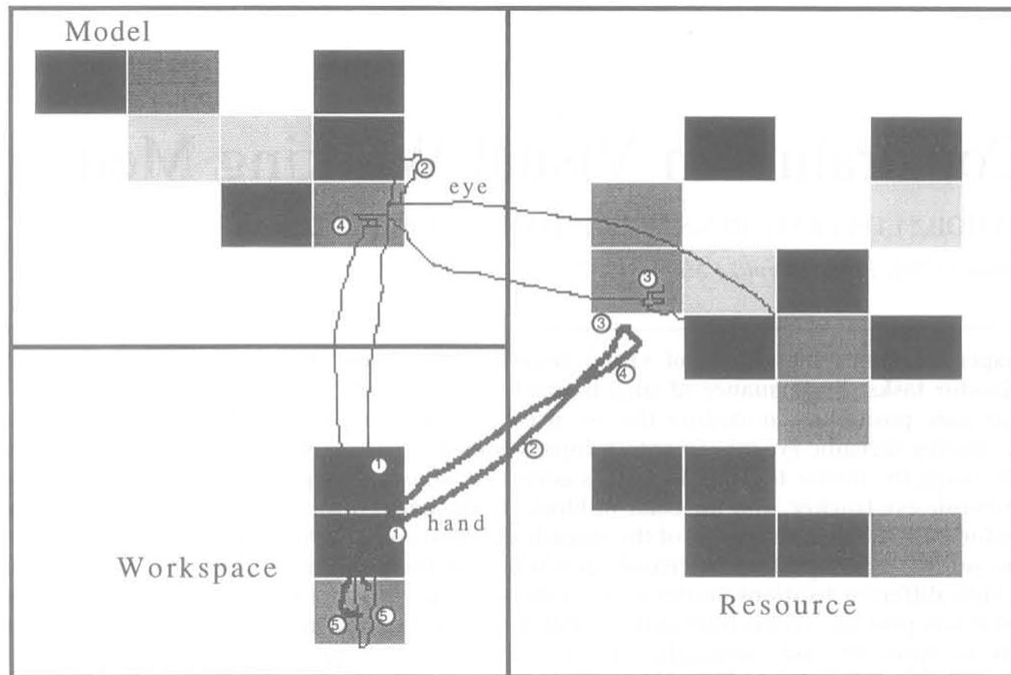


Figure 9. Example of performance in the block-copying task, where the objective is to move blocks from the resource to the workspace in order to copy the pattern shown in the model. Thin lines show eye traces; thick lines show movements of the visible cursor used to move the blocks. From M. M. Hayhoe, D.G. Bensinger, D.H. Ballard (1998) Task constraints in visual working memory. *Vision Research*, 38, 12–137. (fig. 1)

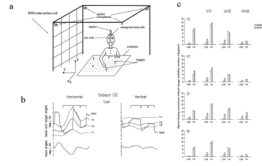


Figure 10.

(a) Cartoon showing subject tapping a set of rods placed on a worktable. Rotations of head and eye are recorded by the revolving field monitor. Translations of the head are recorded by an acoustic tracking system. (b) Sample traces of gaze, 3 targets and head. Rotational motions of the target are produced by translations of the head, which occurred both during and between gaze shifts. (c) Average speeds of head, eye, gaze and retinal image during both tapping and looking-only tasks. “Search” refers to speeds before the locations of the tapped rods were learned; “sequence” after the locations were learned. From J. Epelboim (1998), Gaze and retinal-image-stability in two kinds of sequential looking tasks, *Vision Research*, 38, 3773–3784, Figs. 1, 3, and 5.

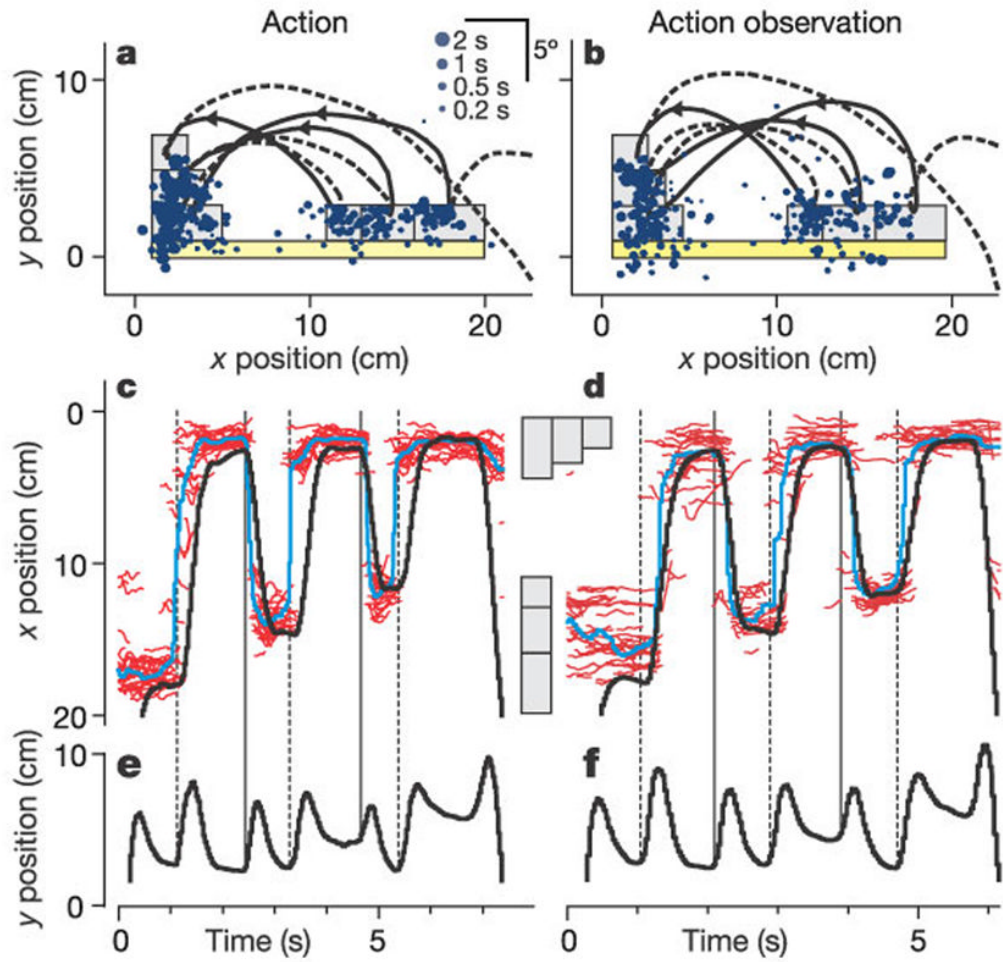


Figure 11.

Eye movements while stacking a set of blocks (a, c, e) or observing someone else stack the blocks (b, d, f). a,b, show positions at end of saccades (diameter of dot proportional to fixation duration); lines show path of hand. c,d show eye positions over time; e,f show eye velocities. From J.R. Flanagan, R.S. Johansson (2001) Action plans used in action observation. *Nature*, 424, 769–771 (fig. 1).