Attention and Eye Movements

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Synopsis:

Eye movements and visual attention both enhance perceptual processing of selected portions of visual scenes. Attention filters out visual backgrounds and ensures that smooth or saccadic eye movements are programmed solely on the basis of selected visual signals. Attention can do so nearly perfectly, while still allowing some broader perceptual analysis of the scene. This cooperative interaction meets the needs of both perception and eye movement control during inspection of visual scenes.   Behavioral and neurophysiological research is focused on understanding the coordination of eye movements and attention, and the processes that determine where people look during the performance of natural tasks.

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Eye movements are inextricably linked to visual attention because both are the principal tools available for selecting interesting portions of visual scenes for enhanced perceptual and cognitive processing. Selection is crucial for animals that rely on foveal images for making decisions about the visual environment or for guiding action. As a result, most of what is known about eye movements and attention derives from studies of human and non-human primates.

Eye movements are often taken to mark the path of attention through a scene, where "attention" refers to the internal (or "covert") distribution of processing resources. Eye movements and attention are assumed to serve useful purposes connected to the visual task, an assumption that has fueled decades of efforts to use eye movements to study how people search, read, study pictures of scenes, or carry out all manner of visually-guided actions involving reaching, pointing, manipulating objects, walking, or driving. All of these tasks require serial processing of different parts of a scene, and all routinely call upon eye movements.

For eye movements to be useful, they must be able to bring the line of sight to relevant locations quickly and accurately, and keep it there, with no deliberate effort or laborious decision stages beyond those already incorporated into the task itself.   In order to meet these requirements – speed, accuracy and low cognitive load – eye movements must be sensitive to both the physical structure of the visual array and to the momentary needs of the task. To see why this is the case, consider the two extreme possibilities: If eye movements were completely under the control of the stimulus, with gaze attracted to the most vivid or salient portions in a scene, cognitive load would be minimal, but the eye would continually be dragged off to useless and irrelevant locations. It would be impossible to choose targets according to the needs of the task. (Nevertheless, there are many models based on just this assumption.) On the other hand, too much emphasis on volition, choice or effort to control gaze would create undue cognitive demands and interfere with the ongoing flow of the task. The effort devoted to eye movement control would be a continual distraction from the job of recognizing objects and making task-related decisions and plans.   Over the past decades, oculomotor scientists have struggled to find ways of integrating these two extreme modes of eye movement control. The focus of these attempts, in behavioral, psychophysical and neurophysiological studies, has been the attempt to find and understand the relationship between the control of eye movements and the mechanisms of visual attention.

What is attention?

Before considering the relationship between eye movements and attention, it is useful to briefly summarize some aspects of attention as they apply more generally to perception.

In his classical treatment of attention in 1890, William James acknowledged that while everyone knows what attention is ("experience is what I agree to attend to") the question of what attention does is difficult to answer. Attention is credited with being able to enhance certain experiences at the expense of others, but at the same time it must do so without distorting the nature of these experiences.   Attention, James said, might make it possible to notice a faint sound or light, but paying attention to faint sounds or lights does not make them suddenly appear unusually loud or bright.

Modern researchers grappling with James' paradox have devised a number of clever experimental paradigms to explore the effects of attention on perception in many different contexts.   Attention can be summoned to locations or to objects by various sorts of cues or signals, or it can be drawn away by imposition of a competing task. Studies using these techniques have led to broad agreement about several characteristics of attention: (1) Attention can lower detection thresholds and increased perceived contrast, producing improvements equivalent to those produced by modest increases in the contrast of the stimulus itself. These effects may correlate with attention-induced changes in cell firing patterns (e.g., increased contrast gain) at neural levels as early as V1 or the LGN. (2) Improvements in perceptual thresholds can be produced either by paying attention to a selected location (the so-called "attentional spotlight"), to a selected feature, or to a selected object. In the case of "feature-based" attention, the attentional benefits can spread across broad regions of space; in the case of "object-based" attention, the benefits of attention can extend to the different features (color, size, orientation) making up the attended object. (3) Attention to an object serves to overcome potential perceptual interference from visual objects nearby. The importance of attention in the presence of competing stimuli has contributed to the view that attention should be viewed as an internal processing resource that can be distributed among features, objects or regions, as needed, to accomplish task goals. The importance of competition for limited resources has also been reflected at the neural level (areas V4 or MT, for example) with observations showing that, in the presence of multiple stimuli falling in a cell's receptive field, attention determines the relative contribution of each to the response of the cell. (4) Attention may also control access to limited capacity visual short-term or visual working memory, including the visual memory that preserves information from one fixation to the next.

All four of the above characteristics – demonstrated in experiments that took pains to eliminate a role for eye movements, often by restricting stimulus presentations to very brief intervals of time—have influenced thinking and research about the role of attention in oculomotor control and the role played by eye movements and attention in visual processing.

Attention and gaze stabilization

One of the most important functions of eye movements is to maintain stable gaze. Even modest rotations of the head, if not compensated by counter-rotations of the eye in the orbit, can create sufficient motion of the retinal image to impair visual resolution, carry important visual details away from the fovea, and create the illusion that the environment itself is moving. The oculomotor system is equipped with sophisticated systems that use both visual and vestibular signals to compensate for head movements and maintain stable gaze. These traditional full-field gaze stabilization reflexes, however, are not ideally suited to environments containing multiple objects at various distances and locations, viewed by observers who continually pick up and handle some of these objects, and who continually shift their own position in myriad ways. These situations require maintenance of stable gaze on only one thing at a time, and this means overriding the global visual or vestibular gaze stabilization reflexes, or at least restricting the portion of the scene on which they are allowed to operate.

In the early 20th century, physicist and philosopher Ernst Mach described the situation well. The problem, said Mach, is that the retinal motion generated by head movements and body movements as we move through the environment may "exert a peculiar motor stimulus upon the eye, and draw our attention and our gaze after them".   But this attraction can be overridden:

"No special apparatus is necessary for observing the foregoing phenomena. They are to be met with on all hands. I walk forward by a simple act of the will. My legs swing to and fro without my having to attend to them particularly. My eyes fixed steadfastly upon my goal without suffering themselves to be drawn aside by the motion of the retinal images consequent upon progression. All this is brought about by a single act of the will….The same process must also be set up if the eyes are to resist for any length of time the stimulus of a mass of moving objects."   (Mach, E., 1905, *Analysis of Sensation*.)

Mach's impression that we can override flows of motion on the retina and maintain stable gaze on chosen targets has been confirmed and extended many times in the modern oculomotor laboratory. It is possible, for example, to maintain gaze on even very small stationary targets superimposed on large and vivid moving backgrounds. It is also possible to smoothly track a target moving across a stationary background (although this has proven to be the more difficult task), and to track a target moving in the presence of a nearby moving non-target.   In the case of the target and non-target, it may require about 100 ms or so for complete selectivity to be achieved.   Observations like these have been made in many studies since 1930, with different kinds of backgrounds and with fixation targets of different sizes and retinal locations, each time showing that it is possible to maintain fixation on selected targets and override the effects of the more plentiful motion signals originating from the background (Fig. 1).

The ability to select the target for smooth eye movements has also been demonstrated with superimposed transparent sheets of dots, each moving at a different velocity (Fig. 1B and Movie 1). With such patterns, attending to a discrete location would not be sufficient to select one sheet as the target because dots are superimposed everywhere. Thus, effective selection with transparent motions requires attending to a selected object or surface, rather than to a discrete location within the pattern. Interestingly, the selection of one of the transparent surfaces does not disrupt the perceptual impression of transparency, nor does it disrupt perceptual interactions between the superimposed fields.   For example, if one of the fields is moving and the other stationary, the stationary field seems to be moving opposite in direction to the other, ignored moving field. The percept of induced motion shows that the selection of the target for the eye movements leaves intact basic operations of sensory and perceptual motion processing. This raises the possibility that the selective mechanism that determines the target for smooth eye movements may use its own dedicated attentional filter whose operation has minimal consequences for perception.

The role of attention in perception vs. the role of attention in smooth eye movements

One way to find out whether smooth eye movements and perception share a common attentional mechanism is to expand the eye movement experiment to include a concurrent perceptual task. In one representative situation, an observer is presented with two sets of moving targets and asked to smoothly track one set and ignore the other (Fig. 2). In this situation

perceptual judgments made about the tracked target are more accurate than those made about the untracked background (even after taking into account any differences in retinal position and retinal velocity), implying that a single filter and a single attentional decision determine the strength of signals reaching both perceptual and oculomotor systems. But there are important differences between eye movements and perception. While the smooth tracking eye movements are nearly perfect, with virtually no effect of the unselected background motion, perceptual judgments about the unselected background are above chance, showing that some perceptual registration of the background remains. Thus, there is an asymmetry between the effects of attention on perception and eye movements. Analogous results have been obtained from neurons in extrastriate cortical areas MT and MST, the presumed sources of the motion signals that guide smooth eye movements and serve perception. Neurons in these areas respond more vigorously to attended and tracked motion than to unattended, untracked motion, but the differences in firing patterns are small, and do not explain the high degree of selectivity that can be demonstrated in smooth pursuit eye movements (although they are in general agreement with the magnitude of selectivity observed at the perceptual level). The observed differences between the effects of attention on eye movements and perception, and the small effects observed in the motion areas MT and MST during the selective tracking tasks, imply that a given distribution of attention across target and background has different consequences for perception and for eye movements. This rules out "early selection" models, in which attention operates primarily at an early sensory level of visual processing shared by perception and eye movements.

The ability to eliminate almost all influence of the unselected motion signals from the eye movements has suggested the involvement of a winner-take-all (WTA) network operating on the set of attentionally-weighted motion signals emerging from areas MT and MST. Winner-take-all networks are often used in models of attention or perception, and are effective ways to remove weak, and potentially interfering, signals. Although such a network operating downstream from sensory motion areas could account for the perfect or near-perfect selectivity observed for eye tracking performance, an unconstrained WTA network places a strict limit on the options. It would not, for example, allow people to divide attention between target and background, and track at a velocity intermediate between the two. An alternative to the WTA network is an executive controller that determines the relative weights assigned to different sets of sensory motion signals. A single executive controller could be used by both perceptual and oculomotor systems with different effects on each.   For example, assigning maximum weight to a target could completely attenuate the representation of non-targets in neural areas devoted to smooth tracking, and only partially attenuate the non-target representation in perceptual areas. Different assignments of weight would produce different performance outcomes. Given that the neural circuitry that controls smooth eye movements includes several high-level cortical areas (FEF, SEF and LIP) that also play roles in perceptual attention, there is considerable opportunity for executive intervention in the attentional weighting of motion signals from target and background.

Summary: attention and gaze stabilization

Selective attention plays a crucial role in the control of smooth eye movements by ensuring that stable gaze can be maintained on either stationary or moving targets, regardless of the signals present in the background. Attention ensures that eye movements are controlled only by signals originating from the selected object. Performance of concurrent oculomotor and

perceptual tasks have shown that a single attentional decision affects both: it is not possible to maintain gaze on one object while fully attending another. Unselected objects nevertheless remain perceptible, and continue to generate neural signals in areas sensitive to motion. This outcome rules out early selection models of attentional control, and raises still unanswered questions of how a common attentional decision can have different consequences for smooth eye movements and for perception.

Attention and saccadic shifts of gaze

Saccadic eye movements are used to inspect the visual environment, with saccadic shifts of gaze occurring anywhere from once every several seconds to several times a second. Visual processing occurs during the pauses between saccades. Unlike smooth eye movements, described above, which cannot be generated without some sort of representation of smooth motion, saccadic eye movements can be made at will to look at arbitrary locations.

Saccades are typically directed to useful or informative locations and are often taken to disclose the path of attention during performance of natural tasks. Attention, however, need not be locked to the fovea even as the eye jumps from place to place. Attention to locations remote from the line of sight is valuable for broad surveys of the scene, and is indispensable for ensuring that saccades land on the selected object, regardless of the visual structure of the immediate surround.

Eye position as an overt marker of the locus of attention

Figure 3 shows examples of saccadic patterns made during various visual tasks: reading, counting, geometry problem-solving, and visual scene recall. Figure 4 shows eye movements during visual search. Figure 5 replicates and extends the well-known experiment described by Yarbus in his 1967 book *Eye Movements and Vision*, in which people are asked to inspect the same painting in order to answer different questions. The scan patterns differ depending on the question, showing that the physical features of the pictures do not by themselves determine the landing locations of the eye, but there is considerable influence of purpose and intent. Figure 6 looks at this issue from another angle, showing scan patterns obtained when looking at two versions of the same photograph, where in one version the image has been filtered and fine detail removed. Although the task is the same in each, the scatter of the fixated locations is different.

Similar efforts to document sequences of fixations in different tasks have been made in more complex and dynamic situations, where observers move about the environment, handling various objects for some specific purpose. Movie 2 depicts sequences of fixation positions of the two eyes when observers are tapping a set of rods in prescribed order, grooming a fellow primate and assembling a doll.

Data like these have always been intriguing. They prove that ordinary visual experience, which seems smooth, continuous, and flowing, is really made up of sequences of brief, still frames and snapshots, whose detailed contents escape awareness. We don't notice each individual glance because we remember only what is most essential – the cumulative number of dots counted, or the meaning of a word or phrase – or we use what we see to guide an immediate

action. Observing sequences of eye movements reveals the sequential nature of vision and provides a view of underlying goals and strategies that would be hard to recover through other means.

Decisions, attention and saliency maps

Understanding the rules that govern saccadic planning in everyday life tasks is an enormous undertaking that must be based on generalized models of the task, combined with knowledge of the relevant visual, cognitive and motor capacities that limit performance and affect the strategies adopted. Although we still lack comprehensive and general models, progress has been made toward the goal. One of the influential constructs developed to account for the eye movements made during scanning of a scene is the "salience map". As originally proposed by Koch & Ullman, the salience map is derived from the output of banks of visual filters, modeled after those present in early levels of the visual system (V1). These filters respond on the basis of local feature contrast (luminance, color or orientation contrast) present in the scene. Models for the generation of salience maps integrate all three types of feature contrasts, taking effects of retinal eccentricity into account. Saliency maps have been used to predict where people direct saccades, and how they distribute visual attention (i.e., processing capacity) across a scene even when eye movements are not made.

In order to use a global salience map to predict a sequence of fixations, two additional assumptions have to be made.   The first is that a "winner-take-all" network (similar to that discussed in the context of smooth eye movements, above) establishes the ordering of the fixations, with the region with the highest salience level designated as the next one to be fixated. The second assumption is that the salience map is subjected to "inhibition of return", that is, once a location is examined its strength in the salience map will abruptly diminish, thus allowing the line of sight to proceed to new places and avoiding the need to store a list of already-scanned locations. Armed with a salience map and these two supporting assumptions, it has been possible to generate precise predictions about where people look during unconstrained free-viewing. The predictions have proven to be reasonably accurate, at least when computed salience is compared to the global aggregate of fixated locations over some period of inspection. Nevertheless, the approach has not been without controversy.

The main criticism of the salience-map approach is the obvious one, recognized and discussed even by proponents of the approach. Strict control of eye movements or attention based solely on physical salience becomes counter-productive as soon as people are faced with real world tasks, such as those illustrated in Figs. 4-6 and Movie 2.   In real world tasks people look at the objects and details that are important, regardless of the physical salience levels. Gaze and attention may be drawn to novel or unexpected objects, or to highly familiar objects, depending on the situation. None of these characteristics is represented by physical salience. Physical salience also does not capture the long-term changes in gaze preferences that develop as the contents of the scene are learned, nor does it capture effects of motivation. Do you look at something because it attracts your interest, because it contains some new information you need to perform a task, or because you need to confirm a detail that you already know is present? All of these so-called "top down" variables that influence gaze and attention can be viewed as

displacing the concept of a saliency map, or, alternatively, as imposing an additional set of weights on the physical salience levels.

Neurophysiological studies using a variety of active saccadic tasks involving visual search or visual discriminations have addressed a portion of the problem of incorporating "top-down" variables by showing that neurons in areas related to saccadic planning (LIP, FEF, SC) may be able to encode the top down salience level at a given location.   The evidence for this assertion is that neurons in these areas show enhanced activity when objects in their receptive fields contain information relevant to the guidance of an upcoming saccade, even when the location of enhanced activity does not correspond to the location of the saccadic target. Visual areas (V4 or IT, for example), also show sensitivity to top-down salience. In these areas neurons tuned to specific features show effects of attention, as well as patterns of pre-saccadic enhancement. Thus, there has been considerable progress in identifying brain areas that modulate responses to objects depending on their immediate behavioral significance, and these areas may constitute the core of a network that directs attention and saccades to objects or locations relevant to a task.

Incorporating top-down factors and physical salience levels into a single map may be a physiologically plausible means of deriving a single message to guide saccades and attention. Alternatively, there may be multiple maps that compete for control. Studies of eye movements during visual search have provided some support for the notion of competing maps. In these studies saccades are drawn to physically salient locations that are not likely to contain the search target, followed quickly by "corrective" saccades to more appropriate, but less salient, places (Fig. 4c). These rapid saccadic sequences could represent the results of the competition between different maps for momentary control of the neural centers that produce saccades. Although such competition seems inefficient, the amount of time lost by an occasional errant saccade may be small enough that an investment of time and resources in more prudent saccadic planning may not be warranted.

Saccades and attention

Saliency – either stimulus-driven or top-down – is said to predict the distribution of both attention (internal processing resources) and saccades over time and space. Is there any important or necessary distinction between the distribution of attention and saccades? According to "pre-motor theories of attention", saccadic eye movements and shifts of attention are essentially the same process, originating in the same neural areas, with an attention shift occurring only when the saccade is suppressed or inhibited.   The pre-motor theory is supported by finding several neural areas (SC, FEF) whose activity can evoke, or is correlated with, both attention shifts and saccades. Nevertheless, it is troubling for pre-motor theories that attention can be distributed in parallel across the visual field, or aligned symmetrically about the line of sight, spatial patterns do not readily map onto trajectories of saccades.

If we view attention not as a subthreshold saccade, but rather as an internal processing resource that influences both perception and motor control, we can then ask how attention and saccades interact. Attention plays an important role in saccadic guidance in that, while it is

possible to shift attention independently of the saccade, it does not appear possible to plan and carry out an accurate saccade without shifting some attention to the saccadic goal.

Dual-task studies, similar to those described earlier for smooth eye movements, have examined the distribution of visual attention prior to saccades, using various psychophysical tasks as indicators of local attentional strength. These dual-task studies require observers to do two things at once (in as brief a time as possible), namely, prepare look to at a specified object, and identify a perceptual target presented while preparation of the saccade is in progress. The perceptual target appears either at the saccadic goal or elsewhere. These experiments can succeed only if care is taken that the two tasks are done in the same brief interval of time because otherwise observers can decide to delay saccades in order to improve perceptual performance.

Dual-task experiments have shown that perceptual performance is better at the saccadic goal than elsewhere (see illustrative study in Fig. 7), showing that saccades and attention do not functional independently. Yet, as was the case with smooth eye movements, perceptual performance at non-goal locations remained well above chance even when efforts were made to produce the saccades as quickly and accurately as possible (i.e., with the same latency and accuracy as observed with no concurrent perceptual task). Moreover, it only required a modest sacrifice in saccadic performance (10-20% latency increases) to achieve pronounced improvement in perceptual performance at non-goal locations.

Similar connections between attention and saccades are found during the execution of sequences of saccades (Fig. 8a). Best perceptual performance is found at the saccadic goal, with elevations in perceptual thresholds at other locations, the amount of elevation depending on when and where the perceptual target appears. The pattern of activity observed during saccadic sequences suggests that the reduction in the attentional levels at non-goal locations is important for providing sufficient "attentional contrast" to guide an accurate saccade and prevent the line of sight from landing at salient, but incorrect, locations during scanning tasks. Thus, the main role of top-down attention in saccadic guidance may be to suppress the attraction of physically salient, but irrelevant, locations.

When the scan path to be followed is marked by a feature difference, rather than being followed from memory, the distribution of attention changes significantly. Attention spreads to locations along the feature-cued path, including targets of subsequent, as well as previous saccades (feature based attention) (Fig. 8b). An interesting question raised by these results is how the saccades remain accurate when so many locations are attended at once. As was the case with smooth eye movements, there are two main alternatives. The first is a "winner-take-all network" that directs the eye to the location where attentional strength is greatest. The second alternative requires the intervention of a central executive controller that imposes its own attentional weights. The controller could, for example, focus all active, effortful attention on the upcoming target. The perceptual enhancement observed elsewhere along the featured-cued path could result from a passive process that facilitates the spread of attention across space to the selected features.

Summary: Attention and saccades

The picture of saccades and attention that emerges from the psychophysical and behavioral studies described above, which is in agreement with neurophysiological work, is that saccades and attention normally operate in a connected fashion, with saccades landing at the object that is the main focus of attention.   Nevertheless, attending to the goal of saccades still allows significant perceptual processing at different locations, perhaps with the aid of other mechanisms that passively distribute attention to relevant locations in parallel across the visual array.

Overall summary and conclusions

The connection between eye movements and attention described in this article justifies the prevalent assumption that eye movements can provide reliable indicators of the main focus of attention in active visual tasks, such as reading, search or object manipulation. Attention plays a crucial role in oculomotor control by enhancing signals from selected targets relative to those in the background, thus ensuring that eye movements are planned and programmed on the basis of selected visual signals, regardless of the visual configuration of objects nearby. Following the classical treatment of William James, it is useful to distinguish between the distribution of attention and the effects of attention. Attending to a given target can completely eliminate the influence of visual backgrounds on eye movements (smooth or saccadic) while continuing to allow perceptual processing, albeit at reduced levels. This asymmetry between perception and eye movements has the desirable consequence of allowing eye movements to be accurate while global perceptual analysis continues across the visual field.

Further Readings

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Figure Captions

Figure 1. Smooth eye movements and attention. (A) Examples of horizontal smooth eye movements maintaining a stable line of sight on a stationary fixation target superimposed on a background moving grating. Data from two observers, RS and BW. The left trace in each panel shows the stimulus motion (5, 48, or 480 '/s); the right trace shows horizontal eye movements. Horizontal lines are one-second time markers, with time beginning at the bottom. The horizontal bar below the panels for each observer represents a 1 deg eye rotation. From: Murphy B.J., Kowler E. & Steinman R.M. (1975) Slow oculomotor control in the presence of moving backgrounds. *Vision Research* 15, 1263-1268. (B) Another example of the independence of smooth eye movements from background motion. Each trace shows horizontal smooth eye movements with two full-field superimposed arrays of random dots, one array stationary and the other moving at 1.2 deg/s. In the upper panel the observer was told to fixate the stationary array, and in the lower panel to pursue the moving array. There was virtually no effect of the unattended field on performance. From: Kowler E., Van der Steen J., Tamminga E.P. & Collewijn H. (1984), Voluntary selection of the target for smooth eye movements in the presence of superimposed, full-field stationary and moving stimuli. *Vision Research*, 24, 1789-1798. (C) Average eye velocity in response to a single target moving either downward (top) or rightward (bottom) (thin eye traces, labeled "Rt" or "Dn") or to a pair of targets, one moving rightward and the other downward (bold traces labeled "Rt&Dn"). Traces labeled "target" shows the stimulus which traveled over 20 deg for 400 ms. After 150 ms one of the target motions of the pair disappeared leaving only a single stimulus moving downward (top) or rightward (bottom). Eye velocity when both target motions were present was the average of the two target velocities until about 80 ms after one of the motions was removed (marked by the arrows) when the traces diverged. From Lisberger S.G. & Ferrera V.P. (1997) Vector averaging for smooth pursuit eye movements initiated by two moving targets in monkeys. *Journal of Neuroscience,* 17, 7490-7502. (D) Horizontal eye velocity in the presence of two visual arrays of noise elements moving in opposite directions, one located above and the other below the line of sight.. The eye trace shows the change in pursuit direction when first one, and then the other, moving field is selected as the pursuit target.   From Liston D. & Krauzlis R.J. (2003) Shared response preparation for pursuit and saccadic eye movements. *Journal of Neuroscience*, 23, 11304-11314.

Figure 2. Smooth eye movements with a concurrent perceptual task. The 3 display frames show four rows of letters moving rightward with the top and third rows moving at half the velocity of the second and bottom rows. Letters remained within the confines of the frame so that as portions reached an invisible boundary on the right they re-appeared immediately on the left side of the display.   Vertical eye position remained in the gap between rows 2 and 3, while subjects attended and tracked either the faster or slower pair of rows. Frames 1 and 3 are masks. Frame 2 is the critical display containing 2 numerals that had to be identified at the end of the trial. Tracking gains were > .8. Perceptual performance shown in the top graphs for 2 observers depended on instructions. When attending and tracking the slower pair of rows (open symbols) identification accuracy was better for the slower rows than the faster rows. When attending and tracking the faster pair of rows (closed symbols) identification improved for the faster pair at the expense of the slower pairs. Separate analyses showed that these results were not due to differences in retinal speed of tracked and untracked rows and were due solely to attention.

Based on: Khurana, B. and Kowler, E. (1987). Shared attentional control of smooth eye movements and perception. *Vision Research 27*, 1603-1618.

Figure 3. Examples of eye movements during various visual and cognitive tasks. (A) Fixation positions of one observer during one stage of solving a problem in geometry. The problem is presented above the diagram and the excerpt from the protocol is below. Important features of the diagram were refixated at regular intervals. Analyses of the timing and locations of fixations showed frequent revisits, consistent with a working memory capacity of 5 visual features of the problem. From Epelboim J. & Suppes P. (2001) Eye movements during problem solving in geometry. *Vision Research* 41, 1561-1574. (B) Eye movements during reading. The same pattern of eye movements is shown as individual fixation locations superimposed on the text (above) and as a trace of eye positions over time (bottom). Eye position is on the abscissa and time moves from top to bottom. These eye movements are typical of reading in that saccades were about 7 characters long and intersaccadic pauses were about 275 ms. More than 40 readings of this same text showed little change in the pattern of eye movements and a high level of consistency in the distribution of landing locations. From Schnitzer B.S. & Kowler E. (2006) Eye movements during multiple readings of the same text. *Vision Research* 46, 1611-1632. (C) Eye movements while counting an array of dots are shown both superimposed on the dot array and also as horizontal and vertical traces over time. (D) Eye movements made during a visual recall task. Subjects had to report the contents of the picture after periods of scanning ranging up to 4 seconds. Analyses showed that memory for the content of the pictures was preserved across successive viewings separated by several minutes and several intervening viewed scenes. From: Melcher D. (2001) Persistence of visual memory for scenes. *Nature* 412, 401.

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Figure 5. Effect of task motivation on eye movements. (A) Adapted from Yarbus' (1967) *Eye Movements and Vision*, showing that people looking at Requin's painting, The Unexpected Visitor, alter the choice of fixation positions depending on the question they had to answer. (B) A replication of Yarbus' experiment.   Subject A shows the same sensitivity to task as Yarbus

demonstrated, while subject B tends to look in the same places regardless of the task. From
Lipps, M., & Pelz, J. B. (2004). Yarbus revisited: task-dependent oculomotor behavior
[Abstract]. *Journal of Vision 4*, 115a.

Figure 6. Fixations made by 10 viewers while looking at two variants of the same photograph
under instructions to remember the picture for a subsequent recognition task. The original
photograph is on the left; fixations are tightly clustered in a few key areas. On the right
computer graphics techniques were used to create a drawing-like version of the scene and
remove detail throughout the image. Fixations are more uniformly distributed. Based on
DeCarlo D. & Santella, A. (2002) Stylization and Abstraction of Photographs, ACM
Transactions on Graphics (Proceedings of ACM SIGGRAPH), 21, 769-776; and Santella A. &
DeCarlo D. (2004) Visual Interest and NPR: an Evaluation and Manifesto. Proceedings of the
3rd international symposium on Non-photorealistic animation and rendering, 71-78.

Figure 7. Saccades and attention. (A) The display contained 8 randomly chosen letters. The
task was to make a saccade (downward, in this case) while simultaneously identifying the letter
in the righthand position. Display timing was adjusted so that the critical letters appeared only
during the saccadic preparation interval. (B) Attentional-operating characteristics for 2 subjects
showing the tradeoff of saccadic and perceptual performance under two different conditions,
saccade to a randomly chosen location (filled circles) or saccade to the same location on each
trial (open circles).   The 3 data points in each function show performance under 3 instructions:
(1) minimize saccadic latency (lowermost symbols); (2) sacrifice latency for improved
perceptual accuracy (uppermost symbols) or (3) perform at a level intermediate between these
two extremes.   Achieving best perceptual identification accuracy required a sacrifice in saccadic
latency (analysis of saccadic precision showed analogous results). Perceptual identification
reached near perfect levels with latency increases of only 10-20%. From Kowler E., Anderson
E., Dosher B. & Blaser E. (1995) The role of attention in the programming of saccades. *Vision
Research* 35, 1897-1916.

Figure 8. Attention during performance of sequences of saccades. (A) Repetitive sequences of
saccades: Two subjects made saccades to rectangular boxes following a triangular pattern
(shown by arrows) in which saccades were made to every other box. During a randomly selected
fixation pause an oriented Gabor patch was shown in one of the boxes either during the early
(top) or later (bottom) portion of the pause. Current fixation position is in the top box. Colors of
the boxes and the numbers in the boxes show the ratios of contrast threshold for correct
orientation identification relative to thresholds during steady maintained fixation.   Thresholds
were significantly elevated at all locations except the currently-fixated position (top of each
graph) and target of the next saccade (lower left box in each graph). From Gersch T.M., Kowler
E., & Dosher B. (2004) Dynamic allocation of visual attention during the execution of sequences
of saccades. *Vision Research* 44, 1469-1483. (B) Non-repetitive sequences of saccades:
Arrows represent a segment of a saccadic path. Current eye position is the top circle (dotted
outline). Shading and numbers in the circles show percent correct orientation identification (2
alternative forced-choice) for a Gabor patch shown briefly in one of the circles during a
randomly selected intersaccadic pause. Perceptual performance is best for locations on the
saccadic path, including the targets of the next two saccades. Performance at on-path locations is
better than that of off-path locations, including off-path locations of equal or smaller retinal

eccentricity.   From Gersch T.M., Schnitzer B.S., Sanghvi P., Dosher B., & Kowler E. (2006). *Visual Cognition*, 14, 104-107.

Movie Captions

Movie 1:

Three examples of the effect of attention on smooth eye movements. The stimulus in each is a pair of superimposed dot fields, one moving horizontally and the other vertically.   Eye movements – shown by the moving red dot – follow the motion of the attended field, horizontal in the first example, and vertical in the second. In the third example attention was distributed across both moving fields. The eye followed an oblique path reflecting the pooling of signals across both fields.

Move 2:

Three examples of eye movement patterns during performance of realistic visuomotor tasks requiring binocular eye and head movements. The tasks were: tapping a set of rods, grooming a primate, and assembling a doll. The movie first shows each task in progress, followed by a visualization of the trajectories of the movements of both eyes as seen from overhead. Based on Steinman R.M., Menezes W., & Herst A.N. (2005) Handling real forms in real life. In M.R.M. Jenkin, L.R. Harris (Eds.) Seeing Spatial Form (pp. 187-212). N.Y, N.Y.: Oxford University Press.
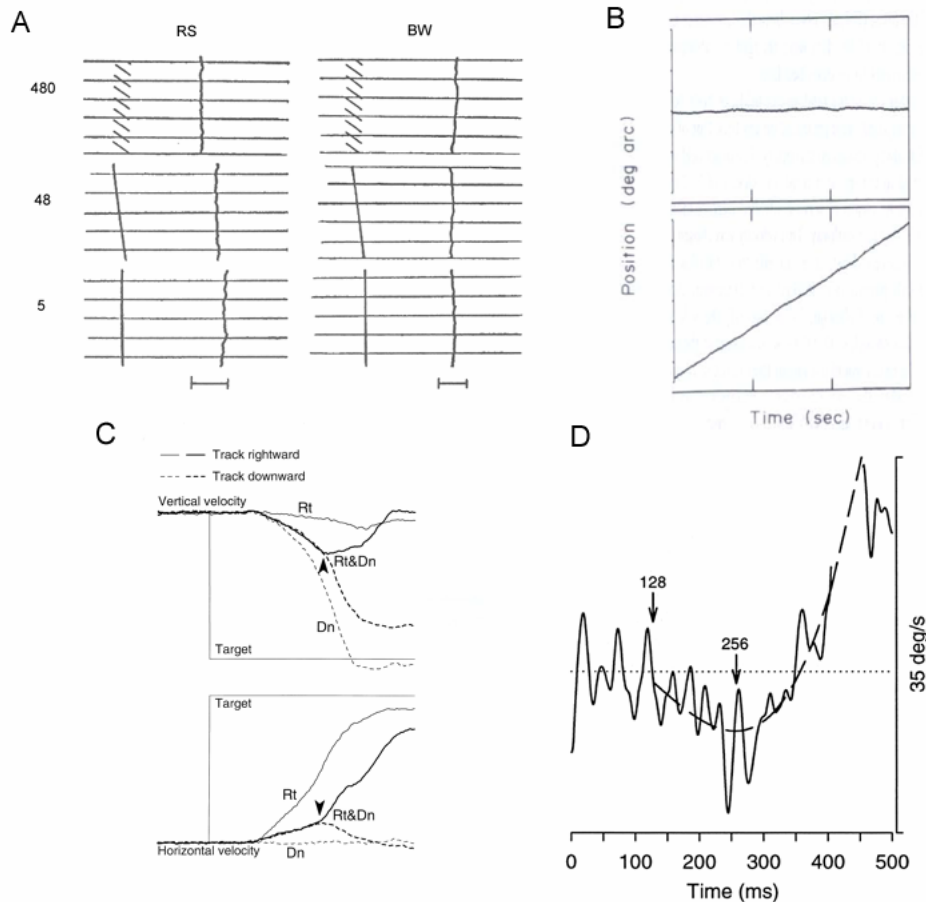
Figure 1. Smooth eye movements and attention. (A) Examples of horizontal smooth eye movements maintaining a stable line of sight on a stationary fixation target superimposed on a background moving grating. Data from two observers, RS and BW. The left trace in each panel shows the stimulus motion (5, 48, or 480 '/s); the right trace shows horizontal eye movements. Horizontal lines are one-second time markers, with time beginning at the bottom. The horizontal bar below the panels for each observer represents a 1 deg eye rotation. From: Murphy B.J., Kowler E. & Steinman R.M. (1975) Slow oculomotor control in the presence of moving backgrounds. *Vision Research* 15, 1263-1268. (B) Another example of the independence of smooth eye movements from background motion. Each trace shows horizontal smooth eye movements with two full-field superimposed arrays of random dots, one array stationary and the other moving at 1.2 deg/s. In the upper panel the observer was told to fixate the stationary array, and in the lower panel to pursue the moving array. There was virtually no effect of the unattended field on performance. From: Kowler E., Van der Steen J., Tamminga E.P. & Collewijn H. (1984), Voluntary selection of the target for smooth eye movements in the presence of superimposed, full-field stationary and moving stimuli. *Vision Research*, 24, 1789-1798. (C) Average eye velocity in response to a single target moving either downward (top) or rightward (bottom) (thin eye traces, labeled "Rt" or "Dn") or to a pair of targets, one moving rightward and the other downward (bold traces labeled "Rt&Dn"). Traces labeled "target" shows the stimulus which traveled over 20 deg for 400 ms. After 150 ms one of the target motions of the pair disappeared leaving only a single stimulus moving downward (top) or rightward (bottom). Eye velocity when both target motions were present was the average of the two target velocities until about 80 ms after one of the motions was removed (marked by the arrows) when the traces diverged. From Lisberger S.G. & Ferrera V.P. (1997) Vector averaging for smooth pursuit eye movements initiated by two moving targets in monkeys. *Journal of Neuroscience*, 17, 7490-7502. (D) Horizontal eye velocity in the presence of two visual arrays of noise elements moving in opposite directions, one located above and the other below the line of sight.. The eye trace shows the change in pursuit direction when first one, and then the other, moving field is selected as the pursuit target. From Liston D. & Krauzlis R.J. (2003) Shared response preparation for pursuit and saccadic eye movements. *Journal of Neuroscience*, 23, 11304-11314.
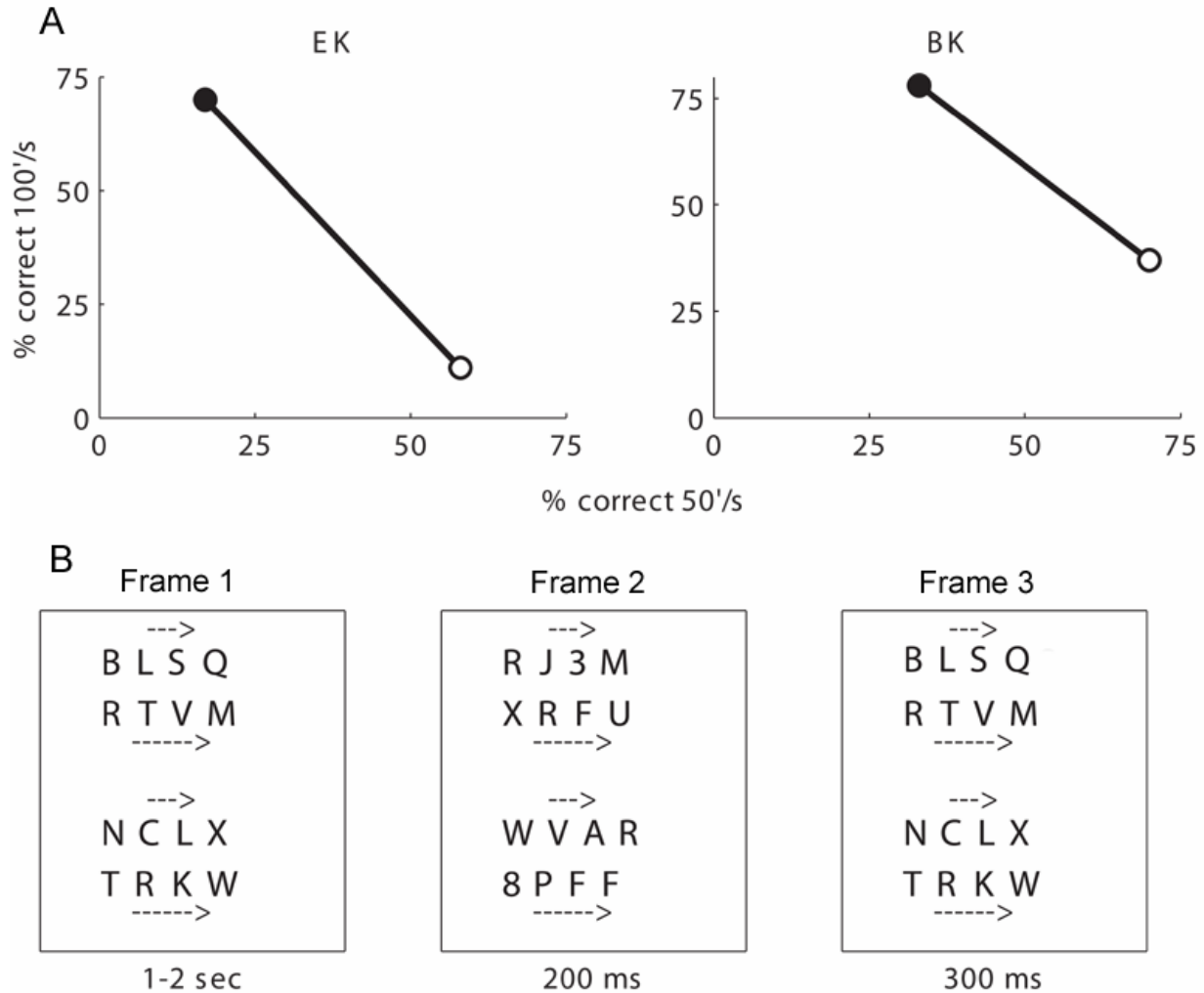
Figure 2. Smooth eye movements with a concurrent perceptual task. The 3 display frames show four rows of letters moving rightward with the top and third rows moving at half the velocity of the second and bottom rows. Letters remained within the confines of the frame so that as portions reached an invisible boundary on the right they re-appeared immediately on the left side of the display.   Vertical eye position remained in the gap between rows 2 and 3, while subjects attended and tracked either the faster or slower pair of rows. Frames 1 and 3 are masks. Frame 2 is the critical display containing 2 numerals that had to be identified at the end of the trial. Tracking gains were > .8. Perceptual performance shown in the top graphs for 2 observers depended on instructions. When attending and tracking the slower pair of rows (open symbols) identification accuracy was better for the slower rows than the faster rows. When attending and tracking the faster pair of rows (closed symbols) identification improved for the faster pair at the expense of the slower pairs. Separate analyses showed that these results were not due to differences in retinal speed of tracked and untracked rows and were due solely to attention. Based on: Khurana, B. and Kowler, E. (1987). Shared attentional control of smooth eye movements and perception. *Vision Research 27*, 1603-1618.
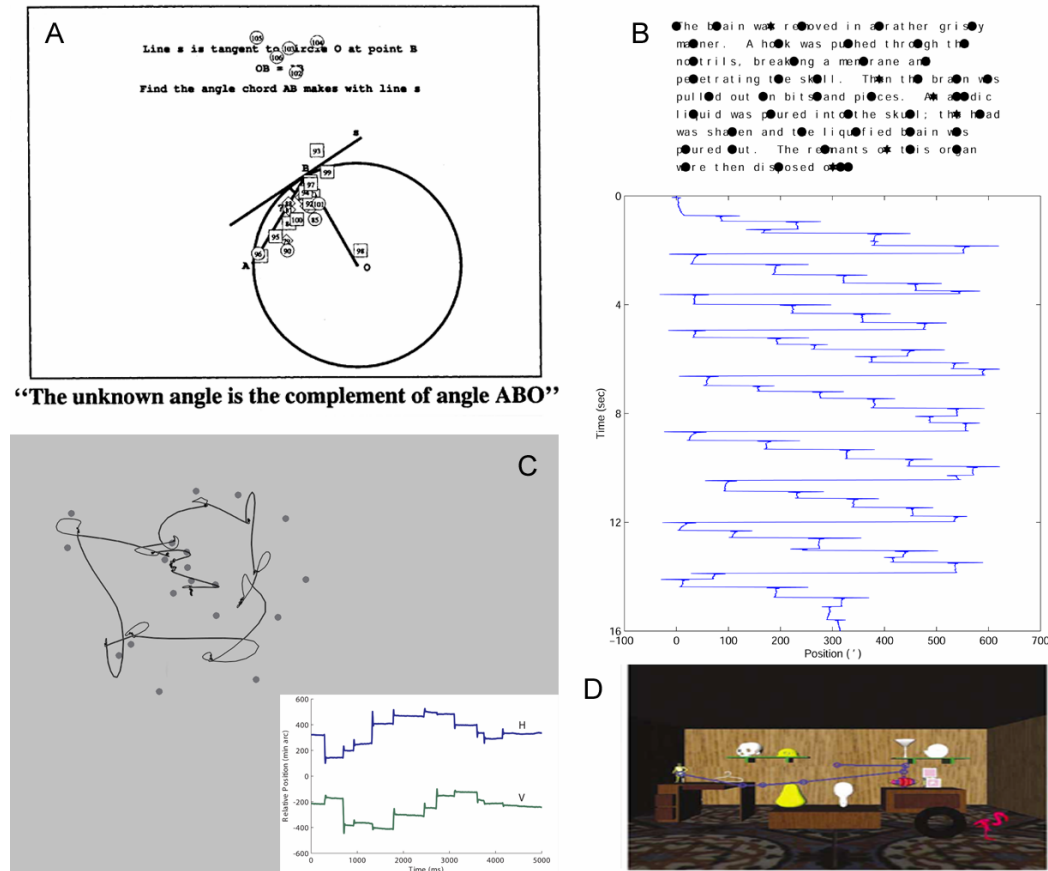
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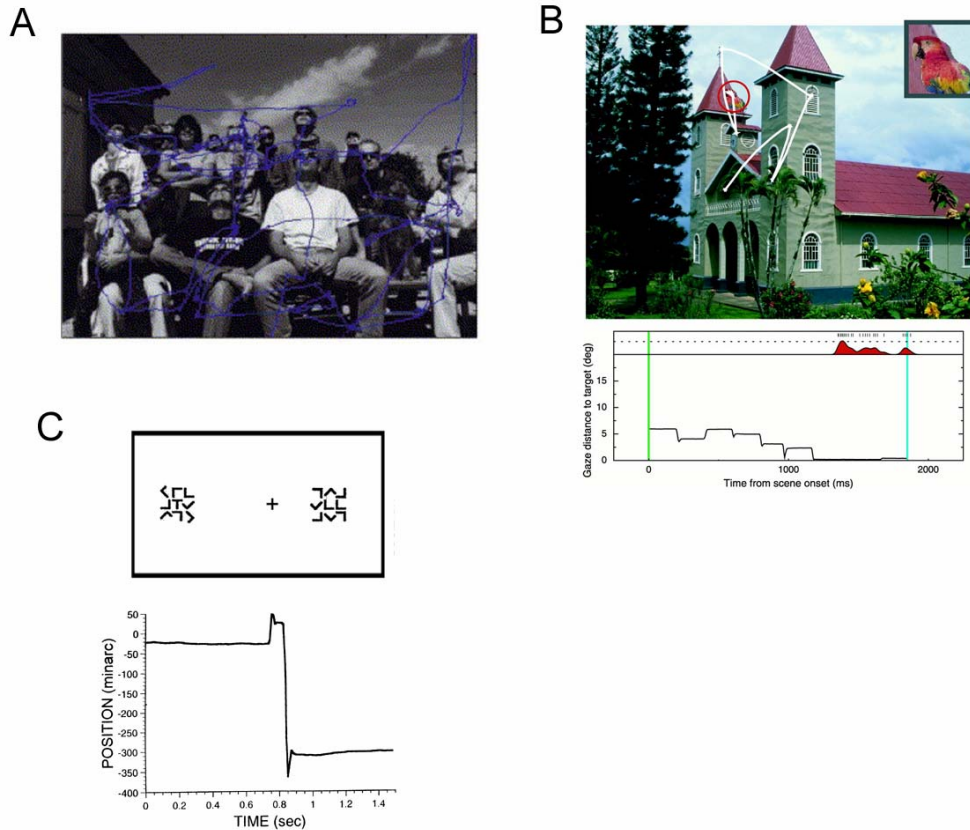
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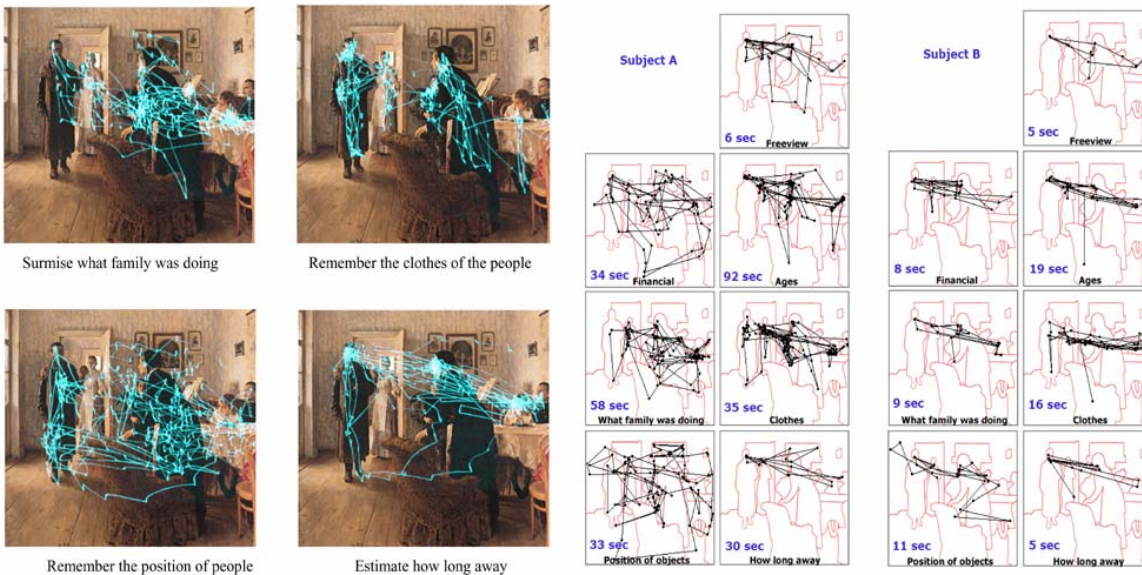
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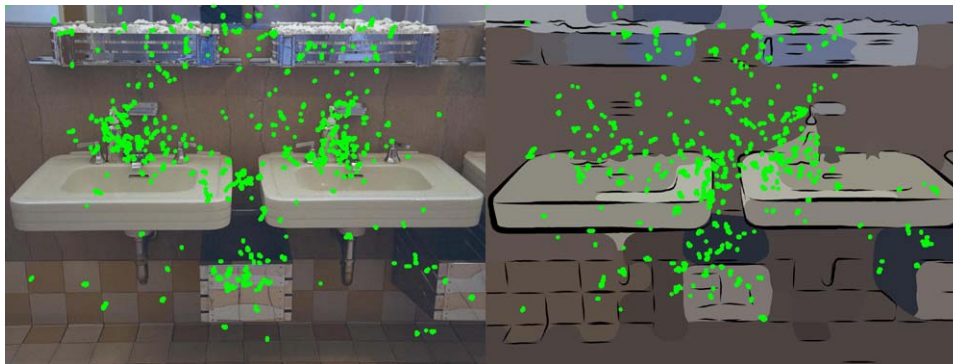

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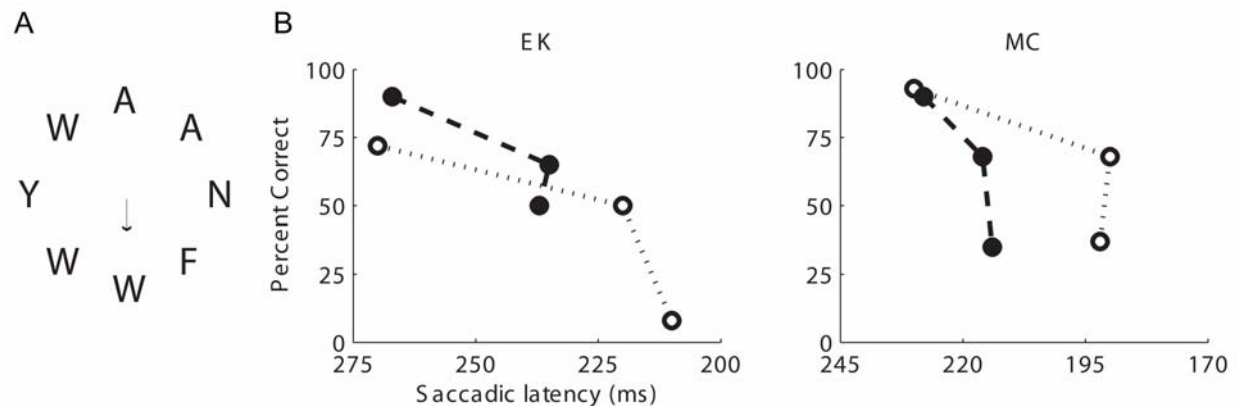
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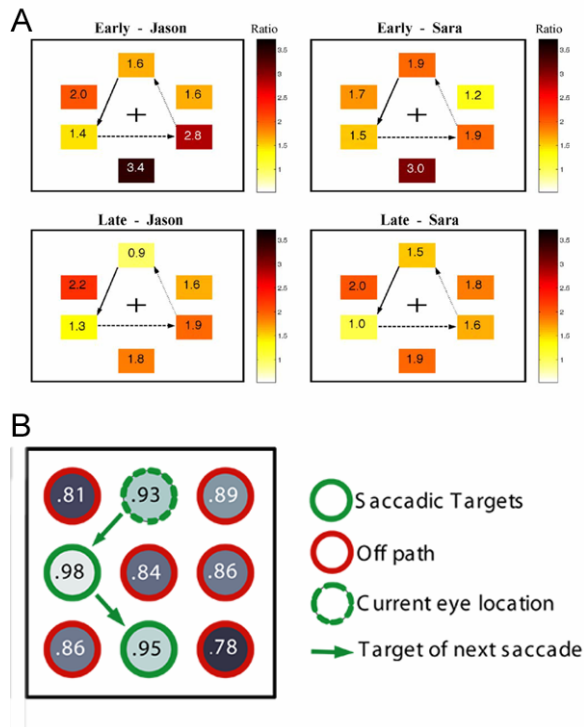
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