

Attention in Active Vision: A Perspective on Perceptual Continuity Across Saccades

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Abstract

Alfred L. Yarbus was among the first to demonstrate that eye movements actively serve our perceptual and cognitive goals, a crucial recognition that is at the heart of today's research on active vision. He realized that not the changes in fixation stick in memory but the changes in shifts of attention. Indeed, oculomotor control is tightly coupled to functions as fundamental as attention and memory. This tight relationship offers an intriguing perspective on transsaccadic perceptual continuity, which we experience despite the fact that saccades cause rapid shifts of the image across the retina. Here, I elaborate this perspective based on a series of psychophysical findings. First, saccade preparation shapes the visual system's priorities; it enhances visual performance and perceived stimulus intensity at the targets of the eye movement. Second, before saccades, the deployment of visual attention is updated, predictively facilitating perception at those retinal locations that will be relevant once the eyes land. Third, saccadic eye movements strongly affect the contents of visual memory, highlighting their crucial role for which parts of a scene we remember or forget. Together, these results provide insights on how attentional processes enable the visual system to cope with the retinal consequences of saccades.

Keywords

eye movement, visual attention, transsaccadic, remapping, visual memory, visual stability, priority

Introduction

Vision begins with the retinal image—a changeful ocean of light and darkness covering the back of the eyes. In the middle of that ocean sits the fovea, densely packed with small sensors that capture every ripple in the water, every shade of color. The waters in the distance remain largely mysterious, charted only by a coarse radar. Until we need a closer look. Suddenly the eyes jerk into a new position, sweeping the image across the retina. Like a nippy boat, the fovea cuts across the ocean in these rapid voyages of conquest called saccades, before it rests again.

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Yarbus (1967) was one of the pioneers who recognized this inquisitive nature of the human gaze. By recording observers' eye movements while looking at paintings, he showed that the fovea's itinerary across the retinal image is not random—it depends largely on the nature of the observer's task. In a search task like *Where is Waldo*, the objective is clear—find the big-eyed fellow with the red and white striped shirt and bobbled hat—and the fovea will target parts of the busy scene that contain the critical features. Yarbus showed that similar observations can be made when a target is not defined explicitly. To stick with his choice of Russian paintings, consider *Morning in the Pine Forest* (Figure 1(a)). A task like finding the bear with the lightest fur will cause eye movements to scan the image quite systematically, going back and forth between the bodies of the cubs and their mother (Figure 1(b)). In contrast, in the absence of an explicit task, the eyes' itinerary may look quite different (Figure 1(c)); nevertheless, our nature is curious enough to send the fovea across the image, exploring a scene that may ultimately be inconsequential for behavior.

Rapidly placing the fovea on different parts of the image thus allows us to process relevant visual information quickly, cheaply, and in incredible detail, while avoiding the overhead of processing the entire scene at a high resolution at all times. But the eyes' hasty trips come with a number of challenges to the visual system. My current list contains five such challenges:

- (1) *Ignoring intrasaccadic smear.* As the retinal image dashes across the back of the eyes, the receptors' sluggish response causes them to average signals from all locations in the image they travel past. The resulting streaky and greyed out intrasaccadic input is rarely perceived. Some researchers have argued for an active suppression of incoming motion signals around the time of a saccade (e.g., Burr, Morrone, & Ross, 1994). Others have shown that masking from the pre- and postsaccadic input is sufficient to eradicate any percept of intrasaccadic motion or smear (e.g., Castet, 2002).

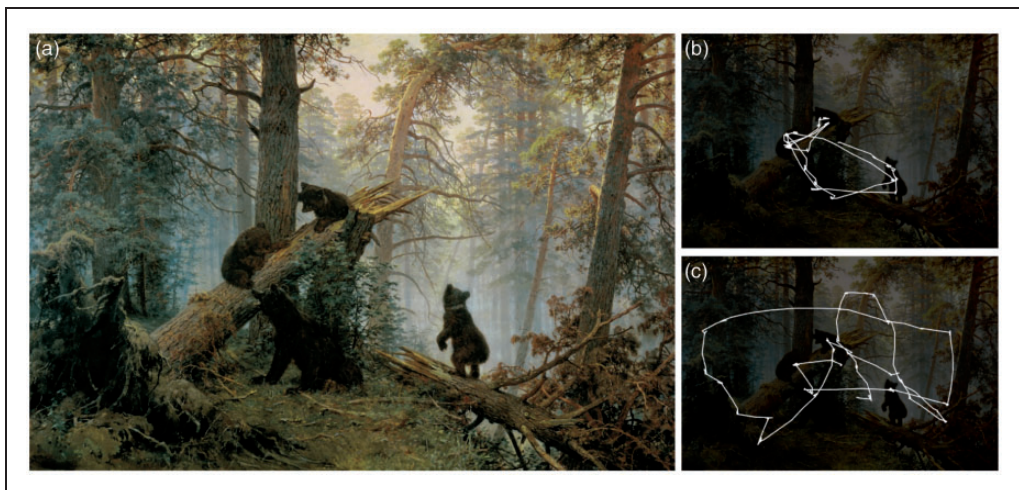


Figure 1. Eye movements across *Morning in the Pine Forest* (1889) by the Russian artists Ivan Shishkin (who drew the scenery) and Konstantin Savitsky (who drew the bears). (a) Original stimulus. (b) An observer's scan path across the image while finding the bear with the lightest fur. (c) The same observer's eye movements during free exploration of the scene.

- (2) *Bridging temporal gaps.* Saccades are fast, yet each time they take the fovea to a new location, the stream of input to the visual system is disrupted for a brief moment. We do not usually experience these discontinuities, but the stopped-clock illusion illustrates this phenomenon: When you make a saccade to a clock face, the second hand sometimes appears to stick to its location for more than a second. The visual system appears to bridge these gaps predictively, anticipating the visual consequences of the eye movement; indeed, subjectively, we think we are looking at the clock face before the eyes arrive there (Hunt & Cavanagh, 2009).
- (3) *Telling self-motion from world motion.* The changes in retinal input around the time of a saccade are, in principle, compatible with two very different scenarios. Either the eyes moved, dragging the retina across the image, or the entire world moved while the eyes remained stationary. The challenge to find out what actually happened is ubiquitous in any spatial sensory modality, including audition and touch. Efference copy signals—that is, copies of the motor command that can be used to generate predictions about the visual consequences of eye movements—may help resolving this dichotomy. This idea goes back to von Helmholtz (1867): Motion is seen only if there is a (large) discrepancy between the motion on the retina and the motion expected from a saccade.
- (4) *Keeping track of where things are.* As the eyes move across the scene in a sequence of fixations, the fovea is placed on different parts of the scene (Figure 2(a)). With each saccade, the objects in the scene are displaced in the direction opposite the saccade, such that the same stimulus will be processed by very different parts of the retina (Figure 2(b)), and thus, very different parts of any retinotopically organized brain area (i.e., most stages of visual processing). A major challenge for the visual system, therefore, is to know at any point in time where the currently relevant objects are both on the retina (so we can look at them or process them attentively) and in the world (so we can grasp, point at, or walk toward them).

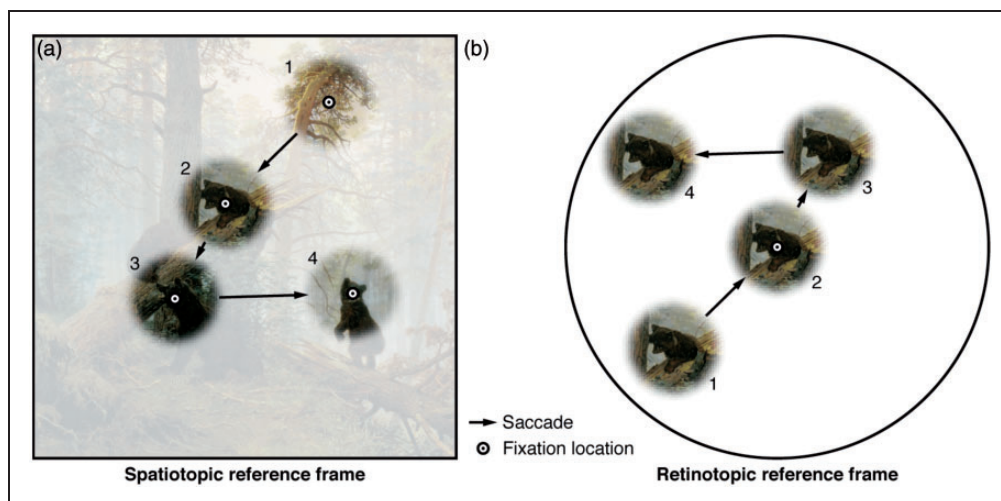


Figure 2. Retinotopic consequences of saccadic eye movements. (a) As the eye moves, the fovea visits a number of locations in the image. (b) During this sequence of fixations, the same object (here, the bear cub in the center of the image) will fall on very different parts of the retina.

- (5) *Keeping track of what was there.* Knowing the locations of the relevant items in a scene solves part of the problem of perceptual continuity across saccades. However, the relevant locations must be linked to the identities of the currently relevant targets. We have called this the hard binding problem (Cavanagh, Hunt, Afraz, & Rolf's, 2010): How does the visual system attribute the same identity to a target that changes locations with every flick of the eyes? Even for a single relevant object in the scene, when the association between its location and its identity may seem straight forward, assigning object identity is challenged by the largely different patterns of retinal stimulation resulting from the retinas heterogenous resolution (Herwig & Schneider, 2014).

The findings reviewed in this article have implications for all of these challenges, but the focus of my discussion will be on the last two. In particular, I will argue that an understanding of the relation between eye movements and visual attention is fundamental to comprehending how the visual system knows where things are and what is there. First, I will present the results of studies investigating how the preparation and execution of saccadic eye movements affect the selective allocation of visual attention and, thus, what we see. Second, I will review evidence suggesting that perceptual continuity is a result of updating the landscape of spatial attention every time we prepare a saccade. Finally, I will argue that presaccadic attention creates a natural bottleneck for visual memory across saccades, protecting identity information for targets and discounting it elsewhere. Together, these results provide a perspective on transsaccadic vision in which perceptual continuity is achieved by continuously prioritizing visual information at currently relevant locations in the scene.

Preconditions for Transsaccadic Vision

An early view of perceptual continuity across saccades proposed that the brain reconstructs a representation of the world. By compensating for the saccadic shifts of the retinal image, information from subsequent fixations could be fused into a coherent spatiotopic code of what is out there. Spatiotopic representations are mapped in a world-centered coordinate system and are thus immune to the challenges associated with jerky retinal input resulting from saccades.

The earliest tests of this idea involved the presentation of two half patterns (Figure 3(a)), one before a saccade (presaccadic stimulus) and the other after (postsaccadic stimulus), with the following rationale: If the visual system integrates the two halves of the patterns, the observer should be able to identify the complete pattern once the eyes land and see the second half. Observers fail miserably at this task (Bridgeman & Mayer, 1983; Irwin, Yantis, & Jonides, 1983; O'Regan & Lévy-Schoen, 1983; Rayner & Pollatsek, 1983), even if they had excelled when no saccade intervened between the two presentations (Figure 3(b)). Indeed, it seemed as though fragile traces of the scene in visual memory were entirely erased during the execution of a saccade (Irwin, 1991; see *Paying attention to what was there* section for an update on this issue).

Later tests of spatiotopic representations of visual feature information tested the reference frame of early visual processes such as feature integration and visual adaptation. Indeed, some authors found evidence for transsaccadic spatiotopic motion integration (Melcher & Morrone, 2003), and for world-centered negative aftereffects following adaptation to motion (Ezzati, Golzar, & Afraz, 2008), duration (Burr, Tozzi, & Morrone, 2007), tilt, form, and faces (Melcher, 2005). Unfortunately, more often than not other authors could not replicate

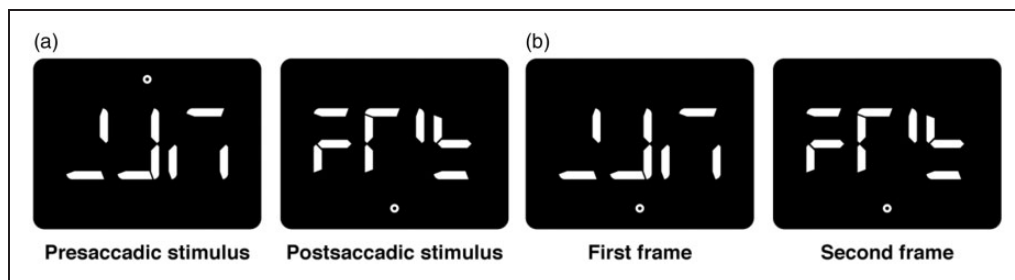


Figure 3. Testing visual fusion of temporally segregated patterns. (a) In a test of spatiotopic fusion, the observer sees one part of a stimulus before a saccade (presaccadic stimulus) and the other part upon saccade landing (postsaccadic stimulus), at the same screen location. Observers' performance is very poor in this condition. (b) If the two half patterns are presented in the same temporal sequence but without an intervening saccade (hence, at the same retinal location), observers have no problem recognizing the entire pattern (here, the number 2015 in an LCD display font). Indeed, by moving the eyes back and forth between the two fixation spots in panel (b), retinotopic afterimages may allow the reader to see the fused version of the patterns.

these findings, or pointed out control conditions that—if tested—led to the opposite conclusions. As a consequence, for each of the original studies, there is at least one other that contests the finding of spatiotopy and instead supports fully retinotopic processing (motion integration: Morris et al., 2010; motion adaptation: Knapen, Rolfs, & Cavanagh, 2009; Turi & Burr, 2012; Wenderoth & Wiese, 2008; tilt adaptation: Knapen, Rolfs, Wexler, & Cavanagh, 2010; Mathôt & Theeuwes, 2013; Morgan, 2014; face adaptation: Afraz & Cavanagh, 2009; duration adaptation: Bruno, Ayhan, & Johnston, 2010; Latimer, Curran, & Benton, 2014). While these discrepancies cast a shadow on the field in general, current efforts are trying to understand their origin (see Zimmermann, Morrone, & Burr, 2014). New studies explore the reference frame of other visual processes at a regular pace (e.g., Arrighi, Togoli, & Burr, 2014; Nakashima & Sugita, 2014), and the last word may well depend on the specific process in question (e.g., Turi & Burr, 2012). For now, the idea of a representation of visual features in explicit spatiotopic maps is based on unsteady empirical footing; if they exist, these representations may not be robust enough to support perceptual continuity (see Burr & Morrone, 2012, for a different view).

Indeed, there is no need (or even no use; see O'Regan, 1992, for a persuasive discourse) for compensating for the retinal consequences of eye movements, or the existence of an explicit world-centered representation of the visual scene. The visual scene is generally available at any point in time and vision can prioritize the processing of the scene's currently relevant parts over others. These selective processes, which we refer to collectively as attention, enable the visual system to deal with the abundance of information entering the eyes. Beyond orienting the fovea toward new locations in the scene (i.e., overt attention), they include covert processes that regulate processing up and down for any given location, feature, or object on the retina (see Carrasco, 2011, for a review). The most striking demonstration of the critical role of attention in visual perception comes from two phenomena that capitalize on its absence—change blindness (Rensink, O'Regan, & Clark, 1997) and inattention blindness (Rock, Linnett, Grant, & Mack, 1992). Change blindness is the failure to notice even salient changes in a visual scene, an ability that relies to some extent on visual memory (Simons & Rensink, 2005). In contrast, inattention blindness is the inability to notice an object to begin with, which occurs even for high-contrast stimuli presented right in foveal vision (Mack & Rock, 1998). Of course, change blindness and inattention blindness do not rule

out detailed visual representations of the visual scene, but they reveal how strikingly continuous perception is even in the presence of salient changes in the visual input. The key to this continuity is the deployment of attention, foreshadowing a key role of covert attention in transsaccadic perception.

Goal-Directed Movements Shape Visual Priorities

Fixation of attention directed towards an element of a stationary object is accompanied by fixation of the gaze.

(Alfred L. Yarbus, 1967)

Indeed, it turns out that covert attention is strongly intertwined with the control of saccadic eye movements. A large body of evidence makes a strong case that attentional selection of the target of a saccade begins before the eyes start moving to their new position (see Zhao, Gersch, Schnitzer, Doshier, & Kowler, 2012, for a review). This presaccadic attention shift can be revealed using observers' performance in difficult visual discrimination tasks: Observers identify stimuli more accurately if they appear at the goal of a saccadic eye movement than if they appear at any other locations in the display (Deubel & Schneider, 1996; Kowler, Anderson, Doshier, & Blaser, 1995; White, Rolfs, & Carrasco, 2013), independent of whether the saccade was willfully planned or triggered involuntarily by a salient visual event (Peterson, Kramer, & Irwin, 2004). In an actively behaving observer, therefore, visual selection and the planning of saccadic eye movements go hand in hand.

Thanks to the dedicated work of a number of research groups, the neurophysiological mechanisms underlying the link between attention and saccades is rather well understood. To illustrate these mechanisms, consider an observer looking at the picture presented in Figure 4(a). Figure 4(b) shows an (admittedly, greatly simplified) outline of the observer's

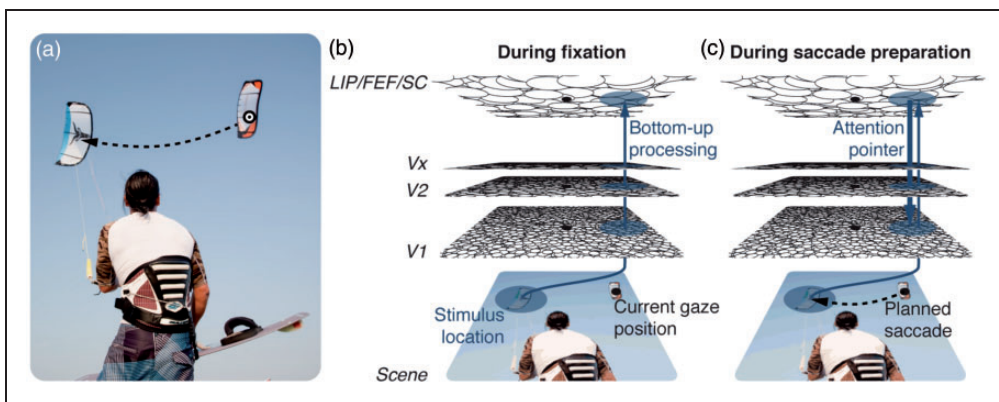


Figure 4. The concept of attention pointers. (a) A visual scene of a kite surfer with an observer's fixation on the red kite; the blue kite will be the target of the next saccade. (b) Outline of a hierarchy of visual areas processing the scene, each organized in retinotopic coordinates. Early stages (V1, V2, through Vx) encode the visual features present at each location (say, the orientation, motion, or color of the blue kite). The map displayed at the top (LIP/FEF/SC) encodes the current priority (i.e., the combination of salience and behavioral relevance) for each part of the scene. (c) If a stimulus becomes behaviorally relevant (here, the blue kite is the target of the next saccade), activity increases at the corresponding location in the priority map and triggers a feedback signal to earlier visual areas. Activity in the priority map can thus be viewed as an attentional pointer, indexing relevant locations in other retinotopic maps. See text for details.

visual system, organized in a layered hierarchy of visual areas, processing the picture shown at the bottom. Each layer in the hierarchy encodes certain aspects of the visual stimulus (e.g., orientation in Layer V1; contours in Layer V2, etc.). While receptive fields tend to increase in size with every layer, each of them is retinotopically organized—that is, adjacent locations in the image are encoded by adjacent populations of neurons in the map. If the observer is looking at the red kite in the upper right corner of the image, the blue kite will be to the left of fixation and—due to the crossed mapping of visual hemifields onto cortical hemispheres, starting in the optic chiasm—be processed to the right of the foveal representation at each level of the system. At the top of this hierarchy is a priority map, a layer that is agnostic to the visual features at a given position in the image. Instead, it integrates bottom-up saliency in the image—how conspicuous each part of the image is across a number of feature dimensions—with the current behavioral relevance of that part of the image. Activity in this priority map, it turns out, is tightly linked to the preparation of goal-directed eye movements (Fecteau & Munoz, 2006).

Several visual areas behave like priority maps, including the frontal eye fields (FEF), the lateral intraparietal area (LIP), and, at the subcortical level, the superior colliculus (SC). Each of these areas is tightly linked to the generation of eye movements, such that electrical stimulation of a local population of neurons will generate a stereotypical saccade targeting the location of the neurons' receptive (or movement) fields. Their causal contribution to the control of covert attention has been established in a series of elegant electrophysiological studies. First, microstimulation (below the threshold that would generate a saccade) in FEF and SC increases visual performance selectively at the corresponding location in the scene (Cavanaugh & Wurtz, 2004; Moore & Fallah, 2001, 2004; Müller, Philastides, & Newsome, 2005). Second, reversible inactivation of LIP, FEF, and SC results in spatially constrained covert attention deficits (Balan & Gottlieb, 2009; Lovejoy & Krauzlis, 2010; Wardak, Ibos, Duhamel, & Olivier, 2006; Wardak, Olivier, & Duhamel, 2004; Zénon & Krauzlis, 2012). And finally, sub-threshold microstimulation in FEF results in an increase in the visual responsiveness of neurons in earlier visual areas (Armstrong & Moore, 2007; Moore & Armstrong, 2003). The resulting boost in the encoding of visual information at the corresponding location resembles the consequences of saccade preparation on processing in these areas (e.g., Moore, Tolias, & Schiller, 1998).

On the basis of these findings, several authors have proposed a mechanism for presaccadic attention shifts (Armstrong & Moore, 2007; Bisley, 2011; Cavanagh et al., 2010; Hamker, 2005; e.g., Moore & Armstrong, 2003): During saccade preparation, activity builds up at the target location in the priority map. This sub-threshold activity triggers a feedback signal that facilitates processing at that part of the retinotopic map in earlier visual areas, resulting in performance benefits that are spatially confined to the target region (Figure 4(c)). In this framework, activity in the priority map can be viewed as a location index to relevant locations, and we refer to these indexes as attention pointers (Cavanagh et al., 2010).

Interestingly, in a seminal review paper, Reynolds & Chelazzi (2004) pointed out a striking similarity between the changes in visual responses of neurons that result from a deployment of attention to a stimulus, to those resulting from an increase in the stimulus' physical contrast. The linking hypothesis that a deployment of attention is perceptually comparable to an increase in stimulus contrast (Treue, 2004) has indeed received strong empirical support (e.g., Carrasco, Ling, & Read, 2004). Inspired by these findings, we designed a psychophysical study to address if movement preparation indeed affects sensory processing by integrating visual salience and behavioral relevance. Specifically, we asked whether saccade preparation results in an increase in perceived contrast of visual stimuli at the target of the eye movement as the saccade onset approaches.

To approach this question, we developed a paradigm in which observers compared a test stimulus presented at different times during the preparation of a saccade, to a standard stimulus presented some time before a movement cue was available and, therefore, before saccade planning could be initiated (Figure 5(a)). Critically, the test stimulus—an oriented grating—differed from the reference in two ways (Figure 5(b)). First, its orientation was slightly tilted clockwise or counterclockwise; second, its contrast was either higher or lower than that of the standard stimulus. By asking subjects to report both differences in a single button press (Figure 5(c)), we obtained an objective measure of visual performance (orientation discrimination) and a subjective report of stimulus intensity (perceived contrast), on each trial. We compared subjects' reports in this presaccadic condition to a

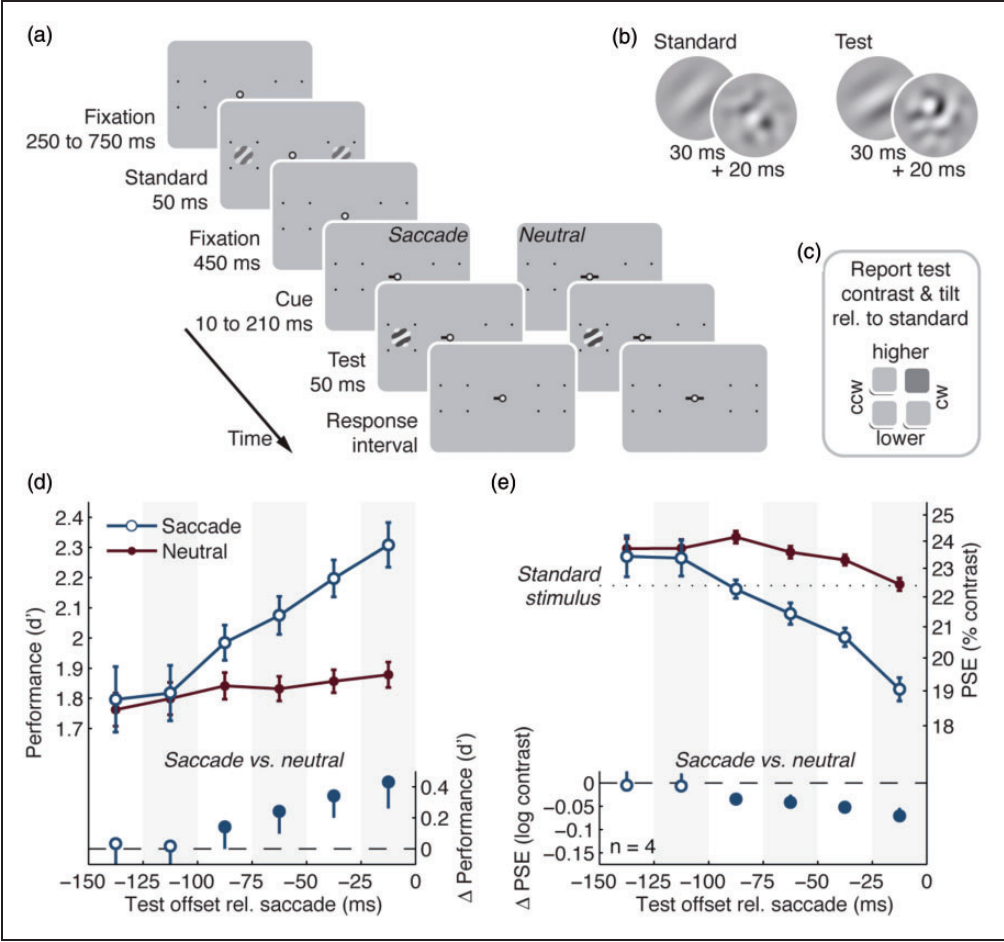


Figure 5. Objective and subjective changes in visual perception go hand in hand during saccade preparation. (a) Trial procedure used to assess simultaneously changes in orientation discrimination performance and perceived contrast before saccades. (b) Standard and test stimuli were oriented gratings that differed in both contrast and orientation. (c) On each trial, and in a single button press, observers reported how the test stimulus differed from the standard stimulus on these two dimensions. (d, e) Presaccadic time course of orientation discrimination performance (d') and the test contrast needed to equate the standard stimulus contrast (point of subjective equality, PSE). (Adapted with permission from Rolfs & Carrasco, 2012.).

fixation condition, in which a neutral cue instructed observers to keep fixation in the center of the screen throughout the trial.

The experiment yielded two remarkable results. First, performance in the orientation discrimination task increased rapidly over the last 100 ms before a saccade (Figure 5(d)). Indeed, this increase in performance was evident within 60 ms of the presentation of the movement cue and, therefore, much faster than expected from a willful deployment of covert attention following cue onset. Moreover, as performance increased at the target location, so did the subjective impression of stimulus strength: As time approached a saccade, the contrast of the test stimulus necessary to equate that of the standard stimulus decreased continuously (Figure 5(e)). Therefore, during saccade preparation, an increase in the subjective intensity of the stimulus at the target location accompanied the well established boost in objective perceptual performance. This increase in subjective stimulus strength may thus be a direct perceptual correlate of visual priority (defined as the combination of physical contrast and current behavioral relevance). In combination with the results of the physiological literature reviewed above, the case can be made that before a saccade, vision prioritizes those parts of the scene that are relevant to the movement.

While visual processing is inextricably linked to eye movements, its relation to other effector systems could be less direct. Nevertheless, selective visual processing has also been observed before other types of goal-directed movements, including reaching (Deubel, Schneider, & Paprotta, 1998) and grasping (Schiegg, Deubel, & Schneider, 2003). However, there are a number of findings that suggest differences in the consequences of reach preparation and saccade preparation. First, results from behavioral studies (Jonikaitis & Deubel, 2011) suggest that performance benefits before reaches may draw on different attentional resources than presaccadic attention shifts (but see Khan, Song, & McPeck, 2011). Second, attention can be withdrawn from reach targets (but not from saccade targets) once the movement has been prepared (Deubel & Schneider, 2003). Finally, reach preparation may rely on different priority maps than saccade preparation. Indeed, in the parietal cortex, LIP is involved in saccade preparation, whereas the parietal reach region is involved in the preparation of reach movements (Snyder, Batista, & Andersen, 1997). While parietal reach region is also retinotopically organized, its relation to visual selection has yet to be established. In FEF, where a clear relation to attention has been established, visual neurons encode remembered target locations for saccades, but not for reaches (Lawrence & Snyder, 2009). Yet, other areas (e.g., the SC) may encode priority irrespective of the specific effector (Song, Rafal, & McPeck, 2011).

To shed more light on this multifaceted picture, we translated the experimental design of our saccade task (Figure 5) into a study of goal-directed reaches (Rolfs, Lawrence, & Carrasco, 2013). In this study, observers kept fixation at the center of the screen, while a central cue instructed them to move the index finger as quickly as possible from the center of a touch screen device to a peripheral target location. We presented the test stimulus at the movement target (as in Rolfs & Carrasco, 2012), or at the opposite location. In line with previous studies (Deubel et al., 1998), we found a reliable performance difference in the orientation discrimination task—observers were more sensitive at the movement target location than at the opposite location, but this relative benefit was not locked in time to the onset of the movement (see also Deubel & Schneider, 2003). Moreover, in the course of reach preparation, stimuli presented at the movement target appeared increasingly higher in contrast than stimuli presented at the opposite side of fixation.

Thus, the preparation of goal-directed movements—saccades and manual reaches—reliably alters subjective visual experience and objective visual performance, supporting the linking hypothesis that movement preparation alters effective signal

strength in the visual system. Indeed, this goal-directed enhancement of sensory processing is not limited to the visual domain (e.g., van Ede, van Doren, Damhuis, de Lange, & Maris, 2015) and may thus represent a general strategy of the nervous system to emphasize currently relevant information over inconsequential input.

Keeping Track of Where Things Are

The image is then seen as stationary, and a large enough saccade is always perceived as a change of the points of fixation (transfer of attention) on a stationary object.

(Alfred L. Yarbus, 1967)

Above, we considered the retinotopic nature of the visual system, arguing that attentional benefits at the target of eye movements arise from a peak of activity in a priority map. This activity, in turn, provides an attention pointer to the corresponding retinotopic location in earlier visual areas, enhancing visual responses to stimuli in that target region (Figure 4(c)). Indeed, there is strong evidence that, natively, attention operates in a retinotopic reference frame (e.g., Golomb, Chun, & Mazer, 2008). That being the case, however, how does the visual system keep paying attention to where things are in the world? If with every eye movement, the objects of interest fall on new parts of the retina, while the attentional signals remain in the same location in retinotopic coordinates, how do we keep track of these objects' locations in the world?

The answer to this fundamental question has been inspired by a neurophysiological finding, originally published by Duhamel, Colby, and Goldberg (1992). They recorded from neurons in area LIP of the macaque cortex. For each neuron, they characterized a classical visual receptive field, which are relative large in LIP but still highly spatially specific in retinotopic coordinates. It was quite a surprising finding, therefore, that if the monkey prepared (and executed) a saccade, these neurons started responding to stimuli at the postsaccadic location of the receptive field. Neurons in LIP thus appear to anticipate the visual consequences of the eye movement. This finding is now commonly known as predictive remapping and, from the outset, it has been linked to perceptual continuity across saccades (Duhamel et al., 1992).

As pointed out earlier, LIP is a key area in the control of visual priority, and similar results have been obtained in other potential priority maps, including the SC (Walker, Fitzgibbon, & Goldberg, 1995) and the FEF (Umeno & Goldberg, 1997). Moreover for LIP, there is evidence that the predictive response of a neuron scales the priority of its future location (Mirpour & Bisley, 2012). Significant increases in neural activity are observed only for locations that are currently attended, either as movement targets or because they are visually salient (Gottlieb, Kusunoki, & Goldberg, 1998).

On the basis of these findings, we hypothesized that as priority maps update before saccadic eye movements, so should attentional pointers (Cavanagh et al., 2010). Consider an observer preparing a sequence of two saccades across the image of the kite surfer, first from the red to the blue kite, then on to the kite handles (Figure 6(a)). During the preparation of this movement sequence, both saccade targets would be attended (Baldauf & Deubel, 2008; Gersch, Schnitzer, Sanghvi, Doshier, & Kowler, 2006; Godijn & Theeuwes, 2003), providing the corresponding attentional pointers (for clarity, Figure 6(b)–(c) focus on the pointer for the second target). An efferent copy signal of the imminent saccade (Sommer & Wurtz, 2008) would then update the priority map, shifting the attention pointer to its postsaccadic location in retinotopic coordinates (Figure 6(b)). For a brief moment before saccade onset, this updated retinotopic location corresponds to an irrelevant location in space (Krauzlis

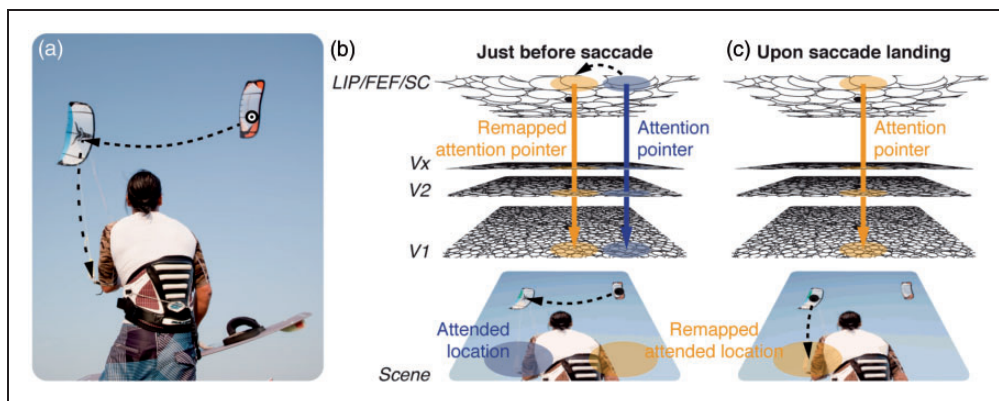


Figure 6. Updating attention pointers across saccades. (a) The observer plans a sequence of two saccades, the first to the blue kite, the second to the kite handles. (b) The second saccade target is attended prior to the first saccade. Just before the execution of the first movement, the priority map is updated, increasing the activity of neurons that will process the attended location after the eye movement. This predictive remapping results in a new attention pointer, indexing the postsaccadic retinal location of the second target. (c) As a consequence, attention is at the relevant location in the scene (at the kite handles) as soon as the eyes land. Conventions as in Figure 4. See text for details.

& Nummela, 2011), where it should be evidenced by an increase in visual performance (Figure 6(b), “Remapped attended location”). The benefit of this predictive remapping is that attention will be at the relevant location in space at the moment the eyes land (Figure 6(d)), facilitating the visual processing at the second saccade target, and ultimately the movement itself. In a series of studies, we found strong support for this scenario.

In the first of these studies (Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011), we developed a paradigm that allows mapping visual performance at a fine temporal scale (Figure 7(a)). Specifically, we instructed observers to make a sequence of two saccades in an array of visual stimuli, first to a cued stimulus location and then to a neighboring one. Each location in the array contained a flickering stream of vertical Gabors, rapidly alternating with noise patches. On every trial, and at some point during saccade preparation, one of the Gabors briefly changed orientation, allowing us to probe visual performance at that location and presaccadic moment. Critically, as the probe itself was embedded in a flickering stream, its onset transient did not interfere with saccade preparation. Using this setup, we were able to track the dynamic deployment of attention across the array as the observer planned a sequence of two saccades. We found that performance increased sharply at both the first and, to a lesser degree, the second saccade target over the course of 200 ms before the saccade (Figure 7(b)). Most importantly, just before saccade onset, performance increased at the remapped location of the second saccade target, providing evidence for a predictive deployment of attention to that target’s future retinotopic location.

Our results also revealed functional consequences of predictive remapping of attention. In particular, in a sequence of two saccades, the second movement was significantly faster on trials in which there was strong evidence for predictive updating of attention to the second target’s remapped location (as evidenced by correct reports of the orientation at that location before the first saccade) than on trials in which there was no such evidence (incorrect reports of the orientation at the remapped location before the first saccade). Thus, rapid updating of attention in retinotopic coordinates supports the generation of fast sequences of movements.

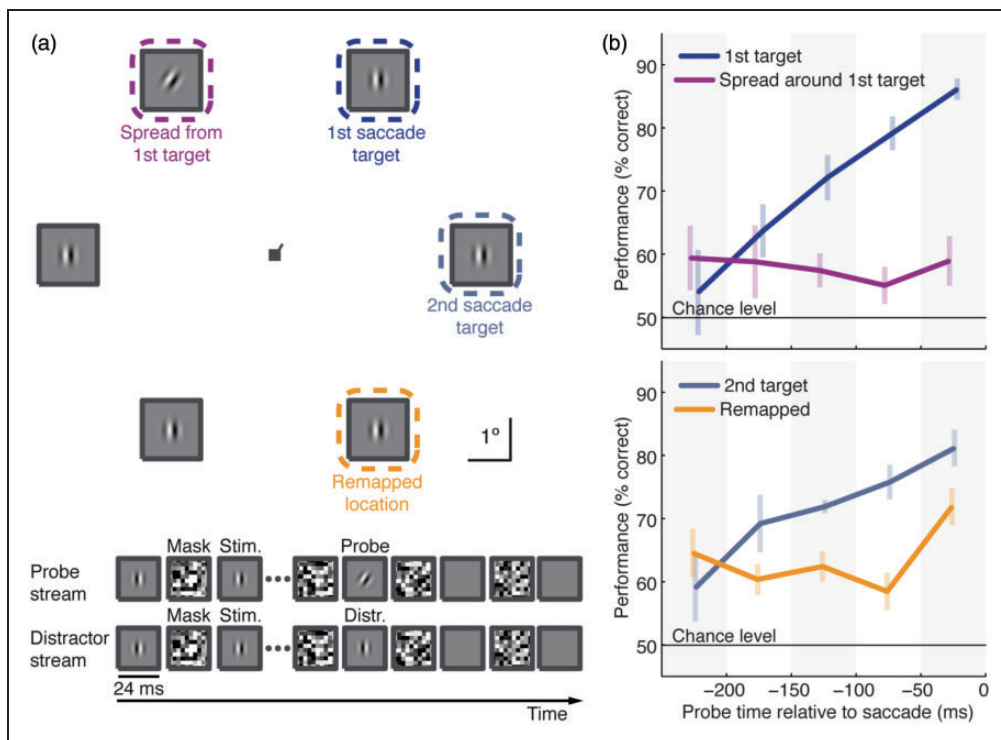


Figure 7. Probing remapping of attention. (a) Layout of the display in a two-step saccade task (first to the cued location, then to the next location in clockwise direction). Each location contained a flickering stream of gratings (embedded in noise). A brief change in the orientation of one of them probed the allocation of attention at different times before the first saccade. (b) Performance at the probe locations as a function of time before saccade onset. (With permission from Rolfs, Jonikaitis, Deubel, & Cavanagh, 2011.).

It keeps track of the targets of movements, but also of the locations of distractors across saccades (Jonikaitis & Belopolsky, 2014).

In a subsequent study, we extended the finding of predictive remapping of attention to the domain of transient attention (Jonikaitis, Szinte, Rolfs, & Cavanagh, 2013) and probed its consequences for the postsaccadic deployment of attention. In a series of two experiments, we drew observers' attention to a peripheral location using an irrelevant, colored flash. In line with our previous results (Rolfs et al., 2011), attention shifted to the remapped location of the flash briefly before saccade onset. Importantly, this presaccadic remapping of attention translated to a postsaccadic benefit at the spatiotopic location of the flash. That is, after the saccade, when the retinal coordinates of the remapped location coincided with the flash's location on the screen, the attentional benefit was apparent at the location in space that indeed contained the salient flash (Jonikaitis et al., 2013). These results add further substance to the idea that—beyond facilitating rapid sequences of movements—remapping supports perceptual continuity across the saccade.

From a certain perspective, these findings may appear to contradict earlier work showing that attention lingers in retinotopic coordinates even upon saccade completion (e.g., Golomb et al., 2008; Mathôt & Theeuwes, 2010). These studies found that if attention is allocated to a visual object before a saccade, it leaves a retinotopic trace even after the eyes have landed,

resulting in performance benefits at the retinal location the object initially occupied. Note, however, that predictive remapping of attention and a retinotopic trace both are the result of coding attended locations in retinotopic coordinates and, indeed, can co-occur in the same experimental setting (Jonikaitis et al., 2013). Nonetheless, at least two factors play role in whether attention is efficiently updated across a saccade. First, spatial updating of attention depends on the presence of visual objects following the eye movement (Lisi, Cavanagh, & Zorzi, 2015), such that spatiotopic attentional benefits occur only if an object is present upon saccade landing. Indeed, studies that failed to find updating of attention across saccades invariably removed the attended objects before saccade landing. Second, these studies often required observers to memorize attended objects willfully, over long periods of time (cf., Jonikaitis & Belopolsky, 2014). In contrast, studies that found predictive remapping of attention (or rapid updating of locations) used exogenous cues or defined saccade goals to attract attention involuntarily (and transiently), which may more readily activate the oculomotor system (Jonikaitis & Belopolsky, 2014).

Indeed, in the first two studies of predictive remapping of attention (Jonikaitis et al., 2013; Rolfs et al., 2011), we had investigated saccade preparation and transient (exogenous) attention because for these conditions there was strong evidence for remapping in the neurophysiological literature (Gottlieb et al., 1998). But what about locations that we track covertly while looking somewhere else? Some behavioral evidence suggests that endogenous shifts of covert attention play a minor role, as goal-directed eye movements largely restrict the voluntary allocation of attention to competing locations (e.g., Montagnini & Castet, 2007). However, in many everyday situations like fast-paced sports or driving, keeping track of objects in the periphery is essential. To better understand scenarios of this kind, we studied the deployment of attention when observers covertly tracked the location of an object moving in a predictable fashion across the display (Szinte, Carrasco, Cavanagh, & Rolfs, 2015). Specifically, we assessed observers' ability to discriminate brief pulses of coherent motion at any location along the object's motion path, using sensitivity in this task as an indicator of the observer's focus of attention. At any given time during fixation, observers' sensitivity peaked somewhat ahead of the tracked object's current location. In contrast, during saccade preparation, attention was reflexively drawn to the future retinal location of the tracked object, leaving its current spatial location (in the world) unattended. This result suggests that voluntary covert attention is not ineffective during saccade preparation. Instead, the visual system appears to trade off attentional resources, prioritizing being ready for new input once the saccade lands.

A curious side effect of the predictive remapping of attention is that, for a brief moment before a saccade, the visual system appears to process information at an irrelevant location—the remapped location that will become relevant only after the saccade (see also, Krauzlis & Nummela, 2011). It is unlikely that this additional focus of attention interferes with the generation of the saccade itself, because remapping occurs in the last moments before the saccade, when the saccadic system has committed to the next movement. However, under certain circumstances, this association of two locations with a single object may result in an integration of visual information across the two locations (W. J. Harrison, Retell, Remington, & Mattingley, 2013; Hunt & Cavanagh, 2011), as if the visual features from two locations were integrated into a single object (Pelli & Cavanagh, 2013). This “brief window of vulnerability” (Krauzlis & Nummela, 2011) may be the result of the temporal limits of spatial updating of attention in the visual system, and a small price to pay for the benefit of attending to the correct locations as soon as the eyes land.

The findings summarized here show that, before saccadic eye movements, attention remaps predictively from currently relevant locations in the world—the targets of

goal-directed movements, salient events, and voluntarily tracked visual objects—to their future locations in retinotopic coordinates. This updating of attention tracks relevant locations as the eyes move, facilitates perception and action after saccade landing, and thus supports continuity in perception and action.

Paying Attention to What Was There

Usually changes of attention remain in our memory, but not changes of points of fixation.
(Alfred L. Yarbus, 1967)

Transsaccadic updating of spatial attention is valuable, as it provides a way to cope with the retinal position changes of relevant objects across saccades. But knowing where things are only solves part of the problem of perceptual continuity in the face of eye movements. What is missing is how these relevant locations are tied to the identities of the relevant objects that inhabit these locations. This problem is particularly relevant if there are multiple relevant objects in the scene, and a one-to-one correspondence between identity and location is no longer possible. Thus far, we only understand part of this hard-binding problem (Cavanagh et al., 2010); to tackle it, we need to scrutinize the link between saccades and visual memory.

Indeed, the field looks back on a comprehensive series of studies establishing the features and intricacies of transsaccadic visual memory. In particular, the seminal work of David Irwin and colleagues has revealed that transsaccadic memory largely relies on visual short-term memory (VSTM), which is long-lasting and comparably robust, but of very limited capacity (Irwin, 1996). As a consequence of this focus on a limited number of objects in the scene, change blindness is very effective across saccades (Grimes, 1996; McConkie & Currie, 1996). It is interesting that, no matter how little they remember of the presaccadic visual scene (see also the discussion in *Preconditions for transsaccadic vision* section), observers are most likely to store information about the stimulus presented at the target of the saccade (Currie, McConkie, Carlson-Radvansky, & Irwin, 2000; Irwin & Zelinsky, 2002; e.g., McConkie & Currie, 1996). This dedication of memory resources to the current most relevant part of the scene is in a good position to support perceptual continuity for object identities across the eye movement. Moreover, it may serve motor functions, such as the fast corrective saccades, which are triggered when a saccade missed its target (Hollingworth, Richard, & Luck, 2008).

Neurophysiological research suggests that short-term storage of sensory information could be accomplished by brain areas and circuits that also encode the relevant stimulus feature in the first place (see Pasternak & Greenlee, 2005, for a review). This sensory recruitment hypothesis has recently found strong empirical support in studies of the human brain (Ester, Anderson, Serences, & Awh, 2013; S. A. Harrison & Tong, 2009; Serences, Ester, Vogel, & Awh, 2009; Xing, Ledgeway, McGraw, & Schluppeck, 2013). For instance, Harrison and Tong (2009) had participants maintain a memory of the orientation of a grating. Applying pattern classification techniques to data from concurrent functional magnetic resonance imaging, they were able to decode that orientation from recordings in early visual cortex.

Given these results, it seems possible (or, in fact, likely) that an attention pointer indexing the target of a saccade would not only enhance visual sensitivity at that location in the scene but may also boost memory of visual information that has disappeared from view, as long as retinotopic brain areas have been recruited to store their memory traces. While the literature on transsaccadic memory reviewed above might appear to confirm this prediction (memory is better for saccade targets than for other locations), these previous studies invariably probed observers' memory for stimuli that disappeared with the onset of the saccade. This procedure

leaves open the possibility that the memory benefit for the saccade target, as observed in these studies, results primarily from enhanced sensory encoding (see *Goal-directed movements shape visual priorities* section), not an impact of the saccade on the memory itself.

Ongoing research in our lab addresses this question directly. In a set of experiments that we presented at the 2014 meeting of the Vision Sciences Society (Rolfs & Ohl, 2014), we briefly presented an array of four oriented stimuli, one of which observers were asked to remember at the end of the trial. About half a second after the disappearance of the array, we presented a movement cue, instructing observers to quickly move their eyes to one of the four locations. Two specific experimental features are critical here. First, eye movement planning could only start some time after the array had disappeared from view, isolating the impact of the saccade on items held in visual memory at the time of saccade preparation. Second, observers were aware that the movement cue was not predictive of the probe location because memory was probed at the saccade target as often as at any other location in the display. Despite these facts, observers remembered an item more often when the location probed was congruent with the saccade target. In contrast, items seen at other locations were often forgotten. This relative advantage for the congruent location was highly spatially specific and largest soon after the disappearance of the visual array, when visual memory was in a volatile state, transitioning from iconic memory to the more robust VSTM (e.g., Gegenfurtner & Sperling, 1993). These results suggest that saccades actively protect fragile traces of visual information if that information appeared at the current behaviorally relevant location.

In summary, saccades strongly affect what we remember and what we forget, imposing spatial priorities on visual memory beyond sensory encoding. Indeed, signals originating in the oculomotor system appear to actively protect the memory of behaviorally relevant information across saccades. Little more survives the movement.

Conclusions

Saccades send the fovea on rapid trips, sweeping the image across the back of the eyes. Indeed, looking at the retinal input, the benefits of a foveate eye appear to come with a number of challenges for the visual system. Here, I have made the case that visual processing around the time of a saccade is ideally suited to overcome some of these challenges by prioritizing relevant information in the input stream, without the need of compensating for motion in the retinal image or constructing a spatiotopic representation of the visual scene.

This case was built mainly on three results. First, priority controls visual attention and is concerted with the planning and generation of goal-directed movements. Second, visual attention supports perceptual continuity across saccades by facilitating perception predictively at those retinal locations that will be relevant after the eye movement. Third, saccadic eye movements strongly affect the contents of VSTM, highlighting their crucial role for which parts of a scene we remember once the eyes have landed. I have suggested that retinotopic visual areas provide the crucial interface between attention, visual memory, and the oculomotor system, as they maintain the most relevant visual information and saccades directly affect their processing. Ultimately, saccades may establish the link between relevant locations and the identity of relevant objects in the scene, but solving this hard-binding problem is a prize to be won in the next decade.

Many more questions remain unanswered of which I can only name a few. How does the visual system deal with more complex movements (of the head, the torso, or the whole body) whose visual consequences may be less predictable? What roles do object-based and feature-based attention play in active vision? How is motion in the outside world incorporated in the

predictive shifts of attention accompanying eye movements? If we understand the deployment of attention across saccades, the fovea's voyages through the ocean of light on the back of our eyes may appear less of a challenge to the visual system than a look at the retinal image suggests.

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