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The Interplay of Visual Attention and Saccade Planning in Active Vision

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The Interplay of Visual Attention and Saccade Planning in Active Vision

by

Afsheen Khan

A dissertation submitted to the Graduate Faculty in Biology in partial fulfillment of the requirements for the degree of Doctor of Philosophy, The City University of New York

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The manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Abstract

by

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Advisors: Josh Wallman and Jonathan Levitt

Vision is a highly active process. When we view the world, we do not hold our eyes still, but constantly move them around in order to view the object or area of interest with the fovea (the region of the retina with the highest acuity). Saccades are the step-like movements that we most often employ for this purpose. In addition, our attention is constantly being covertly attracted or directed to points of interest. Combining these different aspects of viewing: visual processing, the orienting of attention, and eye movements can be referred to as ‘active vision’.

Most work on active vision or attention and saccades has concentrated on performance improvements preceding saccades, but relatively little is yet known about how attention affects later stages of saccade planning. That is the focus of this thesis. First we look at the temporal dynamics of the scaling of attention and what influence that attention scale exerts on the decision to make a saccade. We are able to infer the attention scale during individual trials from their saccade latencies. We find that the scale of attention changes very rapidly, and faster than previously reported. The remainder of the thesis concentrates on the effects of attention scale and locus on post-saccade adaptive processes: how the success of the current plan influences learning.

Saccades maintain their accuracy through an adaptive process, slowly to compensate for muscle weakening, or rapidly in a lab setting using intra-saccadic steps. Little is known about how covert attention interacts with this process. The second study of this thesis looks at how the scale of attention can affect the magnitude of saccade adaptation. We use a novel paradigm in
which the intrasaccadic steps change from trial-to-trial so that over many trials the displacement produces a sine wave pattern. We find that when attending to larger targets, there is proportionally greater adaptation than when attending to smaller targets. Finally, we demonstrate that the locus of attention at the end of a saccade contributes to the error signal for saccade adaptation. Instead of intra-saccadically moving the target in order to induce saccade adaptation, we present a distractor briefly after the saccade on the near side or far side of the target. By drawing attention away from the saccade target immediately after the saccade, the distractor is able to induce saccade adaptation. The magnitude of the saccade adaptation depends on the novelty of the distractor.

These experiments highlight the interplay between attention and saccades. Using novel paradigms, we show that the locus of attention can induce saccade adaptation, and that the scale of attention influences both the magnitude of saccade adaptation as well as the decision to move. While conventionally, saccade experiments are performed using very small stimuli, we see that using larger stimuli can greatly change saccade performance. Use of larger, more complicated stimuli as compared to simple spot targets is a step closer to natural viewing and very important to our understanding of active vision.
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Introduction

General Overview

Vision is very important for humans to gain information about the world, and consequently the area in the human brain devoted to vision is the greatest compared to all of the other senses. However, if we were to hold our eyes perfectly still, the visual perception of the world would fade due to the retina encoding changes in light intensity (the Troxler effect). Vision is therefore an inherently active process; microscopic movements of the eyes (or head) are constantly required to see at all. This dynamic visual input is increased further by very frequent (2-3 times per second) macroscopic step movements of the eyes to align our best central vision with targets of interest, known as ‘saccades’. In addition to all this overt action, our attention is constantly being covertly attracted to potential points of interest. The way we combine these different aspects of viewing, of vision, attention and eye movements is sometimes referred to as ‘active vision’. This term is also increasingly used to underline that our visual perceptual experience is created in an integrated, active way and that studying passive processes of the system can miss critical, essential features of the system.

Traditionally, vision, attention and saccades have been studied in very passive or simplified ways. For example, vision has often been studied in anesthetized animals, which has allowed researchers to precisely control where on the retina images were being presented. A tremendous amount has been learned from passive vision about the function of the visual cortex from the pioneering work by Hubel and Wiesel (1959) to more recent essential findings (e.g. Levitt and Lund, 1997). Anatomical studies have also provided much information about the structure of the visual system. One example is the development of the non-uniform distribution of cells of the human retina (Abramov et al., 1982) with the highest concentration of cones
located within the fovea, giving the highest acuity vision, and decreasing hyperbolically with eccentricity (Figure I.1).

![Figure I.1](image)

Figure I.1. (A) Distribution of rods and cones across the human retina relative to the fovea. (B) Visual acuity across the retina is highest at the fovea (the location with the greatest concentration of cones) and declines rapidly with distance (Rattner and Nathans, 2006).

Covert attention has often been studied while maintaining fixation, which isolates attentional processes, but this is not how we normally tend to explore the world. Visual attention is key in filtering of unwanted information as well as in target selection for eye movements. However, eye movements and covert attention have historically been studied in opposition to each other. Early eye movement research was performed in a very sparse, isolated manner with very simple stimuli. But, we make an eye movement to an object of interest, which is typically spatially extended and embedded in a richly cluttered visual array.

Because vision, attention and saccades are naturally interconnected in everyday viewing, the frequency of studying more active vision has been on the rise. The number of citations for papers about active vision has steadily been increasing since the 1960’s (Figure I.2).
Figure I.2. The number of citations for active vision has risen steeply since the 1990's.

Remarkably little is known as to the interplay of these aspects of active vision. For example, how is saccade planning affected by the scale of visual attention, and not just the more studied locus of attention? We will be looking at the interplay of these factors in three experiments.

We will highlight the influence of attention throughout each stage of saccadic eye movements planning (Figure I.3). In brief these stages are: (1) A pre-saccadic shift of attention that is involved with a target selection and choice of saccade goal. (2) Next, a decision to actually start the saccade must be made. In Chapter 1 we explore the temporal dynamics of the scale of attention, which influences the decision to start the saccadic eye movement. (3) A saccade is made. (4) Following the saccade itself, assessment of the accuracy of the saccade takes place. We study how both the scale of attention (Chapter 2) and the locus of attention at the end of the saccade (Chapter 3) influences accuracy assessment of saccades.
Overview of Attention

What is attention?

In a complicated visual environment such as driving down a highway, there is so much visual information all around us, but much of it is unhelpful for our task. The driver for instance does not need to pay attention to the beautiful fall colors of the trees on either side of the highway while the car is in motion, but to the traffic and the road signs. The observation that not all of the stimuli presented to us needs to be perceived, instead perceptual resources could be focused on particular stimuli, has been attributed to Aristotle (Hatfield and Wright, 1998). Attention filters unwanted information and enhances those objects that either draw attention or that are voluntarily focused on. Attention is a very broad process with so many different aspects to it. For example, when walking down the street, one can voluntarily choose to pay attention to a nearby couple’s conversation or it can be involuntarily drawn to a dog’s barking. The voluntary and involuntary nature of attention is referred to as endogenous and exogenous attention, respectively. Endogenous attention allows us to attend to an object or an area of interest for an extended period of time, while exogenous attention is more fleeting. We can also pay attention to a certain location or to specific objects in the environment (spatial compared to feature-based attention). In addition, if when walking down the street, you pay attention to a group of people instead, you are less likely to notice individual traits of each person. This is because if attention is distributed over multiple objects or locations, the clarity of each of these is reduced. We are susceptible to differences in motivation with vigilance and arousal affecting how we are attending.
When we pay attention to something, our information gathering at that location is facilitated. Attention in the absence of eye movements, or ‘covert attention’ has been found to improve perception and behavioral responses. Sperling and Melchner (1978) have shown that cueing a target location allowed subjects to direct covert attention to that location. In an early search task in which subjects had to detect number targets amongst an array of distractor letters, subjects were more accurate if they were previously instructed where the target would appear. Similarly, Posner (1980) demonstrated that attention could be directed to an expected location if cued to that location. Using a paradigm that has since often been used (Figure I.4), subjects’ reaction times to a detection task were faster when the target appeared at an expected location compared to an unexpected one.

Figure I.4. Cueing of target location employed by Posner paradigm. The ‘neutral cue’ was presented in 50% of trials and was not informative of the target direction. Alternatively, a ‘valid cue’ correctly indicated the target location in 80% of trials, or an ‘invalid cue’ indicated the wrong direction in 20% of trials (adapted from Posner, 1980).

Attention can enhance perception in many different types of tasks by increasing resolution, spatial or feature selectivity, etc. It is has been shown that attention enables this enhancement by an increase in spatial resolution (Yeshurun and Carrasco, 1998). Using a texture segregation task (in which increased resolution decreases performance), it was demonstrated that task performance was worse at the fovea when it was precued compared to the periphery and neutral cue conditions. Attention can also increase the perceived contrast of an attended object when comparing two stimuli (Carrasco et al., 2004). Search tasks have also been widely used in
order to study how attention can be allocated in various conditions (Figure I.5). Using visual search tasks, it was proposed that first stimulus properties or simple features (such as color, orientation, spatial frequency, etc.) are initially attended and perceptually processed before these features can be combined to form objects, this is referred to as feature-based attention (Treisman, 1998). Therefore, when searching for a target that varies from distractors by only one simple feature, the target should “pop-out” and the number of distractors should not matter (Figure I.5A). Alternatively, if looking for a target that varies in a conjunction of features, a serial scan of the search array would be necessary and would take more time as the number of distractors was increased (Figure I.5B).

![Feature Search and Conjunction Search](image)

**Figure I.5.** (A) Example of a feature-based search task. The target is identical to the distractors in all but one key feature, such as orientation in this example. (B) A conjunction search task in which the target contains a unique combination of features different from the distractors. In this example, both color and orientation, so that the target was the unique, purple, vertical bar (adapted from Anton-Erxleben and Carrasco, 2013).

This leads to the idea that salient features of a scene or stimulus can capture attention, as can an abrupt onset. However, an abrupt onset may not capture attention if it is voluntarily being directed elsewhere (Yantis and Jonides, 1990), as someone who is already engrossed in a riveting book could attest that the sudden actions of a friend trying to gain their attention would not necessarily be successful. Therefore, attention can be stimulus-driven as long as attention is not being intentionally focused elsewhere (reviewed in Egeth and Yantis, 1997).
Spotlight of attention

The different experiments linking attention and reaction time have led to a spotlight analogy to describe the way in which we shift our attention to highlight areas of interest. This “spotlight of attention” can be shifted from one location to another, enhancing or highlighting one area of the visual field by bringing the attentional resources to the area that is of interest, while leaving other areas in the dark. As mentioned earlier, target can draw attention, or attention can be voluntarily directed (Yantis and Jonides, 1990). The ability for attention to shift from one area to another has been supported by experiments demonstrating subjects were faster to respond for an attended target that was precued (Sperling and Melchner, 1978; Posner, 1980). The Illusory Line Motion illusion has also supported the spotlight of attention, in that attention facilitates neural processing, such that a simultaneously presented line appears to be drawn from a cued location (Hikosaka et al., 1993) (Figure I.6A). We used this to measure the speed at which attention can be shifted (Figure I.6B), which ranged from 60-120ms in the four subjects shown. These measurements of the speed of covert shifts of attention were similar to other studies showing that exogenous cues draw attention in approximately 100 ms, or after a much longer latency by voluntarily willing attention to another location by an endogenous cue (approximately 200 ms) (Nakayama and Mackeben, 1989; Wolfe et al., 2000).
Figure I.6. (A) The Illusory Line Motion Illusion demonstrates that by pre-cueing a location, a simultaneously presented line appears to be drawn from that location due to faster processing due to attention at the cued location (Hikosaka et al., 1993). (B) Training subjects to report where they perceived the line origin, we were able to measure the time for attention to shift from fixation to a peripherally cued location (Appendix 1). Four subjects’ sigmoidal curves are shown.

In addition to behavioral experiments, Brefczynski & DeYoe (1999) have supported the spotlight of attention model with neuroimaging evidence. They found that while performing a task requiring covert shifts of attention and not eye movements, a shift of activity was seen in the visual cortex corresponding to the attention shift in visual space.

Alternatively, there have been studies that have argued against the spotlight analogy of attention. Since they have found no effects of distance on shifts of attention, Remington and Pierce (1984) concluded that attention does not shift in an analog manner but suddenly. An alternative that has been suggested over a spotlight of attention is an Activity-Distribution Model (LaBerge et al., 1997). In this type of model attention shifts neither in an analog nor discrete manner, but attention is evenly distributed over possible targets and gets concentrated to where the target is likely to appear. But the spotlight model has proven to be a useful analogy whether it is strictly accurate or not, in particular with regards to changes in spatial scale.
Scale of Attention

When we look around the world, we don't always attend at the same scale, but could pay attention to large or small things as they attract our interest. Therefore, expanding on the attentional spotlight, a “zoom lens” model of attention also incorporates a changing scale of attention (Eriksen and St James, 1986). The zoom lens adds two properties to the spotlight model, the first being that when a larger area is attended, the attentional resources are more diffusely spread out, decreasing the processing efficiency. A second addition of the zoom lens is that the processing efficiency gradually diminishes along the edge of an attended area rather than having a clear boundary. Eriksen and St James (1986) demonstrated that when multiple locations within a circular array were precued, subjects expanded the area that they attended. If this precue was informative of the size of the target, then the response time was faster then when the target size was unknown. This indicates that all the precued locations were being attended, and that the spotlight of attention can be expanded to encompass a larger area.

Various behavioral and imaging experiments have supported the zoom lens model of attention. By using different sized target location boxes, it was shown that attentional resources are spread over the entire boxed area and that as the attended area increases, the processing efficiency decreases (Castiello and Umilta, 1990). In addition, when two sets of ‘rapid serial visual presentation’ (RSVP) lists were presented without a precue, and thus had to both be attended simultaneously, reaction times increased as the distance between the two lists increased, demonstrating that the scale of attention was expanded to incorporate both lists (Barriopedro and Botella, 1998). In an imaging experiment, an area of activity proportional to the size of the attended visual area was seen in the cortex (Muller et al., 2003). When a large visual area was precued for the possible target location, the corresponding neural area’s activity increased even before the target appeared.
Given that the size of the attentional scale can be modified, one can ask how quickly can it be changed? Stoffer (1993) used a series of composite letter stimuli in which larger letters were made up of small letters. Subjects were instructed to discriminate either the large or the small letters. The attention scale was precued with either a small or large cue and reaction times were compared, from which he concluded that it takes approximately 400 ms to change the scale of attention. We also explore the question of how long does it take for attention to change scales, and we take advantage of the link between the scale of attention and the decision to move in order to measure the time it takes to change this scale in Chapter 1. We will also look at how the scale of attention affects the assessment of saccade accuracy in Chapter 2.

**Neural correlate of attention**

An enhancement in activity associated with the effects of attention has been observed in various cortical areas from higher order areas through feedback projections. The visual system is arranged in a hierarchical manner with visual inputs received by the primary visual cortex (V1) from the retina (through the lateral geniculate nucleus), sending feedforward connections to the parietal and temporal lobes, which proceed to higher order areas in the frontal cortex (Figure I.7). Nearly all neural areas involved in visual processing have shown top-down feedback control from attention starting from area V1 all the way to the frontal eye field (FEF) (reviewed in Gilbert and Li, 2013).

Attentional effects have been found as early as V1 for a luminance detection task in humans (Kelly et al., 2008). Attending to a specific target color can even increase activity for ignored object properties that shared that color selectivity in areas V1, V2, V3, V3A, V4 and MT (Saenz et al., 2002). Attentional effects are most likely to be seen in the presence of competing visual stimuli in the receptive field, where possibly one target is preferred while distractors are
ignored. For example, single cell recordings in V4 in the early Ventral pathway (associated with identification of stimuli) have shown that when comparing responses to two objects in the corresponding receptive field, the response to an unattended object is much lower than to an attended target (Moran and Desimone, 1985; Chelazzi et al., 2001). Additionally, by simultaneously recording from cells in V4 and the FEF during a search task, bottom-up enhancement of activity was detected in area V4 for a preferred target feature as well as top-down attentional enhancement in the FEF for the target feature (Zhou and Desimone, 2011). The lateral occipital complex is active for large-scale targets and area V4 for small-scale targets (Hopf et al., 2006).

Similar attention-related activity effects have been observed in areas of the Dorsal pathway (associated with target location and motion processing), such as the middle temporal area (MT) and medial superior temporal area (MST) (Treue and Maunsell, 1996). Also, the parietal cortex, in particular the lateral intraparietal area (LIP) is thought to be involved in the top-down control of spatial attention and the locus of attention.

Distractors presented during the delay period of a memory-guided saccade task demonstrated that LIP activity tended to reflect the locus of attention, rather than the saccade target (Goldberg et al., 2002). Microstimulating the FEF improved performance in a luminance change detection task in a similar manner to the spotlight of attention (Moore and Fallah, 2004).

In the brainstem, the Superior Colliculus (SC) has been shown to be involved in the locus of attention as well. Inactivation of part of the SC caused a deficit of the ability of attention to focus on a target over a distractor stimulus in the corresponding visual area (Lovejoy and Krauzlis, 2010). Additionally, while saccades can be elicited by stimulation of SC cells above their activation threshold, subthreshold stimulation of cells in the SC can counter change
blindness in the same way that a cue could (Cavanaugh and Wurtz, 2004). This suggests that this subthreshold stimulation actually directs attention to the corresponding visual location.

Figure I.7. Feedforward (blue) and feedback (red) connections in the human brain. Abbreviations: PF= prefrontal cortex, FEF= frontal eye fields, IT= inferior temporal area, PMd= dorsal premotor area, TeO= tectum opticum, PMv= ventral premotor area, AIP= anterior intraparietal area, LIP= lateral intraparietal area, MIP= medial intraparietal area, MST= medial superior temporal area, MT= medial temporal area, MD= medial dorsal nucleus of the thalamus, PL= pulvinar, SC= superior colliculus, V1= primary visual cortex, LGN= lateral geniculate nucleus, (taken from Gilbert and Wu, 2013).

**Attention precedes saccades**

If we were walking down an empty hall, and noticed a person unlocking their door, the person would first draw our attention and then we would tend to make an eye movement to him or her. Since we often make an eye movement to what draws our attention, the connection between the two has been the subject of much inquiry. What is the extent of their connection? Are the attentional and eye movement systems independent of each other? We know that the goal of both these processes is to increase clarity and visual perception of areas of interest. The
connections between attention and saccades led to the pre-motor theory, which is the idea that attention and saccades are one orienting system and that covert attention is merely a planned saccade that was not executed (Rizzolatti et al., 1987; Sheliga et al., 1994). They found that the locus of attention in an unrelated task could affect the trajectory of saccades to a target (Sheliga et al., 1994).

To test the idea that covert shifts of attention always precede the eye before an overt shift such as a saccade, subjects are typically required to perform a “dual task” in which an attention-related task in addition to a saccade task is performed. For example, Kowler et al. (1995) showed that identification of a target was better at the saccade goal than at other locations, as well as that saccades were facilitated in that they had shorter latencies and were more directionally accurate than saccades made to another location. This suggests that for an accurate saccade to the target, attention is involved at that location and that the locus of attention cannot be completely separated from the saccade target. Hoffman and Subramaniam (1995) also demonstrated that attention first goes to the saccade goal, by showing that if a target was displayed immediately before a saccade, detection accuracy was best if the target was presented at the saccade goal, and if subjects were instructed to attend to a particular location, target detection was still better at the saccade location even if it differed than the instructed attended location. In a similar dual attention and saccade task, Deubel and Schneider (1996) found very little difference in the accuracy or latency of saccades, however discrimination accuracy was the highest when the discrimination target and saccade target were the same, but was near random when saccades were made elsewhere (Figure I.8).
All of these experiments support the idea that attention generally precedes the eyes to the saccade target. It has been suggested that attention could act as a placeholder that can track targets across saccades contributing to our perceived stability of the world (Cavanagh et al., 2010).

Further evidence for the idea that attention precedes saccades, can be seen in an experiment in which we gradually adapted the size of the shifts of attention in the absence of saccades (see Appendix 1). Having measured subjects’ attention shift times (Figure I.6B), we shifted our line-illusion array backwards at the mid-point of each subjects’ attention shift time. This “intra-attentional shift” gradually adapted the perceived locus of the illusory line motion in the direction of the shift, thereby adapting attention in a similar manner to the classic “intrasaccadic shift” paradigm of saccade adaptation (McLaughlin, 1967). Interestingly, even though no saccades were made, after the shifts of attention were adapted the saccade goal was also adapted. Therefore saccades were made to the adapted-attention goal location instead of to
the saccade target. This suggests that gaze follows the attentional locus, even if that location has shifted.

In addition to behavioral studies, electrophysiology also supports the idea that attention precedes saccades. For example, Moore et al. (1998) found cells in V4 which displayed orientation specific activity that declines over time and then increases immediately before saccade onset for stimuli within their receptive field. This pre-saccadic activity was higher if the saccade was going to be made to the target that was in the receptive field of the measured cell compared to outside of it. This reactivation suggests that attention precedes the saccade and can act as a place holder for saccades (Moore et al., 1998).

Other shared processes between attention and saccades, which would be consistent with the pre-motor theory, include, for example, express shifts of attention, which is similar to express saccades have also been recorded (Mayfrank et al., 1986; Mackeben and Nakayama, 1993).

Similarly, a tight coupling between attention and saccades can be demonstrated by the fact that many brain areas that have been shown to demonstrate attention-related activity are involved with saccades as well. Through lesion studies of monkeys we know the following areas to be involved in saccade planning: the parietal eye field (PEF), lateral intraparietal area (LIP), frontal eye field (FEF), supplementary eye field (SEF) (as reviewed by Gaymard et al., 1998). In humans as well, the frontal and parietal cortices were shown to be involved with saccade planning using fMRI (Curtis and Connolly, 2008). Additionally, in humans, fMRI scans were compared in subjects making covert shifts of attention and eye movements to the same peripheral visual stimuli found that both tasks caused an increase in activity in the FEF, SEF, and areas in the parietal & temporal lobes (Corbetta et al., 1998). More precisely, direct electrical stimulation of single cells in the superior colliculus (SC) and the FEF (both of which are known to be
involved in the saccade preparation) can evoke saccades. And interestingly, in the same areas, a subthreshold microstimulation too small to evoke a saccade can evoke a covert shift of attention to the corresponding visual location, as shown by an improvement in attention-related tasks (SC: (Cavanaugh and Wurtz, 2004; Müller et al., 2005); FEF: (Moore and Fallah, 2004; Armstrong et al., 2006)).

**Dissociating attention and saccades**

Despite all the above evidence for the tight coupling of attention and saccades, dissociations of covert attention and saccades have been found that argue against the premotor theory. For example, Juan et al. (2004) stimulated monkey FEF during a search version of the classic anti-saccade task, which separates the initial (presumed) covert attention shift to the target from the saccade that the subject actually makes in the opposite direction to the target (Hallett, 1978). On prosaccade trials, stimulating the FEF to induce saccades orthogonal to the target, led to saccades deviated away from this orthogonal direction towards the saccade target, indicative that a saccade was already being prepared towards the target. However, when monkeys were to make an anti-saccade, the evoked saccades deviated away from the visual target in the direction of the upcoming saccade. This suggests that a saccade was not being planned towards the target, but away from it even though attention must have shifted to the target for the target to have been discriminated as requiring an anti-saccade.

Patient studies have also shown that attention and saccades can be dissociated. For example, it was found that a patient with parietal damage could perform the saccade portion of a dual saccade/attention task normally, but not the attention demanding discrimination task in the direction of the impairment (Khan et al., 2009). Therefore, purely pre-motor planning does not
drive attention shifts and the relationship between attention and saccades is more complex than the pre-motor theory implies.

A potentially simple way of further testing the dissociability of attention and saccades is to use a property that attention has, but saccades themselves do not: extended spatial scale. Of course, while the point-to-point saccadic movements themselves have no spatial scale, spatial scale could still influence saccade planning; but at the start of this thesis very little was known about the effects of spatial scale on saccade planning, and the little reported suggested it had scant effect (Kowler et al., 1995). The possibility to use spatial scale to dissociate attention and saccades was a major motivation behind the work of Chapters 1 (focused on Decision to Move) and 2 (focused on Accuracy Assessment).

Decision to Move

Visual attention has been shown to be involved in the decision to move the eyes by influencing the latency of saccades. Cueing the spatial location of the saccade target speeds up saccade reaction times (Crawford and Muller, 1992). As the dual task paradigm demonstrated, saccades latencies are faster if the saccades are made to the locus of attention (Kowler et al., 1995). But is this exogenous attentional facilitation due to increased visual processing, as suggested in the illusory line motion example above, or reductions in saccade planning and the decision time to move? Khan et al. (2010) elicited this exogenous attention facilitation by presenting a distractor at the target location shortly (66.7 ms) before the target appearance. They used saccade adaptation to separate the presaccadic shift of attention to the initial saccade target from the saccade endpoint goal. The facilitated saccade latencies were then to the endpoint goal,
not the initial target location, suggesting that the facilitation speeds the saccade planning itself and the decision to initiate the saccade instead of the visual processing of the target.

Attention has also been implicated to affect saccade preparation decisions to move in the ‘gap’ task. In the “gap” condition, if fixation is removed around 200ms before the saccade target appears (Saslow, 1967), leaving a temporal gap with no target visible, saccade latency is decreased by about 30ms. The gap effect is often thought of in terms of attention being disengaged from the target, allowing motor preparation to be higher, or for decreased activity of fixation cells in the SC after the target disappears to result in shorter saccade latencies (Dorris and Munoz, 1995).

Conversely, attention can also cause a delay in the decision to make a saccade. In an “overlap” condition in which the initial fixation remains after the appearance of the saccade target, longer latencies were observed (Kalesnykas and Hallett, 1987). In addition, Walker et al. (1997) methodically demonstrated that distractors presented at the same time as the saccade target, but outside of the path and immediate area of the saccade target delay the saccade onset (Walker et al., 1997) (Figure I.9). The location of stimuli was shown to be very important in the Remote Distractor Effect (RDE). The ratio of the distractor to target eccentricity was shown to be inversely proportional to the effect it had on saccade latency. This RDE has been shown to be caused by an attentional inhibition of cells in the superior colliculus (Honda, 2005). Similarly, saccadic inhibition, as demonstrated by a decrease in frequency of saccades made was demonstrated when a sudden distractor was flashed 60-70 ms before a saccade could be initiated (Reingold and Stampe, 2002; Edelman and Xu, 2009).
Figure I.9. (A) Diagram of the visual field highlighting the area surrounding a target where a remote distractor would be able to increase saccade latency. This area would be outside of a 20 deg window surrounding the target (as indicated by the wedge in which amplitude would be modified). (B) The ratio of the distractor to target eccentricity was plotted against the increase of saccade latency. The target and distractor distances, as well as the radial locations of the distractors were varied (taken from Walker et al., 1997).

These previous effects of saccade latency have been in the order of 20-50 ms, however more recently our lab discovered a much larger effect, the ‘Size-Latency Effect.’ In the Size-Latency Effect (SLE), the spatial scale of attention has also been shown to affect saccade planning and the decision to move (Madelain et al., 2005; Harwood et al., 2008). When a saccade target steps outside its own diameter and therefore its scale of attention, saccade latencies to the target are much faster (~158 ms) than when the target steps within the target diameter (~315 ms) (Figure I.10). For the example subjects shown, this SLE in median saccade latencies is greater than 100 ms for each subject tested. Moreover, the latency distributions are typically so distinct that one can infer from an individual saccade with at least 94% accuracy, which of two scaled features the subject was attending to on a particular trial. We use the robustness of this effect to judge what the scale of attention was on any given trial, and in Chapter 1, to study the temporal dynamics of changing our scale of attention.
Figure I.10. (A) Distribution of saccade latencies small and large targets. (B) Cumulative frequency distributions of saccade latencies while attending to small and large targets, indicating very little overlap between the two. (C) Receiver-operating characteristic curves for data from B, in which the small target CDF curve is plotted against the large target CDF curve (taken from Harwood et al., 2008).

**Decision Models**

Various decision models have been used to model decision-making and the urgency to make a decision. One model, which we explore in Chapter 1, is the LATER model (Linear Approach to Threshold with Ergodic Rate). The LATER model describes that with a target step, a decision signal rises at rate $r$ towards a threshold ($S_T$), which is when a saccade is made. Between trials, the $r$ varies randomly (Reddi and Carpenter, 2000) (Figure I.11). An alternative to the LATER model is the diffusion model, which has been used to describe variability in decision-making. In this model information is also accumulated at a rate termed the “drift rate,” that varies by stimulus conditions and difficulty non-linearly (reviewed in Ratcliff and McKoon, 2008).
Figure I.11. Schematic of the LATER model. Upon stimulus onset, the Decision signal $S$ rises linearly, until it reaches a threshold $S_T$ after which a saccade is made. The rate of rise of this signal $r$, varies randomly between trials (taken from (Reddi and Carpenter, 2000)).

Another model, the leaky competing accumulator model, has been used to model saccadic inhibition (Bompas and Sumner, 2011). The main difference is that in a leaky accumulator model, a target causes a transient, exogenous input and a longer, endogenous input that makes the decision signal rise nonlinearly. Among the possible decision models, the LATER model parsimoniously captures most saccade latency data very well, including the Size-Latency Effect. It appears that the size of the targets modify the urgency of making a saccade by adjusting the rate of rise ($r$) of the decision signal (Harwood et al., 2008). In Chapter 1 we explore the temporal dynamics of the changing scale by taking advantage of the Size-Latency Effect and by changing the size of the target at different times relative to a target step and measuring and classifying the resultant latencies. We also attempt to model the scaling of attention with a modified version of the LATER model.
Saccades

Exactly where the decision to make these saccadic eye movements originates is still unclear, but the execution of saccades clearly proceeds via the superior colliculus. Microstimulation of cells in the FEF, SEF and PEP can evoke saccades (reviewed in Pierrot-Deseilligny et al., 1995), unless the superior colliculus has been ablated (Schiller et al., 1980). These cortical areas send and receive inputs to many different areas, but to the superior colliculus in particular, which also itself receives input from many subcortical areas (Figure I.12).

![Diagram of saccadic system]

Figure I.12. Abbreviations: CN= caudate nucleus, DLPFC= dorsolateral prefrontal, FEF= frontal eye field, GPe= globus pallidus external, LGN= lateral geniculate nucleus, LIP= lateral intraparietal area, SC= superior Colliculus, SEF= supplementary eye field, SNr= substantia niagra pars reticulate, STN= subthalamic nucleus (Munoz, 2002).

The superficial areas of the superior colliculus have been shown to respond to visual stimuli as well as other modalities (reviewed in Sparks, 2002). Microstimulation of cells in the intermediate and deeper layers of the superior colliculus were able to evoke saccades in the contralateral direction. The superior colliculus is also arranged topographically, where a burst of activity is seen in rostral cells before small saccades, and more caudally before large saccades.
Micro-stimulation to these locations would produce the corresponding saccade as well. Also, to evoke upward saccades microstimulation of cells located more medial is necessary, and more lateral for downwards saccades.

The motor output from the superior colliculus goes to the premotor neurons in the pons and midbrain: the saccadic burst generator for horizontal and vertical saccades, respectively. In order to generate the rapid forces required to shift the extraocular muscles quickly, and then hold them in eccentric positions, requires a “pulse-step” in neural activity (Robinson, 1964). These burst pulse-step commands originate in the brainstem with premotor neurons for horizontal movements located in the paramedian pontine reticular formation (PPRF), and those for vertical steps located in the rostral interstitial nucleus of the medial longitudinal fasciculus (riMLF) (reviewed in Sparks, 2002). During fixation, “omnipause neurons” fire at a constant rate, inhibiting both horizontal and vertical burst generators, and cease firing right before a saccade and resumes firing right before the end of a saccade. During the saccade, excitatory burst neurons (EBN) in the PPRF display a high frequency of activity and directly excite the cells of the ipsilateral abducens (VI) and are the main source of the pulse phase of the pulse-step neural activity. The spike frequency, burst duration and the peak rate modulate the amplitude, duration and velocity of the saccades. The step portion seems to originate from the constant rate of activity of cells in the nucleus prepositus hypoglossi (NPH) and the medial vestibular nucleus (MVN). The step portion for vertical saccades is generated by cells in the interstitial nucleus of Cajal (iNC) and the vestibular nucleus which fire at constant rate, again proportional to eccentricity (reviewed in Sparks, 2002).

Eye movements are controlled by the coordinated activity of 6 extraocular muscles (Figure I.13), which are innervated by three motor neurons. The lateral rectus and medial rectus
muscles rotate the eyes in a purely horizontal direction, while the superior and inferior recti muscles rotate the eyes purely vertically. The inferior and superior oblique muscles are involved with both vertical and horizontal movements. The trochlear nerve (Cranial Nerve IV) innervates the superior oblique muscle, the abducens neuron (Cranial Nerve VI) innervates the lateral rectus muscle, and the oculomotor nerve (III) innervates the remaining four extraocular muscles. The activity of the muscle and motor neuron for a movement involves a burst of spike firing activity for the agonist muscle for the duration of the saccade. Simultaneously, there is no spike activity of the motor neuron innervating the antagonist muscle. While fixating, motor neurons display a constant rate of spike activity which is proportional to eye eccentricity. Another feature of saccades is Sherrington’s law of reciprocal innervation which states that if a muscle contracts to move the eye in one direction, the corresponding fellow muscle must relax (reviewed in Ciuffreda and Tannen, 1995).

Why are saccades in particular so often studied in neuroscience? There are several reasons, one of which has to do with the comparable simplicity of eye movements in general. Compared to movement of other limbs, eye movements are very simple in that there are only six muscles involved (Figure I.13), and the movement of the eye appears relatively unaffected by other extraneous factors such as gravity.
Figure I.13. The six extraocular muscles responsible for all eye movements. The medial and lateral recti muscles move the eyes horizontally. The superior and inferior recti muscles move the eyes vertically. And the superior and inferior oblique muscles participate in both vertical and horizontal movements (taken from http://pfoflaserandeye.com/anatomy.htm)

And why saccades in particular over other eye movements? Firstly, because saccades are the most frequently made eye movement; secondly and importantly is that saccades are also very stereotypical in certain properties. For example, a saccade always starts very quickly, with an initial acceleration often \( \sim 30,000 \text{ deg/sec}^2 \). The deceleration at the end of the saccade may be slower than the acceleration, causing a slight overshoot before stopping the eyes. In addition, the peak velocity of the eyes is also stereotypically proportional to the size of the saccade and is typically in the range of 400-600 deg/sec, which also has a proportional saccade duration (Becker, 1989; Leigh and Zee, 1999). This relationship between the peak velocity, or the duration of the eyes and amplitude of saccades is known as the “saccadic main sequence” (Bahill et al., 1975) (Figure I.14).
Assessment of Accuracy of Saccades

The eye can move as fast as 700 deg/sec during a saccade, therefore there is very little visual feedback during the saccade itself (Leigh and Zee, 1999). This means that the size and direction of the saccade is determined before the start. Since saccades are too rapid to be guided by vision, they are thought to maintain their accuracy based on error signal(s) related to the consequence(s) of their movement. Although saccades have been compared to ballistic movements, some online-visual feedback control is in effect during the movement as has been demonstrated with patients with spinocerebellar degeneration that produced slow saccades, but were able to modify their saccades during the movement (Zee et al., 1976). Also, when saccades were halted by stimulating omnipause neurons, the saccades resumed once the stimulation ended (Keller and Edelman, 1994).
The accuracy of saccades is constantly maintained by the oculomotor system. An adaptive control mechanism ensures saccade accuracy in everyday life, since over time saccades may become less accurate with events such as muscle weakness associated with aging or fatigue. When extraocular muscle impairment or weakness occurs, the initial large targeting errors diminish over time, meaning that the motor planning is able to adapt and restore saccade accuracy (Kommerell et al., 1976; Abel et al., 1978; Optican and Robinson, 1980; Snow et al., 1985). Therefore, adaptive control mechanisms are necessary to ensure saccade accuracy. Saccade accuracy is often described in terms of gain (saccade amplitude divided by target distance) where a gain of 1.0 would mean a perfectly accurate saccade. However, the eye rarely makes perfectly accurate saccades, it has been widely observed that the eye consistently undershoots the target (Henson, 1978).

In order to study how saccade amplitude can be adapted by the oculomotor system, McLaughlin (1967) devised a method which caused very rapid saccade adaptation. This was done by surreptitiously stepping a target once a saccade to the target had been initiated (Figure I.15). The eye velocity during the saccade is so high that the visual information is very limited; therefore the oculomotor system is fooled into thinking that an inaccurate saccade was made. This causes successive saccades to have gradually smaller gains (if the intrasaccadic step moved the target closer to the previous location). Further experiments found saccade adaptation gradually modifies saccade amplitude over hundreds of trials, although effects of a single trial can also be observed (Srimal et al., 2008). The magnitude of the adaptation never completely matches the amount of error that is produced (Albano and King, 1989).
Adaptation can also be generalized to other similar saccade sizes in the same direction or vector (Deubel, 1987; Semmlow et al., 1989; Noto et al., 1999). This adaptation procedure can not only decrease, but over a longer rate constant increase gain as well (Deubel et al., 1986). The kinematics of the adapted saccades demonstrated that they were in fact altered and not simply altering the perceived target location (Abrams et al., 1992; Straube and Deubel, 1995). The peak accelerations were smaller, but the saccade duration was not different from unadapted saccades. However, some other experiments have found no changes in the kinematic properties of adapted saccades after a gain decreasing paradigm (Albano and King, 1989; Frens and van Opstal, 1994). It is unclear why the results of these experiments differ, one possibility is that a much smaller degree of adaptation was seen in these latter experiments compared the first two.

The fast, intra-saccadic step (ISS) or McLaughlin method of adaptation has been used to study the mechanism by which saccade accuracy is maintained in everyday life. Even though the timescales are very different, the rapid adaptation that results from the McLaughlin method and the slow adaptation from extraocular muscle weakening are not two completely different
mechanisms (Scudder et al., 1998). Scudder et al. (1998) found an inverse relationship between the complexity of the possible saccade vectors and the rate of adaptation in both kinds of adapt experiments. They were therefore able to show slow adaptation with the ISS paradigm by increasing the number of amplitudes and directions of saccades using a complex stimulus array, and a comparably fast rate of adaptation with a weakened eye muscle and a limited number of possible saccade sizes using a sparse stimulus.

The timing of the error signal is also very important in adaptation. By varying the delay and duration of the postsaccadic stimulus, we see gain reduction only if the stimulus was displayed for a minimum of 32 ms, with the magnitude of adaptation increasing with the duration of the target presentation reaching a maximum at 80 ms (Shafer et al., 2000).

**Neural basis of Saccade Adaptation**

Where in the brain does saccade adaptation occur? Rapid saccade adaptation is specific to the type of saccade that was adapted, and the ability to transfer adaptation from one type of saccade to another has also been studied in order to determine the site of adaptation. Saccades can be divided into two general types: exogenous and endogenous. Exogenous saccades are those that are stimulus-driven. Conversely, endogenous saccades are self-motivated, and are considered to be programmed upstream of exogenous saccades. Adaptation of an exogenous type of saccade does not transfer to an endogenous saccade. The pattern of transfer of adaptation from different types of saccades shows that adaptation of an exogenous type of saccade is unlikely to transfer to an endogenous saccade (Deubel, 1994, 1995). However, adaptation of an endogenous saccade may partially transfer to an exogenous saccade (Deubel, 1994, 1995; Fuchs et al., 1996; Alahyane et al., 2004). This suggests that the neural areas responsible for saccade adaptation are
not in the lower oculomotor areas such as the brainstem where signals from various areas have already been merged.

The most likely site for maintaining saccade accuracy is the cerebellum, since it is known to be involved in motor regulation (Purves and Hall, 2004). Cerebellar lesions did not prevent movement, but lesioning the posterior vermis of the cerebellar cortex in monkeys inhibited their ability to regulate saccade accuracy and to undergo rapid saccade adaptation using the ISS paradigm (Barash et al., 1999). It was shown that saccade adaptation could take place downstream of the superior colliculus, by using near-threshold stimulation of the superior colliculus in monkeys and found that saccade adaptation did transfer to the saccades that were evoked (Edelman and Goldberg, 2002). In addition, human patients with cerebellar lesions or with cerebellar degeneration demonstrated much less saccade adaptation than normal subjects (Straube et al., 2001). An imaging experiment on humans demonstrated an increased level of activity in the medioposterior cerebellar cortex during rapid saccade adaptation (Desmurget et al., 1998). Another experiment suggested that the cortex was involved as well where patients with a lesion of the linking cerebellar thalamus demonstrated less saccade adaptation (Gaymard et al., 2001). Since the activity of the cells did not change, it is possible that saccade adaptation acts on a level downstream of the superior colliculus (Frens and Van Opstal, 1997).

**Error Signal for Saccade Adaptation**

What is the error signal for saccade adaptation? There are several possibilities as to what constitutes the error signal driving such saccade adaptation. One possibility is that the error signal is motoric, meaning that the small corrective saccades to foveate the target after the primary saccade drive adaptation depending on their size and direction (Albano and King, 1989). But, the general view has been that correctives are not necessary for saccade adaptation and
adaptation could occur even when correctives are in the opposite direction (Wallman and Fuchs, 1998; Bahcall and Kowler, 2000). Since saccade amplitude can be decreased when the target is displaced backwards, and increased when the intrasaccadic step is forward, the retinal error—the distance of the target from the fovea when the saccade lands could provide a simple possible error signal to guide saccade adaptation (Wallman and Fuchs, 1998; Noto and Robinson, 2001; reviewed in Hopp and Fuchs, 2004; Havermann and Lappe, 2010). However, a direct test of the potency of retinal error alone in driving saccade adaptation in the absence of an actual intrasaccadic step, showed the difference between where the eye lands and the predicted target location can drive saccade adaptation as well (Collins and Wallman, 2012).

Because of the strong connections between attention and saccades, in Chapters 2 and 3 we test the influence of two different properties of attention on saccade adaptation. In Chapter 2, we test whether the scale of attention affects the magnitude of saccade adaptation. We compare the magnitude of adaptation to a small 1 deg target compared to a large, 8 deg target. In addition, because attention may act as a placeholder that allows the oculomotor system to keep track of the target across the saccade, in Chapter 3, we moved not the target, but the locus of attention. We show that if a distractor can attract attention away from the target at the end of the saccade, it can induce saccade adaptation in the direction of the attentional shift.
Chapter 1: Changing scales in active vision: the interplay of visual attention and motor re-planning

Abstract

Visual attention cannot only shift from one location to another, it can also scale its size. We explore the temporal dynamics of this scaling using the Size-Latency Effect, which has demonstrated that the saccade reaction time is affected by the scale of attention. More specifically, saccadic latency is determined by the ratio of the target step amplitude to the diameter of the target. Based on this relationship, we can reliably infer what the scale of attention was for any given trial. Can we measure the time it takes to scale your attention by changing the size of the target during saccade planning? We randomly either changed the size of the target or not, at a random time, and compared the saccade latencies of size-change trials to non-size-change trials. First we replicated previous finding so that we can classify non-size change trials between small and large attentional scale based on the saccade latencies with 98% accuracy. Second, we show that the scale of attention can be changed before a saccade is initiated and that the scaling is completed within 32 ms, and can alter motor planning up to 149 ms before the start of the saccade. In addition, we found that the size-change immediately before a saccade can lead to either inhibition or facilitation of the saccades depending on whether attention size was increased or decreased. Finally, we were able to model the attentional scaling effect on saccade reaction time using a modified version of a LATER model incorporating a combination of rate change and reset of the decision signal for the saccade execution.

Introduction

Visual attention has often been compared to a spotlight which can be shifted from one location to another, enhancing or highlighting one area of the visual field with attentional
resources, while ignoring others (Posner and Petersen, 1990; Muller and Ebeling, 2008). The ability of attention to shift from one area to another has been supported by experiments demonstrating, for example, a faster reaction time or a better discrimination accuracy for an attended target that was precued (Sperling and Melchner, 1978). In addition to behavioral experiments, neuroimaging evidence has supported the spotlight of attention model. It was found that while performing a task requiring covert shifts of attention (no eye movements), a shift of activity was seen in the visual cortex corresponding to the attention shift in visual space (Brefczynski and DeYoe, 1999). The speed at which attention can be shifted has also been studied. These covert shifts of attention can either be shifted quickly in about 70-150 ms by a reflexive exogenous cue that draws attention, or after a much longer latency of more than 300 ms by voluntarily orienting attention to another location by an endogenous cue (Nakayama and Mackeben, 1989; Theeuwes, 1991; Wolfe et al., 2000).

Building on the spotlight model, the zoom lens model incorporates changes in the size of the area covered by attention (Eriksen and St James, 1986). A number of different methods have been used to assess whether the zoom lens model of attention is tenable or not. Behavioral experiments have mainly relied on either a discrimination reaction time (RT) or accuracy comparison to determine the scale of attention where RT is smaller or accuracy higher when the scale of attention matches the target (Castiello and Umilta, 1990; McCormick et al., 1998). For example, it was shown that when multiple locations within a circular array were cued, the reaction times of a letter discrimination were lower if the target was located within the cued area. Also, reaction times increased as the target distance from the nearest cued position increased (Eriksen and St James, 1986). Imaging experiments (fMRI) have shown that an increase in the scale of attention proportionally increases the area of enhanced neural activity (Muller et al.,
Electrophysiological experiments (EEG, MEG, ERP) have additionally shown differences in the sites of activity, in early visual processing and with the anterior areas of the ventral visual pathway being active for both large and small targets, but the posterior portions of this pathway being active only for small targets (Hopf et al., 2006; Song et al., 2006).

Another behavior that has been found to be largely influenced by the scale of attention is the latencies of saccades. When the amplitude of the saccade is smaller than the scale of attention, saccade latencies are much longer than if the target is outside the attention zone (Madelain et al., 2005; Harwood et al., 2008). They argued that this size-latency effect (SLE) reflects a cost-benefit phenomenon. Targets that remain within the attention zone will benefit little from re-centering saccades, but still incur the cost of disrupted vision during the movement. Conversely, there will be a greater benefit, with increased motor urgency associated with it, for target movements beyond the attention zone. Larger relative movements are consequently prioritized, while smaller relative movements exhibit more procrastination due to their lesser improvement of target perception.

Given the zoom lens model of attention, how quickly can attention zoom? Despite the crucial importance of knowing how fast we are able to adjust our scale of attention as we constantly attend to objects of varied size and shape, there have been only few studies on the timescale of the dynamics of the scale of attention. It was initially studied using a detection task and measuring the RT to stimuli presented within 1, 2, or 3 deg square place holders using a variation of the Posner cueing paradigm. Castiello and Umilta (1990) demonstrated that 40 ms was not sufficient to scale attention while 500 ms was. Another early experiment studied the scaling of attention using compound letter stimuli made popular by Navon (1977), in which a
letter stimulus of a large, global scale was composed of smaller letters. Using these Navon letters, Stoffer (1993) cued either the smaller scale or global scaled stimulus and found that it took approximately 300 ms to change the scale of attention from between 1 deg and 4 deg. In another experiment using a target detection task where either a small or large cue drew attention towards the target location for a variable stimulus delay, zooming out to either 2.5 or 7.5 deg was found to take between 33-65 ms (Benso et al., 1998). More recently, a rapid serial visual processing (RSVP) task was used to detect the time course of scaling attention (Jefferies and Di Lollo, 2009). By observing which range of cue-target delays yielded a higher accuracy in the detection of a second target if it immediately followed the first, they found that the scale of attention changes in a gradual, analog manner and not in a sudden way. Using these various methods, different studies have concluded that zooming attention between 1 deg to 4 deg takes in the range of 40-500 ms. The large range of results might be due to the type of attention involved (exogenous or endogenous) as well as the cue-target relationship (direct or indirect). Top-down voluntary factors are difficult to control and add delay and noise to the measure of the attentional scaling.

In our experiment, we quantify the timescale of the shifts of spatial scale of attention by using a novel behavioral paradigm that prevents the previously described confounds by relying on an automatic, reflexive scaling of attention and a trial by trial measure of the size of the attention zone. Indeed, unlike previous experiments that require many trials at each timepoint to estimate whether the attentional scale had matched the stimuli or not, we rely on the saccade latency effect (SLE), which very reliably identifies the attentional scale in single trials (Madelain et al., 2005; Harwood et al., 2008). As mentioned earlier, saccade latencies are much longer when the target steps within the attended area than outside it. For example, a 1.5 degree step
movement of an 8 degree diameter ring elicits latencies that are twice as long as those from the same movement of a 0.8 degree attended ring. Because the latency distributions are so separate (average 150 ms difference), by measuring a single saccade it can be determined with an average 94% accuracy whether the subject was attending to the large or small stimulus (Madelain et al., 2005; Harwood et al., 2008). We used the saccade latency to judge what the scale of attention was at the time of saccade onset. To measure the timescale of the scaling of attention we changed the target size between rotating ring stimuli of small (1 degree) and large (8 degree) diameters at around the target step and measured the saccade latencies. The scale of attention would have adjusted to the new target size when the saccade latency corresponds to that of the new target size. We find that attention can be scaled within 32 ms of the size-change. And changing the scale of attention can still affect the motor plan to make a saccade up until 150 ms before the start of a saccade.

Methods

Subjects

Five human subjects participated in the experiment (3 female, 2 male), age 20-38. All subjects had either normal or corrected vision. Three subjects (S1-S3) were highly experienced subjects at oculomotor tasks, one of these was naïve to the purpose of this experiment. Experiments were done with approval of the City College Institutional Review Board, and all subjects signed consent forms before the start of the experiment.

Equipment

Stimuli were presented using a 200 Hz 21-inch, monochrome CRT monitor with a fast phosphor. Stimuli were generated using a Vision Research Graphics’ Vision Works system (Durham, NH). Eye movements were recorded at 240 Hz using an IScan system (Woburn, MA).
In order to reduce head movements, all subjects used a bite bar and chin rest during the experiment. Viewing distance for all of the experiments was 57 cm from the screen. All experiments were done in a darkened room.

**Stimulus**

The stimulus used was a segmented, rotating ring with 9 evenly spaced breaks (Figure 1.1). In half of the trials, the ring diameter was 1 deg (small ring), and the size of each break was 4% of the circumference. In the other half of the trials, the ring diameter was 8 deg (large ring), each of the 9 breaks were 2.9% of the circumference. The small and large rings rotated counterclockwise at 30 and 55 rotations per minute, respectively. These speeds and the size of the breaks were similar to those used in previous work, in which they had been found to approximately equalize difficulty in the following discrimination task. Luminance of the background and target was 6.4 cd/m² and 23 cd/m², respectively.
Figure 1.1. Stimuli and trial timing. (A) Both the large and small rotating ring stimulus consisted of 9 segments, which changed briefly into the probe stimuli. The probe had either 5 or 7 breaks, after which the number of breaks reverted to 9. (B) Timings of events occurred pseudo-randomly at the illustrated times. Nearly half of the trials were “zooming” trials in which the ring size would change at one of the possible times. In all of the trials, the ring would change briefly to the probe stimulus and would make a ±2 deg step.

**Discrimination task**

In order to keep attention on the ring, in all of the trials we briefly changed the number of breaks in the ring and required subjects to report the number of breaks. The number of breaks changed briefly from 9 to either 5 or 7 breaks (probe stimulus) randomly at either 1200, 1375, or 1500 ms from the start of the trial (Figure 1.1A). The size of the breaks in the ring were 3.7% and 2.9% of the circumference for the small and large probe stimuli, respectively. Subjectively, this discrimination was very difficult to do without attention “locking on” to the size and motion.
of the ring. It has previously been found that if the small and large rings were presented simultaneously, and the subject is instructed to attend to one of the rings, the discrimination accuracy to the unattended ring is near chance (Madelain et al., 2005). Subjects were required to report whether the number of breaks changed to either 5 or 7 breaks using a numeric keypad. Subjects could take as much time as they required since the trial did not advance until a key was pressed. Performance accuracy was maintained at 75% (±10%) throughout the experiment by varying the probe stimulus duration. A beep at the end of the trial indicated to the subject an incorrect response.

**Target step**

The metric we used to judge the spatial scale of attention was saccade latency, therefore, at a random time (either 1000, 1075, 1150 ms from the start of the trial), the ring made a 2 deg step either to the right or left (Figure 1B) up to ±10 deg from the center of the screen. Subjects were instructed to look at the center of the ring and follow it when it stepped. From previous work we know that if the ring steps by more than its diameter, saccade latencies reach a minimum asymptote, and if the step is smaller than the diameter, the latencies were longer (Harwood et al., 2008). We chose 2 deg steps to elicit short latency saccades for a 1 deg ring and long latencies for an 8 deg ring.

**Size-change**

Size-change trials were used to measure how quickly the scale of attention could be modified. These consisted of 59% of the trials in the experiment, in which, at a pseudorandom time between 500-1500 ms (in 50 ms steps), the ring diameter changed from either small to large or from large to small (Figure 1B). There was a small delay in generating a new stimulus, which we measured on each trial. This resulted in the size-change blocks being offset by 16-18
ms (e.g. in Figure 1.3). To better characterize the influence of size-change during saccade planning, we presented more size-change trials in the 200 ms after the target step (Figure 1.1B). Randomly interleaved with these size-change trials were non-size-change trials in which the diameter of the target remained unchanged throughout the trial.

**Protocol**

To summarize, for each trial, along with the size of the ring at the start of the trial, three events were interleaved in a pseudorandom pattern throughout the experiment (Figure 1.1B). First, whether the size of the target changed (size-change trial) or remained the same (non-size change trial), second, time of the ±2 deg target step, and third, the discrimination task in which the number of breaks within the target would briefly change (probe stimulus) (Figure 1.1A). The different possible timings of these events are illustrated in Figure 1.1B. The experiment consisted of a total of 1836 trials, performed in 4 separate, equal sessions. Subjects were instructed to look at the center of the target and to follow it when it moved, as well as perform a forced-choice task reporting the number of breaks in the discrimination target.

**Analysis**

The saccade latencies of the non-size-change and size-change conditions were compared offline. Subjects who did not make saccades in at least half of the large ring non-size-change trials were excluded; two subjects out of seven were eliminated based on this criterion. Trials in which saccade latencies were less than 100 ms and greater than 500 ms were considered erroneous, and removed from data analysis.

**Results**

**I- Non-size-change**

In trials in which the ring size did not change, we found very large differences in saccade
latencies between the small and large rings. The distributions of latencies for the two ring sizes are plotted for a representative subject (Figure 1.2A). The average median saccade latency for the large non-size-change targets for all subjects was 239 ms (Interquartile Range of 75 ms), and median saccade latencies for the small ring for all subjects was 134 ms (Interquartile Range of 21 ms). The cumulative distribution functions (CDFs) of the small and large non-size-change trials were highly significantly different from each other (Figure 1.2B; Kolmogorov-Smirnov statistics for each subject: 0.96, 0.84, 0.97, 0.82, and 0.96, average of 0.91; each \( P << 0.001 \)). Plotting the small versus large non-size change CDF gives us the receiver-operating-characteristic (ROC) curves (Figure 1.2B), the area under which is a measure of our ability to judge the accuracy of our attention scale classification (i.e. if one had to guess the size of stimulus in each non-size change trial based only on the latency information, not on knowledge of the trial condition). These ROC curves demonstrate that the small and large rings’ non-size-change saccade latency distributions were sufficiently different to judge which attentional scale was employed with a mean accuracy of 97.9% across subjects (each subject: 99.5, 96.4, 99.5, 94.3, 99.7%). The 122 ms differences between latencies for the small and large ring and the ROC calculations were similar to those found earlier from comparable conditions (158 ms difference and 94% ROC areas for (Madelain et al., 2005); 106 ms and 98.6% in (Harwood et al., 2008)).

Figure 1.2. (A) Histogram of the non-zooming trials of a single subject. (B) Cumulative distribution of non-zooming small & large data of all 5 subjects (Kolmogorov-Smirnov tests: average of 0.91; \( P << 0.001 \)). (C) ROC curves of the non-zooming trials for all five subjects (mean accuracy of 97.9% across subjects).
II- Size-change relative to step

The other 59% of trials consisted of size-change trials in which the size of the ring changed at a random time within a range of 500 ms before or after the step (Figure 1.1B). These trials were similar in every other way to the non-size-change trials. It is reasonable to assume that if the size of the stimulus changes during the trial, the scale of attention would also change; therefore we would expect that when the size-change was long before the target step, the saccade latency should also change to reflect the new attention scale. We can see that this is the case when looking at the latencies against the time of the size-change (Figure 1.3). When the size-change occurred long before the target step (left side of each of the panels in Figure 1.3), the attentional system had enough time to scale attention and the saccade latencies were similar to the non-size-change mean (circles on the right side of the scatterplots in Figure 1.3). Conversely, when the size change occurred more than 200 ms after the target step (right side of the panels of Figure 1.3), the saccade latencies reflect the fact that the size change occurred too late in the trial to affect the saccade planning. To visualize the transition between latencies reflecting small and large scales of attention, we fit the latencies from the Large-to-Small and Small-to-Large trials with locally-weighted (Lowess) smoothers (Cleveland, 1979). Depending on when the size change occurred, the Lowess curves appear similar to the mean saccade latency of either the small or large non-size-change trials. Analogous to how saccade amplitudes change when a target is moved during saccade planning (“amplitude transition functions,” Becker and Jurgens, 1979), these Lowess “Latency transition functions” place outer limits on the temporal dynamics of changing scale. Visually, the width of this transition appears to be less than 200 ms (Figure 1.3).
Figure 1.3. Saccade latency of all five subjects (S1-S5) plotted against time of size change relative to target step. The mean values of the non-size change trials are plotted on the right side of the figures with error bars for their SD (blue-small rings, purple-large rings). Red crosses and curve are for Large-to-Small condition along with its Lowess smoother fit, and green circles are for Small-to-Large condition. Gray crosses represent Large-to-Small saccades that were most likely executed in response to the size-change instead of target step. These grey points were fitted with a linear regression and are close to a slope of 1. (S1: y = 0.98719x+160.53; S2: y=0.96221x+152.42; S4: y=1.0015x+171.03; S5: y=0.83992x+212.24).

Some saccades were made not in response to the target step, but to the size-change instead. These are most clearly seen in Subjects 4 and 5 by the Large-to-Small trials highlighted in grey in Figure 1.3. The saccade latencies of these trials increased linearly with the size-change time. The idea that these latencies represent saccade plans starting afresh at the time of the size-change, following the abandonment of all prior planning in response to the step of the original
target size, is dealt with more explicitly toward the end of the Results with the model. For now, we simply observed the linearity of these populations, and excluded them from the Lowess fits of latency transitions. We were conservative in classifying these gray points as only those trials in which saccade latencies were greater than 300 ms and that the size-change occurred 100-250 ms before the saccade onset. The four subjects who had data in this region all showed linear regression slopes close to 1 (S1: \( y= 0.99x+161 \); S2: \( y=0.96x+152 \); S4: \( y=1.00x+171 \); S5: \( y=0.84x+212 \)). These gray populations highlight an apparent difference in response for different stimulus scaling directions, but once removed, the latency transition functions are qualitatively symmetrical between Small-to-Large and Large-to-Small transitions. However, the group average illustrated in the bottom-right panel of Figure 1.3 seems to suggest that the transition between large to small scales is more gradual than the small to large change which seems more sudden.

We explored this idea in the following analysis. For the critical 200 ms size-change window around the target step, we fit Gaussian curves to histograms of the saccades latencies at each size-change time relative to step time (all subjects combined, Figure 1.4). We compared the \( R^2 \) for a single-peak Gaussian and dual-peak Gaussian curves and found that adding a second peak did not significantly reduce the \( R^2 \) for any of the size-change epochs, except the 68 ms Small-to-Large epoch. This epoch showed a very large difference between the calculated \( R^2 \) values of the single and multi-peak fit (0.21 to 0.49, respectively). These Gaussian fits are displayed in Figure 1.4. For the Small-to-Large we found very little variability between the different Gaussian curves and latencies appear to be easily classifiable between small and large scale (Figure 1.4A) displaying a bimodal pattern of latency distributions consistent with a discrete switch between attention scales. Interestingly, the Large-to-Small trials display much
more variability and intermediate latencies (between those appropriate for large and small scales) (Figure 1.4B) and are consistent with an analog “zooming-in” of attention.

![Figure 1.4.](image)

Figure 1.4. (A) Gaussian curve fits of histograms of saccade latencies for Small-to-Large trials of all subjects. Each curve represents a different size-change block as seen in Figure 1.3. The histogram and its Gaussian fit for the 16 and 68 ms curves are shown in the panels to the right. (B) Gaussian curve fits for Large-to-Small trials as in (A).

The discrimination accuracy of the probe stimuli at each of these size-change epochs was calculated for both types of size-change trials. We found that all epochs were within the desired 75% ± 10 range except for the 68 ms Large-to-Small epoch. This Large-to-Small 68 ms epoch had a mean response accuracy of 63.5%. As determined by a 2-Sample t-Test, the response accuracy for this 68 ms block was significantly different from the 16, 116, 168 ms epochs of the
same size-change type. The interpretation of this difference will be explored in the Discussion.

When the ring size changes immediately after the target step, there are very few trials in which a saccade was made. We believe that this is a form of object-substitution masking (Enns and Di Lollo, 2000) where the visual transient masked the target step. For the 16 ms Small-to-Large size-change epoch, saccades were made for only 8% of trials as compared to 76% for the other epochs, therefore the masking was nearly complete (Figure 1.4). Although the number of saccades decreased for the Large-to-Small trials, the masking was not as complete since saccades were made in 27% of the Large-to-Small trials during the 16 ms size-change time compared to 72% for the other epochs.

**III- Size change relative to saccade**

*Facilitation and inhibition due to the size-change before saccade onset*

As the measure that we use for testing the scale of attention was the latency of the saccade, another way to look at the data is from a motor perspective, therefore we also looked at the size-change data relative to saccade onset (Figure 1.5). When viewing the data in this way, we observed that there were no trials with the size-change occurring around 100ms before the saccade in the Small-to-Large condition. To test whether this gap in the Small-to-Large condition were significantly different from what could be produced from a random distribution of latencies, we used a bootstrapping method with 10,000 repetitions. This is similar to the methods used to study inhibition of saccades by a sudden distractor flash (Reingold and Stampe, 2002; Edelman and Xu, 2009). It appeared that the sudden size-change to the large target caused an inhibition of saccades as well. The latency data from all subjects were found to be significantly different from the randomly generated data between the range of 87-163 ms before the start of the saccade. Therefore, we can conclude that the gap in the Small-to-Large latencies could not
have been randomly generated. Conversely, around the time of the inhibition of the Small-to-Large trials, we also see an increase in the number of Large-to-Small trials, particularly when incorporating the data that was grayed out in Figure 1.3. Therefore, right before the saccade, the Large-to-Small trials appeared to be facilitated by the size-change. In the discussion section, we explore the inhibition of Small-to-Large saccades and facilitation of the Large-to-Small saccades caused by the size-change.

Figure 1.5. (A) Histogram of number of trials at different size-change times relative to saccade for all five subjects. Green represents the Small-to-Large condition, while red represents the Large-to-Small condition. The dark grey portions of the Large-to-Small bars represent those trials that were represented as grey crosses in Figure 1.3. A decrease in trial frequency for the Small-to-Large trials is seen in all subjects when the size-change occurred around 100 ms before the saccade. (B) A bootstrapping analysis was done on all of the subjects’ combined latency information. The area on the Data fit curve highlighted in red indicates the range of size-change times relative to saccade where the observed inhibition is significantly different than what could be produced randomly.
How close relative to the saccade onset can the scale of attention still be changed?

To answer this question, we classified each trial as being either a “large” or “small” latency trial (based on whether the latency was within 2 Standard Deviations of the small non-size-change latency). This value was assigned as the cutoff value for a “small attentional scale” so that any latency above this value would be classified as being “large attentional scale.” The small ring’s median latency was chosen over that of the large ring since the SD for the small ring’s latency was smaller. We then calculated and plotted two sets of cumulative distribution functions (CDFs) of each trial type (Figure 1.6). First, we plotted the CDFs based on the original target size (Figure 1.6A). For example, for the Small-to-Large trials (green curves), there were very few counts at the original (small) scale classification in the range -500 to -100 ms before the saccade (since those trials would demonstrate “new” large saccade latency). But the frequency of these trials increased rapidly when the size-change occurred just before or after the start of the saccade as the system could not adjust the movement plan anymore. Again, the SD of the small ring’s latency was much smaller than the large, therefore we see much more variability for the Large-to-Small trials in Figure 1.6A. The elbow of these CDF curves was calculated by fitting two separate linear regressions, one to the size-change time (in a 75 ms window) before the curve started to rise, and the other regression to the region (again of a 75 ms window) that started to show a rise in frequencies. The intersection of these two linear regressions was used in Table 1. The Small-to-Large CDF curves tend to rise at an average of 54 ms (SD = 6 ms) before the saccade onset. In other words, if a Small-to-Large transition occurs closer to the saccade onset than 54 ms, it is too late to change the saccade plan and a latency corresponding to the original scale is observed. For the Large-to-Small trials, the latency cannot be changed 175 ms (SD = 35 ms) before the saccade onset so we observe large latencies. It is interesting to note that the slopes of the CDFs curves for the Large-to-Small condition are much steeper than in the Small-to-Large
condition, especially for subjects 2, 4 and 5, the same subjects that showed the large number of grey trials. We also computed the CDFs based on the new target size (Figure 1.6B). We then determined the elbow on the rise and plateaus of the curves similar to that in Figure 1.6A. The elbow of the Small-to-Large transition was at an average of 148 ms (SD = 22 ms) before the saccade. This means that any saccades made where the size change occurred more than 148 ms before its onset were likely to exhibit the large (new) latency. Similarly, the elbow of the Large-to-Small trials was 150 ms (SD = 7 ms) before the saccade, so that if the size change occurs more than 150 ms before the saccade, those trials will reflect the small, changed latency. The difference between the elbows from the CDF curve for the new and old latencies for the Large-to-Small was not very large. There is however a large difference between the old and new elbows for the Small-to-Large curves. This difference corresponds to the gap due to the inhibition of saccades mentioned earlier.
Table 1.1. Table of values calculated from the Cumulative Distribution curves from Figure 1.6. (A) These values indicate the time (relative to saccade) where the size-change is too close to the start of the saccade and the oculomotor system does not have time to modify saccade plan and attentional scale. (B) The “new” values indicate the time of the size-change relative to saccade that is the latest time at which the oculomotor system is still able to change the motor plan and attentional scale. Therefore, if a size-change occurs before this time, the latency will likely reflect that of the new ring size. It can be seen as the latest time at which the scale of attention can still be modified.

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<th>Small-to-Large</th>
<th>Large-to-Small</th>
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<tr>
<td>(A) Old Saccade Latency (ms)</td>
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<tr>
<td>S1</td>
<td>-62</td>
<td>-143</td>
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<tr>
<td>S2</td>
<td>-55</td>
<td>-154</td>
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<tr>
<td>S3</td>
<td>-51</td>
<td>-145</td>
</tr>
<tr>
<td>S4</td>
<td>-57</td>
<td>-207</td>
</tr>
<tr>
<td>S5</td>
<td>-44</td>
<td>-229</td>
</tr>
<tr>
<td>Mean</td>
<td>-54</td>
<td>-175</td>
</tr>
<tr>
<td>(B) New Saccade Latency (ms)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>S1</td>
<td>-184</td>
<td>-146</td>
</tr>
<tr>
<td>S2</td>
<td>-118</td>
<td>-152</td>
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<tr>
<td>S3</td>
<td>-155</td>
<td>-159</td>
</tr>
<tr>
<td>S4</td>
<td>-140</td>
<td>-138</td>
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<tr>
<td>S5</td>
<td>-141</td>
<td>-152</td>
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<tr>
<td>Mean</td>
<td>-148</td>
<td>-150</td>
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Figure 1.6. Curves for the Cumulative Distribution Functions of the trials for different size-change conditions. Latencies were classified as either large or small, and are represented either in panel A or B depending on whether they were the old, unchanged or new, changed ring size, respectively.
IV- Model

We used a simple decision processes model adapted from a LATER model (Reddi and Carpenter, 2000) to see if we could emulate some of the main features of our results. The LATER model ("Linear Approach to Threshold with Ergodic Rate") posits a simple decision signal that starts rising (accumulating evidence) with a constant rate from stimulus onset until an action threshold is reached, at which point the saccade is executed. Random (ergodic) inter-trial variability of rates reproduces the typical positive skew of latency distributions. We have previously shown (Harwood et al., 2008) that, for a given step size, larger attention scales reduce the rate of the decision signal rather than increase the threshold level (Figure 1.7A1). We wanted to know whether this model could adequately account for the size-change trials. In these trials once the size-change occurred the required movement vector (amplitude and direction) would be the same, therefore the saccadic system could continue with the current motor plan but adjust the rate (Figure 1.7A2). Alternatively, the saccadic system could cancel or “reset” the current saccade and start a new motor plan based on the rate for the new target size (Figure 1.7A3). We modeled the non-size-change data from a representative subject (Subject 4) within the parameters of this LATER model with no resets (1\textsuperscript{st} row), resetting all trials (2\textsuperscript{nd} row), and resetting 70\% of trials (3\textsuperscript{rd} row) (Figure 1.7B). We inferred the rate and the variability of the rate from the complete latency distribution of the non-size-change trials (see Harwood et al., 2008, for more details). We used these two parameters to generate a Gaussian distribution of 1000 random rates and adjusted for whether there was a reset or no-reset in the saccade planning after the size-change. We can see that this model has reproduced the key features of the size-change data, which are the general latency patterns on the scatterplots (Figure 1.7B, 1\textsuperscript{st} column; Figure 1.3), the inhibition and facilitation seen from the histograms (Figure 1.7B, 2\textsuperscript{nd} column; Figure 1.5), and the shape of the CDF curves (Figure 1.7B, 3\textsuperscript{rd} column; Figure 1.6).
Figure 1.7. (A) Schematic representation of the rate to rise for the small and large rings. Panels A1 and A2 represent no reset or resetting, respectively, of the saccade plans after a ring size-change. (B) Representation of Subject 4’s data as modeled using a LATER model with three different reset percentages. Data is displayed in the same manner as Figure 3, 5, and 6.

Discussion

Using an original paradigm we were able to show that the scale of attention can be evaluated dynamically by measuring and classifying saccade latency to a stepping target, which also changes scale. We have shown that attention can be adjusted within 32 ms, and the motor plan to make a saccade can reflect this change up to 150 ms before the start of the saccade. Moreover, in the Small-to-Large condition, the scale of attention change was bimodal, while it was more intermediate for the Large-to-Small trials. We surprisingly also found an inhibition of saccades when the size-change occurred nearly 100 ms before the start of the saccade.

In this experiment, we were able to demonstrate an interplay between attention and motor planning because our stimuli were able to constrain attention very well and our classification for
which target size the saccade was being planned is very precise. This gives us an unprecedented insight into the attentional scale and motor planning. We use the Size-Latency effect to classify whether the scale of attention was large or small at the time of saccade onset since saccade latencies are much longer when the target steps within the attentional window, than when stepping beyond it (Harwood et al., 2008). We observed the transition between the two saccadic latencies soon after the step. Interestingly, for Large-to-Small size-changes we found latencies intermediate between those appropriate for the two target-sizes consistent with analog rescaling of attention. Conversely, in the Small-to-Large trials there are two discrete populations of latencies, and trials can be easily classified as either large or small. The results can be interpreted both with a zoom lens model of attention where the target size-change scales the spotlight of attention, in terms of saccadic motor re-planning, or with a combination of the two.

**Changing the scale of attention**

Our experiment employs a unique method, combining attentional scale and saccade planning, quite different from those used in the past. Previously the changing scale of attention has been mainly studied using a manual response to a discrimination, comparing either reaction times (Castiello and Umlita, 1990; Barriopedro and Botella, 1998; McCormick et al., 1998), discrimination accuracy (Stoffer, 1993; Chen et al., 2009), or a combination of the two (Handy et al., 1996; Muller et al., 2003a). These past experiments have yielded the large range (40-500 ms) of times to scale. Our results however are much closer to another study which found that 33-66 ms was sufficient for attention to zoom-out (Benso et al., 1998) and that 133 ms was required for attention to completely zoom in (Jefferies and Di Lollo 2009). In both experiments, the cue-target delays were varied, while the former study compared RT, the later compared response accuracy. We show that attention has completely changed its scale from the small to large target.
size by about 32 ms. Our results are quite different from many of these previous experiments possibly because our methodology was also quite different in two important ways. The first difference is that subjects do not view the stimuli passively fixating on a spot; instead subjects actively follow the target with saccades. Secondly, instead of cue stimuli determining the scale of attention, our target not only determined but was also the stimulus used to measure the attentional scale. This eliminated a possible processing delay for transferring information from the cue to the target. Target discrimination is not used as a measure of the attentional scale, but to motivate subjects to match the attentional scale to the ring size. In our method, with near 98% accuracy we can determine whether the subject’s scale of attention was large or small at the time of saccade onset for each single non-zooming trial, an accuracy level few behavioral experiments can claim within a single trial. Therefore, we were able to measure and classify the scale of attention over a very wide range of size-changes, with fewer trials at each size-change time.

**Bimodal vs. analog size-change**

Two data features suggest an analog pattern of decreasing attentional scale, but not for increasing. First, while the Small-to-Large trials display bimodality in latency distributions, there are discrete populations of trials that can be classified as large or as small. Notably, when the size-change occurred 68 ms after the step, we observe populations of both latencies within that size-change time from which we conclude that the scale of attention very rapidly changes from the small to the large target size. The Large-to-Small trials however demonstrated more intermediate saccade latencies that would suggest an intermediate scale of attention during this size-change time. We modified the LATER decision model (Reddi and Carpenter 2000; Harwood et al. 2008) to include rapid resets in the motor plan and compared how well it matched our data. The LATER model was able to reproduce the intermediate and bimodal latencies.
during the difference size-change times. Secondly, in the Large-to-Small trials at the size-change time of 68 ms, discrimination performance fell to near chance showing that the scale of attention had not matched the size of the new, target size. It is likely that when the small target ring suddenly changes to the large, the attentional system quickly modifies the attentional scale since the large ring is almost completely outside of its attentional focus, however, since the area within the large ring is still attended (albeit diffusely) there is less motivation to scale attention as quickly.

Visual masking by the target size change

The sudden visual transient of when size-change occurred almost immediately after the step caused backward masking of the target step; therefore very few saccades were made, especially in the Small-to-Large condition (Figure 1.4A, Upper right panel). This is likely object-substitution masking, in which the object mask appears peripheral to the target and is diminished if the target location is already attended (Enns and Di Lollo, 2000). Since there were nearly no saccades made in the Small-to-Large condition we believe that there is almost complete masking of the target step since the new, large target is completely outside the attended area. However, when the size-change occurred immediately after the target step in the Large-to-Small condition, although there were fewer saccades made than at other size-change times, the masking of the target step was not nearly as complete and there were a significant number of saccades still made. When the scale of attention is large, attention is diffusely distributed throughout the target that prevents complete masking of the target step. Since our modified LATER model currently only addresses saccade planning for those saccades that were actually executed, it is not surprising that it did not replicate the step masking.
**Size-change relative to saccade**

We employed saccadic latency as a measure of the scale of attention, therefore we also analyzed the data from a saccade planning point of view by determining how close to the saccade onset can saccadic latency still be modified. We find that the motor plan for the saccade can still be updated before the start of the saccade and that the Small-to-Large trials exhibited the old latency much closer to the saccade start than the Large-to-Small trials (Table 1).

Saccade latencies of planned saccades can be modified if the target size changes before the start of the saccade. Saccade amplitude has previously been shown to be modified, even once preparation for the saccade has been initiated, by changing the target location up to about 90 ms before the start of the saccade (Becker and Jurgens, 1979). It is interesting to see such a strong effect on saccade planning even though the saccade vector is not modified by the size-change (same direction and amplitude). Importantly, our modified LATER model is able to replicate the motor-planning aspect of our ring size-change data and was informative about the source and processes that occurred during the observed inhibition of saccades.

**Saccade inhibition and facilitation**

We unexpectedly observed a gap in frequency of saccades for the Small-to-Large trials in the range of 87-163 ms before a saccade could be made, and facilitation where an increase in the number of saccades when the size-change occurred well before saccade initiation. The gap or inhibition in saccades was 100% in 4 out of the 5 subjects. The bootstrapping technique confirmed that these gaps could not have been produced randomly. A possible cause for the gap is that during saccade planning the oculomotor system requires a static scale of attention during this time, and any sudden change could disrupt the saccade before it was executed. The added task of scaling attention during this critical period could interrupt and delay saccade preparation
until the scaling was complete. Therefore, when the size-change occurs near the start of the saccade, the motor plan is interrupted and the saccade is delayed so that it causes an inhibition of the Small-to-Large trials.

The timing of this gap is consistent with the phenomenon of saccadic inhibition. Inhibition has been shown to be caused by a sudden flash across the top and bottom of the screen (Reingold and Stampe 2002), but can be caused by even a small distractor away from a remembered target 90 ms before saccades (Edelman and Xu 2009). This suggests that the brief visual transient of the increase in ring size shortly before the saccade can cause saccadic inhibition, which we observe only in the Small-to-Large trials where the new target size is outside the attended area. Other studies looking at saccade inhibition present a distractor at some distance from the target (Reingold and Stampe, 2002; Buonocore and McIntosh, 2008; Edelman and Xu, 2009). Nearer distractors do not elicit saccadic inhibition (Edelman and Xu, 2009); similarly, a small target suddenly appearing inside the attended area did not elicit saccadic inhibition possibly because a visual onset within a diffusely attended area of space does not cause inhibition. However, we do see facilitation of saccades for the Large-to-Small trials when the size change occurred near the time of the saccade. This facilitation was highly pronounced in 3 out of the 5 subjects. Facilitation instead of an inhibition around the same 80 ms before saccades when the distractor is presented near the target has also previously been seen (Edelman and Xu, 2009).

Our LATER model reproduces this pattern of inhibition and facilitation through a resetting of the motor plan. The figures produced by the model (Figure 1.7B) are remarkably similar to the data figures (Figures 3, 5, and 6). There are two possible ways that the brain could deal with the sudden target size-change: either by modifying the rate of increase of the current
motor plan (Figure 1.7A2) or by cancelling it and starting a new one (Figure 1.7A3, where a reset fraction of 1 means that every saccade was reset). There is evidence that the size-change could cause either modifying or resetting the motor plan, but we hypothesized that the size-change could cause a combination of the two, and that is what we found. The pattern and timing of saccadic inhibition is very clearly seen in the modeled data of the Small-to-Large trials when the reset fraction was 1 or 0.7. The facilitation and its timing is also clear for the Large-to-Small trials. This further supports how well our LATER model fits the size-change data. Without the reset, inhibition of the Small-to-Large trials is incomplete and due only to a decrease in the rate of rise to the threshold to make a saccade. With a reset incorporated into the model, complete inhibition of saccades is reproduced. This suggests that the sudden onset of the large target halts and resets the motor plan, which resumes at a higher rate of rise. Also, when the target ring changes from Large-to-Small, the rate of rise would increase, resulting in the facilitation of saccades that we observe. It is not clear from the data when the sudden size-change would cause a reset versus a rate change. It is possible that resetting of the motor plan could be due to an attentional or perceptual effect since the model produces a multi-peak gaussian.

Model

We investigated multiple characteristics of our data and compared whether they can be attributed to saccade re-planning, it is clear that our modified LATER model can recreate much of the behavior that we see when the size of the ring suddenly changes. Among the characteristics shared by the modeled data and our behavioral data are: the pattern of latency changes as the target size changes, saccades made in response to the size-change instead of the step, CDF curves, and the pattern of inhibition and facilitation.

Our modified LATER model reproduced saccadic inhibition from the size-change very
well even though a previous study using a distractor onset was not able to (Bompas and Sumner, 2011). In this study, the authors also used a modified LATER model to interpret data from a typical distractor onset paradigm but did not replicate strong saccadic inhibition, but their neuronal field model which was based on the Trappenberg et al. (2001) model did (Bompas and Sumner, 2011). We believe that their LATER model had fallen short because they allowed very weak inhibition in their decision model; therefore not surprisingly, their modeled data also had very weak inhibition. With maximum and immediate inhibition, we replicated complete inhibition. In addition, we were also able to reproduce the observed saccadic facilitation with our LATER model, a phenomenon not adequately addressed by utilizing the Trappenberg model (Bompas and Sumner, 2011).

**Conclusion**

In conclusion, the saccade latency of attention demanding targets that step within and without the target radius allows us to classify the scale of attention. The LATER model allows us to attribute much to saccade re-planning. However, not all of the behavior was replicated with the model. It does not reproduce the masking of the target step that we observe when the target size-change occurs almost immediately after the step. We also find that with the performance in the discrimination task, we can confirm the necessity of the scaling of attention to match the scale of the target ring. This is demonstrated by the incomplete attentional scaling that resulted in intermediate saccade latencies, as indicated by low performance on the target discrimination task when the size-change occurred 68 ms after the target step. The interaction of attention on the saccadic system and similarities in behavior between the behaviors of the two has also been previously demonstrated (Sheliga et al., 1994; McFadden et al., 2002). Therefore, we believe that attention acts on the saccade oculomotor system to effect motor re-planning as we observe here.
References

Chapter 2: Scale of attention affects magnitude and temporal dynamics of saccade adaptation

Abstract

In most saccade adaptation experiments, a small spot target is stepped intra-saccadically to produce an error signal at the end of the movement. In normal viewing, we constantly change our scale of attention, yet we do not know how the scale of attention affects saccade adaptation. In a series of experiments, we tested saccade adaptation using two different target sizes with an intra-saccadic step in an orthogonal direction and found that the larger target induced a greater magnitude of saccade adaptation than the small target. In one experiment, we also used non-fixed intra-saccadic steps that varied from trial-to-trial in a sine wave pattern, and found that the adaptation could occur very rapidly, and that the oculomotor system was easily able to track these non-fixed intra-saccadic target displacements. Using four different target sizes in a subset of subjects, we found a proportional magnitude of adaptation. Therefore surprisingly, the larger, more natural, scale of attention provides a larger error signal to drive adaptation. This suggests that the behavior of the oculomotor system related to the integration of error signal could vary greatly depending on the size of the target.

Introduction

Saccades are the fast eye movements used to direct the fovea to objects or areas of interest in the visual field. Due to the speed at which the eye can travel during a saccade, the oculomotor system cannot use visual feedback to guide the movement (Becker, 1989). Consequently, saccades are often thought to be mostly ballistic or open-loop where the saccade is programmed before the movement is initiated (Robinson, 1975).
As saccades are not guided by visual feedback online, accuracy has to be maintained across trials by some adaptive process. For example, when the eyes consistently fail to land near the target due to eye muscle weakness caused by nerve damage, the saccadic amplitude is modified (Kommerell et al., 1976; Optican and Robinson, 1980). This process of saccade adaptation is studied in the laboratory within a rapid timescale by stepping the target when the eye is in flight creating a landing position error, fooling the oculomotor system to adjust the amplitude of successive saccades (McLaughlin, 1967; reviewed in Hopp and Fuchs, 2004). Although these two types of saccade adaptation processes demonstrate two very different timescales, they are actually controlled by similar neural mechanisms (Scudder et al., 1998). The error signals involved in the modification of the saccade gain have been under dispute, but some of the possibilities include retinal error which is the distance between the eyes’ landing position and the actual target location (Wallman and Fuchs, 1998), prediction error which is the difference between the predicted distance between the eyes and the target location at the end of a saccade and the actual distance (Bahcall and Kowler, 2000; Wong and Shelhamer, 2011; Collins and Wallman, 2012), and motor error which would be the required corrective saccades (Albano and King, 1989). But, it has been shown that other error signals, such as reinforcement of a location either on the near side or far side of a target with a visual or even an auditory cue could induce adaptation (Madelain et al., 2011), and it has been suggested that the distance of the fovea to the locus of attention may also be involved (Ditterich et al., 2000; Madelain et al., 2010).

What is the role of attention on eye movements and their adaptation in the real world? In natural viewing, we normally see very cluttered visual scenes but we use attention to filter out parts so that we can focus on the area or objects of interest. It has recently been shown that saccade adaptation can be induced in a natural visual scene, which demonstrates that the
oculomotor system is able to select the target amongst a natural background with attention still involved in filtering of distractors (Madelain et al., 2013). In addition, saccades have been tightly linked to shifts of attention, which have been shown to be involved in the landing position of normal saccades and for object selection with attention possibly preceding saccades (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996; Castet et al., 2006; Herman et al., 2013). In the natural world in which we can make hundreds of saccades each minute, it has been suggested that attention could act as a placeholder that can track targets across saccades contributing to our perceived stability of the world (Cavanagh et al., 2010). Further involvement of attention in the motor planning of saccades has been demonstrated by the influence of attention on saccade reaction time. A saccade can be delayed both by the presence of a distractor that would initially require both the target and distractor to be attended, or if a large target steps within its attended area (Walker et al., 1997; Madelain et al., 2005; Harwood et al., 2008). With attention occupying so many roles and having so much influence on saccade planning and execution, we wanted to see how attention contributes to the error signal for saccade adaptation.

During normal viewing in everyday life, we look at objects of many different sizes, and accurate saccades can be made not only to small targets but also to large targets (Kowler and Blaser, 1995). However, saccade adaptation experiments are typically performed using isolated point-like targets. The aim of the current experiment is to examine how the scale of attention is involved in saccade adaptation. Saccade adaptation of larger targets has been virtually unstudied in the past, just a portion of one paper that suggested that there is no effect (Bahcall and Kowler, 2000).
Since small objects would provide a more focused target location for the oculomotor system, based on three arguments, we could expect smaller targets to demonstrate a greater magnitude of saccade adaptation compared to larger targets. (1) Compared to when a small target is attended, the attentional resources are more diffusely distributed when a larger area is attended (Eriksen and St James, 1986). (2) A greater visual spread for a large target would be equivalent to a greater amount of visual uncertainty of the target location for the oculomotor system. In addition, it has been shown that increasing the uncertainty about the target location decreases the amount of motor adaptation induced (Kording and Wolpert, 2004). (3) The Size Latency Effect has shown that the scale of attention affects motor planning in that saccade reaction times are faster if the target step is outside an attended area (Madelain et al., 2005; Harwood et al., 2008). This is perhaps analogous to what Collins et al. (2007) observed (although not testing attention scale) that saccades between two different objects demonstrate saccade adaptation while saccades within an object do not.

In order to compare the magnitude of adaptation with different scales of attention, we conducted three experiments comparing adaptation between a small target (either a 2 or 1 deg) and a large, 8 deg target (additionally, 0 and 4 deg sized targets were used, see Experiment 3B). In Experiment 1 and 2, the target made an intra-saccadic step that was a fixed size, and in an orthogonal direction to the primary step. We saw most of the adaptation in Experiments 1 and 2 occurred in a handful of trials, therefore, in Experiment 3A and 3B we studied saccade adaptation in a novel and dynamic manner. We varied the size of the orthogonal intra-saccadic step in a sine wave pattern, varying the size of the intrasaccadic step in each trial (Hudson and Landy, 2012). Over a 27 trial cycle, the intra-saccadic step would vary trial-by-trial so that it ranged from 0 deg at the start of each cycle to a maximum deviation of 2 deg, either up or down.
We expected a greater magnitude of adaptation for smaller targets than for larger targets. However, in all three experiments we observed that the large target induced a greater magnitude of adaptation.

**Methods**

**Subjects:**

Three experienced subjects participated in Experiment 1. Eight subjects participated in Experiment 2, four female and four male. Two were experienced subjects; the remaining six subjects were naïve. Twelve subjects participated in Experiment 3A, 5 male and 7 female. Four of these were experienced subjects; while eight were naïve subjects. The four experienced subjects from Experiment 3A also participated in Experiment 3B. All subjects had either normal or corrected vision. The Institutional Review Board of the City College of NY approved the experimental protocol, and all subjects signed consent forms before participation. Naïve subjects were recruited from the City College Psychology Department’s subject pool and received course credit for their participation. Experienced subjects were either authors, or members of the lab who were naïve to the purpose of the experiment.

**Equipment:**

A Dell PC (2.8 GHz) running Windows XP was used to run the experiment. Custom software programmed in LabView (National Instruments), was used to control, generate and display the stimulus, and collect the data. In Experiment 1, eye movements were recorded at 240 Hz using an IScan system (Woburn, MA). In Experiments 2 and 3, eye movements were recorded using an infrared video eye-tracking system, the Eyelink-1000 (SR-Research, Mississauga, Ontario, Canada), which sampled right pupil position at 1000 Hz. Stimuli were displayed on a 22 inch Compaq color, CRT monitor with a vertical refresh rate of 160 Hz. For all
experiments, luminance of the background and target was 3.5 cd/m² and 2.9 cd/m² respectively. The viewing distance was 57 cm in an otherwise darkened room. Subjects’ head position was held steady during the experiment by use of a chin and forehead rest. Subjects were instructed to look at the center of the target in all experiments. Online saccade detection to trigger the intra-saccadic step was based on a velocity threshold criterion of 30°/sec for all experiments.

**Experiment 1. Orthogonal Adaptation With Rings Stimuli**

Red rings of either 2 or 8 deg in diameter were used as stimuli for this experiment in order to set the scale of attention (Figure 2.1A). The 2 deg ring was 0.4 deg thick, and the 8 deg ring was 0.9 deg thick. They were presented on a grey background. Red stimuli were used in each experiment because the red color decays faster on the screen and is not as persistent. Each size condition was tested in separate sessions, and which size was performed first was selected randomly. In previous experiments studying the scale of attention performed by our lab, including the experiment performed in Chapter 1, we used rotating rings and rings with breaks in them with a discrimination task (Madelain et al., 2005; Harwood et al., 2008). However, attention has been shown to automatically scale to the target size even without cueing the size (Hopf et al., 2006). Furthermore, it has previously been shown that a discrimination task is not required for attention to scale to the target size, since the same saccade latency differences can be observed without an attention task (Harwood et al., 2008).
Figure 2.1. (A) The ring stimuli used for Experiment 1 consisted of red rings of either a 2 deg (small) diameter, or an 8 deg (large) diameter. The stimuli for Experiments 2 and 3 consisted of a pair of lines with either a 1 deg (small) or 8 deg (large) separation. (B) All targets were displayed on a grey background. In Experiment 2, trials started on the left side of the screen with a black fixation ring. After 100 ms, the black ring was replaced with either the small or large line stimulus centered on the ring. The target made a rightwards step, and upon saccade detection was blanked for 100 ms. The target reappeared, orthogonally displaced vertically by 2 deg. (C) The paradigm for Experiment 3 was similar to
Experiment 2, except that the magnitude of the intra-saccadic step oscillated in a sine-wave fashion. Each cycle was 27 trials long, and the peak displacement from the center was 2 deg.

The protocol of this experiment was as follows: starting from the center of the screen, the target first stepped vertically by 12 deg upwards during the Pre-Adapt and Post-Adapt phases of 100 trials each. During the Adapt Phase (250 trials), the target made a 2 deg rightwards intrasaccadic step. Subjects were instructed to look at the center of the target in all experiments. An orthogonal, intrasaccadic step was used to separate the dimension of the primary saccade and any adaptation that may occur. Previously we noticed that some subjects make smaller primary saccades to a larger target, therefore by having the intra-saccadic step dimension separate from the primary step dimension our measure of adaptation would not be affected by this target size dependent hypometria.

In the next experiment, we controlled for the fact that by having a larger circumference, the large (8 deg) sized ring provided more visual information than the small ring.

**Experiment 2. Orthogonal Adaptation with line-pairs**

In order to equalize the visual information between the different sized targets, in Experiment 2 we used a pair of lines that were identical visually, but varied in their spatial separation to set the scale of attention and determine the target size. We chose these stimuli because they were similar to those previously used in our lab that have demonstrated an attention scale effect (Harwood et al., 2008), and also to the large illusory targets used by Bahcall and Kowler (2000). The stimuli consisted of a pair of red bars on a gray background. Each bar was 0.5 deg wide and 0.1 deg tall. The target bars were separated vertically (Figure 2.1B) by either 1 deg (“small target”) or 8 deg (“large target”). The stimulus size varied in the vertical dimension, but was identical in the horizontal dimension so that the primary horizontal saccades would be identical between the two stimulus sizes. The pair of bars was centered vertically on the screen,
subjects were instructed to look at the center of the target and follow it with their eyes when it moved. Trials began from a random position on the left half of the screen where a black ring (0.2 deg diameter) was presented for 100 ms, marking the center of where the target bars would appear. The black ring was replaced by the target, which made a rightward step of an average of 10 deg (between 9-11 deg). Upon saccade detection the target was blanked for 100 ms (because 10 deg saccades last approximately 50 ms, no target was present at the end of the saccade for approximately 50 ms) in order to avoid possible trans-saccadic motion transients, since vision is not completely suppressed during a saccade (Deubel et al., 1996; Panouilleres et al., 2011). During the Adaptation phase, the target made a 2 deg intra-saccadic step upwards. Similar to Experiment 1 an orthogonal, upward intra-saccadic step was used in order to separate the dimension of the primary saccade and any adaptation that may occur.

The small and large targets were adapted in separate sessions with the same subjects. Which size condition subjects first experienced was selected randomly. The experiment consisted of a total of 400 trials, 150 of which were of the Adapt Phase. So that subjects were not habituated to the target size, 50 trials of the other target size were randomly interleaved during the Pre-Adapt phase.

**Experiment 3A & 3B. Sinusoidal, Orthogonal Adaptation with line-pairs**

In Experiments 1 and 2 we observed that the adaptation occurred very quickly. In experiments 3A and 3B, to study adaptation with a more rapid timescale, the vertical intra-saccadic displacement was not fixed but varied in a sine wave pattern, allowing us to also test whether the temporal dynamics of adaptation differed between the two scales of attention. Each sine wave cycle was 27 trials long and had a maximal vertical displacement of ±2 deg (Figure 2.1C). The visual stimuli were the same as Experiment 2, but the protocol varied in three
additional key ways making this methodology novel. First, the target size alternated between the small and large target sizes (starting with the small size) in blocks (after each sine wave cycle) of 27 trials within the same experiment. Second, the first two blocks were baseline trials without any intra-saccadic step. And third, the Adapt Phase consisted of 10 alternating blocks of the small target and 10 blocks of the large target, with no Post-Adapt Phase. The stimuli and procedure used in Experiment 3A were otherwise identical to that used in Experiment 2. The bars were similarly separated vertically by either 1 deg or 8 deg for the small and large targets respectively. Like Experiment 2, the target disappeared upon saccade detection but reappeared 100 ms later at the original step location.

To test whether the difference in the magnitude of adaptation is proportional to the size of the target, we tested two other target sizes in Experiment 3B. The experimental procedure was identical to Experiment 3A, except that the separation of the target bars was either 0 deg (no separation between target bars, so that bars overlap forming target that was 0.1 deg in height) or 4 deg for the small and large targets, respectively.

**Analysis**

Saccades were analyzed offline using a custom written Matlab program. All trials were previewed and those trials containing blinks were rejected. The rate of rejection was 7.6%, 15.4%, 18.6% and 7.3% for Experiments 1, 2, 3A, and 3B respectively.

The corrective saccades for each target size were also compared in both Experiments 2 and 3, their latency and vertical amplitudes for each target size were compared. The resolution of the EyeLink Tracker was approximately 0.05 deg. Therefore to exclude false positives due to eye tracker noise, we used an amplitude criterion of 0.08 deg and a velocity threshold of 10 deg/sec to detect corrective saccades.
Results and Discussion

Experiment 1. Orthogonal Adaptation With Rings Stimuli

We hypothesized that a small, more focused target would provide a stronger error signal for driving adaptation, while a larger target with more diffuse attention would induce a weaker magnitude of adaptation. In this experiment using two different sized ring targets and an orthogonal intra-saccadic step we surprisingly found that the larger stimulus induced more adaptation than the smaller stimulus. The three subjects that performed this experiment showed significantly greater adaptation in the large (8 deg) target condition than the small (2 deg) target condition (Figure 2.2, Table 2.1) and the overall magnitude of adaptation across subjects was significantly different (one-way repeated-measures ANOVA, \( p = 0.025 \)). This result was so unexpected and counter to our hypothesis that we attempted to find alternative explanations or possible confounds that could have distorted the results. We considered whether the larger ring induced more adaptation simply because the larger ring provided more visual stimulation owing to its larger circumference. Because of this disparity, we attempted to balance the targets displayed on the screen by using a pair of identical lines, but varying the space between them to set the size of the target and the scale of attention.
Figure 2.2. Orthogonal intra-saccadic displacement of 2 deg and 8 deg ring stimuli in Experiment 1. The mean horizontal component of the primary saccade was calculated for each 25 trial blocks for all three subjects and averaged together. The Pre-Adapt and Post-Adapt Phase did not have any intra-saccadic step. During the Adapt Phase (gray background), the target made a 2 deg intra-saccadic step to the right. The 8 deg stimulus demonstrates more adaptation than the 2 deg stimulus.

Table 2.1. Mean adapt amplitude for the small and large ring target for Experiment 1. The magnitude of adaptation was tested for each subject using a one-tailed t-test.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Mean Adapt Amplitude</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small (2 deg Target)</td>
<td>Large (8 deg Target)</td>
</tr>
<tr>
<td>1</td>
<td>1.16</td>
<td>1.31</td>
</tr>
<tr>
<td>2</td>
<td>1.47</td>
<td>1.89</td>
</tr>
<tr>
<td>3</td>
<td>1.25</td>
<td>1.36</td>
</tr>
</tbody>
</table>

Experiment 2. Orthogonal Adaptation with line-pairs

Equating visual stimulus size did not alter the fact that the large target induced more saccade adaptation. Using pairs of lines that only differed in their distance of separation did not change the trend in adaptation that we observed in Experiment 1. We still found that the magnitude of adaptation of the large (8 deg) target was greater than the small (1 deg) target, as
can be seen for Subject 3 (Figure 2.3A). Although there was much variability between subjects, in general we find that the magnitude of the adaptation for 6 of the 8 subjects was significantly greater for the large target compared to the small target (Figure 2.3B) as tested using one-tailed \( t \)-tests (Table 2.2). The overall difference for all of the subjects, for the adaptation between the small and large targets was also significantly different using a one-way repeated-measures ANOVA (\( p = 0.016 \)). This adaptation of the vertical component of the primary saccade occurred very rapidly. By the second bin of the Adapt Phase of the combined data, the saccades appeared to be maximally adapted (Figure 2.3A & 2.3B). Also, recovery in the Post-Adaptation phase also appeared to be very rapid.
Figure 2.3. Experiment 2 consisted of a horizontal step of an average of 10 deg, and an orthogonal, 2 deg intra-saccadic step upwards. (A) The raw, vertical component of the primary saccade amplitudes of a sample subject is plotted along with a lowess smoother of that data. The small and large stimuli were recorded in separate sessions. (B) The vertical component of the primary saccade amplitude for all of the eight subjects was averaged in bins of 25 trials. The bands surrounding the mean points represent the
Standard Error for those means. The magnitude of saccade adaptation approached the maximum levels for both the small and the large targets by the second 25-trial bin, but was greater for the large target compared to the small target.

Table 2.2. Mean vertical component of the primary saccade for Experiment 2. We find that for 6 of the 8 subjects, this amplitude was significantly different (one-tailed \( t \)-test).

<table>
<thead>
<tr>
<th>Subject</th>
<th>Mean Adapt Amplitude</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Small (1 deg Target)</td>
<td>Large (8 deg Target)</td>
</tr>
<tr>
<td>1</td>
<td>0.26</td>
<td>1.42</td>
</tr>
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</tr>
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</tr>
<tr>
<td>4</td>
<td>0.42</td>
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</tr>
<tr>
<td>5</td>
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</tr>
<tr>
<td>6</td>
<td>0.78</td>
<td>1.23</td>
</tr>
<tr>
<td>7</td>
<td>0.18</td>
<td>0.44</td>
</tr>
<tr>
<td>8</td>
<td>0.74</td>
<td>1.74</td>
</tr>
</tbody>
</table>

Due to the rapid adaptation of both target sizes where maximum adaptation was achieved in very few trials in this experiment, we wanted to explore the adaptation with a more dynamic paradigm. We considered whether changing the intra-saccadic step amplitude in every trial would highlight target differences and make them more pronounced. This indeed turned out to be the case in Experiment 3 where we used a novel, sinusoidal orthogonal intra-saccadic step pattern (Figure 2.1C).

**Experiment 3A and 3B. Sinusoidal, Orthogonal Adaptation with line-pairs**

Since most of the adaptation for both of the large and small targets in Experiment 2 were completed by the second 25-trial block (Figure 2.3B), in Experiment 3A, we tested how well the oculomotor system could track and adapt to a dynamic intra-saccadic step and whether this differs between a small (1 deg) and large (8 deg) target. The intra-saccadic step varied in 27 trials long sine-wave cycles (Figure 2.1C), alternating between the small and large targets in alternating cycles in the same experimental session (Figure 2.4).
Figure 2.4. Individual subject’s average vertical saccade amplitude averaged at each cycle trial number for the small and large targets. The bands represent the Standard Errors at each value.
We found that the target size affected how well the sinusoidal displacement was tracked, with the large targets adapting more quickly and to a greater magnitude than the small targets (Figure 2.4). In Experiment 3A, compared to the 1 deg target, the oculomotor system was able to track the vertical, sinusoidal intra-saccadic step of the 8 deg target more reliably. Across different cycles, there was no learning of the sinusoidal intra-saccadic step. Therefore, with further exposure during the course of the experiment, the vertical saccade for first trial of each new cycle did not change. The results for Experiment 3A were very consistent across subjects, the maximum vertical gain during the adapt period was greater for the large target compared to the small target for all 12 subjects (Figure 2.5).

![Figure 2.5](image.png)

**Figure 2.5.** For Experiment 3A, the average vertical component of the primary saccade at each cycle trial number was calculated across all twelve subjects for the small and large targets. The bands represent the Standard Errors at each value.

When fitting the vertical saccade amplitudes for the small and large size conditions to the target sine wave pattern of intra-saccadic displacement, the average peak fit amplitude was 0.31 deg for the small target, and 0.78 deg for the large target (Table 2.3). The average adaptation for all the subjects shows the same trend (Figure 2.5). The difference in the peak sine fit amplitude between the small and large target was significantly different (paired t-test, p< 0.0001).
However, neither target size achieved full adaptation to the vertical, sinusoidal intra-saccadic step with a maximum amplitude of 2 deg. The phases of the sine wave fits for the small and large targets (Table 2.3) were not significantly different (paired t-test, p=0.22), so the tracking of the intra-saccadic was not faster for the large target compared to the small.

Table 2.3. For each of the twelve subjects that performed Experiment 3A, the vertical component of the primary saccades were fit to a sine-wave curve. We used the amplitude of the fit to assess the magnitude of adaptation.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Amplitude (deg)</th>
<th>Phase (deg)</th>
<th>Amplitude Difference</th>
<th>Phase Difference</th>
</tr>
</thead>
<tbody>
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<td>8 deg</td>
<td>1 deg</td>
<td>8 deg</td>
</tr>
<tr>
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<td>1.4890</td>
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<td>-31.49</td>
</tr>
<tr>
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By testing a range of target separations, we found that the magnitude of adaptation tended to increase systematically with target separation. Combining subjects’ sessions with 0 and 4 deg target separations (Experiment 3B), to their Experiment 3A data we find that in 3 of 4 subjects, the magnitude of the adaptation was greatest for the 8 deg target and decreased progressively as the target size decreased (Figure 2.6). Thus the magnitude of the adaptation was surprisingly smallest for the smallest target (0 deg). The average amplitudes for the sine wave fits for the four subjects were: 0.39, 0.52, 0.99, and 1.03 for the 0, 1, 4, and 8 deg targets respectively. The saccade amplitudes for the 0 deg and 4 deg targets were significantly different from one another.
(one-tailed \( t \)-test, \( p=0.047 \)), as were the saccade amplitudes for the 0 deg from the 8 deg (one-tailed \( t \)-test, \( p=0.009 \)).

**Figure 2.6.** This figure combines the 1 deg and 8 deg target data from Experiment 3A with the 0 deg and 4 deg data of Experiment 3B for the 4 experienced subjects who performed both Experiments 3A and 3B. Each figure represents the individual subject’s average vertical saccade amplitude averaged at each cycle trial number for each target size. The bands represent the Standard Errors at each value. For three of the subjects, the saccade amplitudes progressively increased with the target size. S1, S2 and S3 are subjects S1, S2 and S3 from experiment 3A, S4 is subject S11 from experiment 3A.
Comparison to previous hypothesis and studies:

Although the results from Experiment 3 that the large target demonstrated more adaptation than the small target was consistent with Experiments 1 and 2, they were very different from our original hypothesis. There have been few experiments in the past that have looked at the connection between the scale of attention and saccade adaptation. One such study concluded there was no difference between adaptation of a small point target and a larger target with a diameter of 3 deg (Bahcall and Kowler, 2000). They compared the time course and magnitude of saccade adaptation between the two sized targets and concluded that there was no difference in either characteristic. However, there were a few ways that our experiments varied that could have contributed to our contrasting results. One important difference between our protocols was that in Bahcall & Kowler’s (2000) study, all of the stimuli and step sizes were much smaller. Their largest target was 3 deg, which they compared to a spot, with target steps that were between 3.8 and 4.2 deg, and a 0.8 deg intra-saccadic step (while we compared a 1 and 8 deg target with a 10 deg step and 2 deg intra-saccadic step). Perhaps these size differences were not large enough to induce differences in adaptation. Although the stimulus sizes we used in Experiment 3B were closer to what Bahcall and Kowler (2000) used, our 2 deg intra-saccadic step was more than double the 0.8 deg tested by Bahcall and Kowler (2000). Also, they tested two or three subjects in each condition, while we tested more subjects in case of variability between subjects. Another key difference was that they discouraged corrective saccades, instructing subjects to try to make a single saccade to the target. However, we believe that it may have vitally contributed to the difference in magnitude of adaptation that we observed.
Contribution of corrective saccades on adaptation and attention scale:

If we consider the possible role that corrective saccades may have on the magnitude of saccade adaptation by comparing in a thought experiment two extreme corrective saccade behaviors, we would expect two very different outcomes. If corrective saccades were made in every trial immediately, with a 0 ms latency, there would be no drive to adapt the saccadic amplitude and we would expect to see very little adaptation. Conversely, if there were no corrective saccades possible then the motivation to adapt the saccadic amplitude would be very high. In this situation, there would be a trade off between the magnitude of adaptation that is induced and the corrective saccades in that when gaze does not land on the target, adaptive mechanisms are engaged to increase accuracy. This is similar to adaptation that was induced without an intra-saccadic step by eliminating the corrective saccades, thereby motivating subjects to make primary saccades which were more accurate (Bonnetblanc and Baraduc, 2007). We observe that the magnitude of adaptation is consistently greater for the larger target, and we know from our previous experiments that the temporal properties of saccades are also influenced by the target size.

We considered not just the spatial dimension of retinal error, but the temporal dimension as well by exploring the possibility that a variable duration of retinal error could result in variable adaptation as well. We believe that the observed differences are due to the Size-Latency Effect, saccades made outside the attended area have a shorter latency than those made inside (Madelain et al., 2005; Harwood et al., 2008). The primary step was outside the attended area for both target sizes, therefore we considered the first corrective saccades made to the intra-saccadic step in the Adapt Phase. Even the peak intra-saccadic step of 2 deg would be within the attended area for the large target, but outside the attended area for the small target. Therefore, if the
corrective saccades to the large target occurred later, the eyes would not be centered on the target for a longer period of time; perhaps this delay increased the motivation to adapt the primary saccades. Alternatively, if the corrective saccades to the small target occurred faster than the large target, there may be less motivation to adapt the amplitude since less time is spent not focused on the target.

We examined the corrective saccades for Experiment 3A and 3B to see if their behavior was consistent with the Size-Latency Effect. We find that corrective saccades to the larger target had longer latencies compared to the small target (significantly greater in 11 of the 12 subjects using one-tailed t-tests, and significant at the group level using Repeated Measures ANOVA, p<0.0001), which was consistent with the Size-Latency Effect. In addition, for comparable corrective saccade amplitudes, the movements toward the larger target have larger latencies (Figure 2.7A). The corrective saccades also displayed an increase in saccade latency proportional to the size of the target for all 4 subjects in Experiment 3B (Figure 2.7B). We observed that the magnitude of adaptation as measured by the peak adaptation amplitude and the median latencies of the corrective saccades have a positive relationship (Figure 2.7C & 2.7D). To test whether the positive slope of the linear regression was significant, we used a bootstrap procedure that resampled our data 10,000 times creating a bootstrap normal distribution and tested the probability that the slope for the linear regression of our data could be arrived at randomly. For Experiment 3A, as the magnitude of adaptation increases, the latencies of the corrective saccades significantly increase as well (m=60.6, p = 0.02; Figure 2.7C). And similarly for Experiment 3B, we find a positive significant relation across the four different target sizes (m=42.9, p=0.02; Figure 2.7D). A possible caveat is that because smaller amplitude corrective saccades also have greater latencies, we also compared the median corrective latencies within a constrained range of
corrective saccade amplitudes of 0.7-1.0 deg. For Experiment 3A, we find a similar positive relationship between adaptation and the corrective saccade latency even though the saccade amplitudes themselves were of a similar size, the slope was not significant however, but the relationship was significant for Experiment 3B. Since both the magnitude of adaptation and the corrective saccade latency were two separate empirical measures, we also tested their positive relation using a bivariate linear regression that would be free of the assumption that the adaptation was an independent variable. This produces a steeper slope for the data and not surprisingly we found that both the relations for Experiment 3A and 3B were significant. Although we cannot definitely conclude that there is a causal relation between the two measures, we observe that there is a strong relation between the Size Latency Effect and the magnitude of adaptation.
Figure 2.7. (A) For each fifth or quintile of the corrective saccade amplitude, the average corrective saccade latency was calculated. This was done for each of the 12 subjects that performed Experiment 3A. The data for all of the subjects, for the small (red) and large (blue) targets were fit using a Power Fit law function ($f(x) = a \cdot x^b$), as well as for a sample subject (S3). (B) The same was done for the four experienced subjects and for their data from Experiments 3A and 3B. We see that as the stimulus size progressively decreased, the corrective saccade latency at each quintile of corrective saccade amplitude also decreased. (C, D) Correlation between the adaptation magnitude at the peak of the cycle and median corrective saccades SRT for every subject in every condition of experiment 3A (C) and 3B (D).

**Line-targeting caveat:**

A possible caveat for this experiment is that subjects may have targeted one of the lines itself instead of the center of the target, since for the smaller (1 deg) target one of the lines is closer after the intra-saccadic step than either line for the larger (8 deg) target, giving the larger target a larger error signal. If it were the case that retinal error to either line alone drove adaptation, we would expect that the 0 deg target from Experiment 3B would induce greater saccade adaptation than the 1 deg target since it would also be further after the intra-saccadic step than the 1 deg target. We found that for the four subjects that performed both Experiment 3A and 3B, the 0 deg did not demonstrate greater adaptation than the 1 deg target, it was in fact smaller than the 1 deg target although not significant as tested by a one-tailed $t$-test ($p=0.20$). Therefore, we conclude that the retinal error at the end of a saccade to one of the lines that the targets were composed of could not be responsible for the variable adaptation and that a single line of the target was not likely to be the saccade goal, but the center of the target was.

**General Discussion**

With an unconventional paradigm of saccade adaptation where the intra-saccadic step was orthogonal to the initial target step, we show that different sized targets demonstrate very different magnitudes of adaptation. In Experiment 1 and 2, we show that compared to a small target (2 or 1 deg), a larger sized target (8 deg) is able to induce a greater magnitude of saccade
adaptation to an orthogonal intra-saccadic step. The maximum magnitude of saccade adaptation, for when the intra-saccadic step was fixed and the visual stimuli equated in Experiment 2, was also closer to the intra-saccadic step of 2 deg for the large target compared to the small. But more interestingly, we show that the oculomotor system demonstrated saccade adaption in all target sizes to non-fixed intra-saccadic steps, which varied in each trial in a sine-wave pattern orthogonal to the primary step. Also, the magnitude of saccade adaptation induced increased proportionally to the size of the target. Therefore, the magnitude of the adaptation was closest to the peak intra-saccadic step deviation of 2 deg for the large 8 deg target, and the smallest amount of adaptation for the smallest target of 0 deg separation.

We consistently found across experiments that the magnitude of adaptation for the larger target was greater than the small target, which was contrary to our original hypothesis, and the reason for such remains unclear. Since increasing the uncertainty about target location decreases the magnitude of motor adaptation that can be induced, (Kording and Wolpert, 2004), we were surprised that the larger target which would provide a more diffuse error signal actually produced greater adaptation. Even though we did not include an attentional task, it has been shown that the scale of attention changes quickly and automatically to match a presented target (Hopf et al., 2006). Therefore, we assume that the scale of attention automatically adjusted to the target separation size. And thus, a possible mechanism that we explored since we observed such a large difference in the behavior of the corrective saccades between the target sizes, is that a mechanism similar to the Size-Latency Effect for different attention scales (Madelain et al., 2005; Harwood et al., 2008) could be involved. We observe that not only did the larger targets demonstrate a greater magnitude of saccade adaptation, but they also demonstrated longer corrective saccade latencies. Perhaps the delay in corrective saccades for the larger targets
encourages the oculomotor system to adapt to the intra-saccadic step faster. This is supported by the positive relationship between the adaptation and the latency of the corrective saccades.

Alternatively, if the oculomotor system was simply using retinal error alone to drive adaptation, such that subjects were targeting the nearest point of the stimulus- the closer line (at the end of the intrasaccadic step) that the target was composed of instead of the center of the target (as instructed) then that would explain why the large target induced more saccade adaptation than the small. Both lines for the 8 deg target were further than those from the 1 deg target. However, the lines for the 0 deg target were also further than those from the 1 deg target at the end of the primary saccade, which would have yielded a greater retinal error, and yet it did not induce greater adaptation than the 1 deg target. The 0 deg target in fact demonstrated less adaptation than the 1 deg target, allowing us to exclude this explanation. Together, this suggests that a combination of motor error and visual error at the different attention scales for the different target sizes were responsible for the larger magnitude of adaptation to the larger target.

Saccade adaptation experiments have typically used small targets, but our results were also very different from the conclusion of the previous saccade adaptation experiment that had employed larger targets (Bahcall and Kowler, 2000). However, our results were very consistent throughout our different experiments and across experienced and naïve subjects alike. We therefore decided to more closely examine the results from the Bahcall and Kowler (2000) study. In their (2000) paper, they describe that the small, point-like target was able to induce saccade adaptation that was 77% of the intra-saccadic step but do not state what the magnitude of adaptation was to the large (3 deg) target, just that it was “quite similar.” From their summary figure, we graphically calculated the magnitude of adaptation for each subject and condition, and found that the small target induced an average of 77% adaptation, but the large target induced an
average of 86% adaptation. It was difficult to compare the magnitudes of adaptation for the small and large targets for each subject directly since each subject was not tested in every condition and/or were tested twice. But for the two subjects that performed both conditions, both demonstrated a greater magnitude of adaptation in the large condition (90 and 83%) compared to the small target (83 and 72%). This greater magnitude of adaptation for the large target may not have been significantly different from the small target (it would be difficult for us to test based on the limited data we have), but the trend of the data from Bahcall and Kowler (2000) appears similar to our results.

Another possibility that we would like to explore is whether the larger visual target or the larger scale of attention provides a larger error signal for greater saccade adaptation? Even though it has been shown that the scale of attention adjusts to the size of the target (Hopf et al., 2006), we would like to use identical visual stimuli in both size conditions and require a voluntary scaling of attention. An experiment that we would like to perform in the future would be to combine the large and small targets into a single target while instructing subjects to attend to one target size, with the addition of an attentional task. This would also be a step closer to the viewing of the real world where we voluntarily select which targets (and therefore which scale) are attended.

Our experiment highlights the importance of performing experiments that are more visually complex than simple, point-targets. The reasoning and body of evidence that supports conclusions for very sparse targets may not be applicable to behavior in the natural world where we view targets of a much larger attentional scale as well. Past work led us to expect a more focused target and scale of attention to induce more adaptation. However, outside of saccade adaptation studies, behavior and physiological comparisons have been made with larger targets.
and the scale of attention that could suggest that the opposite would be true. One such study found that a larger target displayed a larger area of attentional enhancement in the cortex, with the most modulation observed in V1 (Muller et al., 2003). Also, activity for a larger scale of attention has been associated with the higher-level, more anterior visual area (the lateral occipital complex) compared to a smaller scale of attention which has been associated with the lower, the more posterior area (V4) (Hopf et al., 2006). Therefore, perhaps the differences in which cortical areas are engaged with larger scales of attention- higher cortical areas, as well as the larger area of recruited cortex to attend to a larger target results in a proportionally greater magnitude of adaptation as well.


Chapter 3: The locus of attention can induce saccade adaptation

Abstract

When a saccadic eye movement consistently fails to land on an intended target, saccade accuracy is maintained by gradually adjusting the movement size of successive saccades. The proposed error signal for saccade adaptation has been based on the distance between where the eye lands and the visual target (retinal error). We studied whether the error signal could alternatively be based on the distance between where the eye lands and the locus of attention. Unlike conventional adaptation experiments that surreptitiously displace the target once a saccade is initiated towards it, we instead attempted to draw attention away from the target (which stepped but then remained in place) by briefly presenting a novel visual distractor on one side of the target after the saccade was initiated. To test whether a less novel distractor would induce less adaptation, we used a random noise pattern in a separate experiment and compared the magnitude of downward adaptation. We found that both visual attention distractors were able to induce a small degree of downward saccade adaptation, which was also significantly smaller for the random noise pattern. As in conventional adaptation experiments, upward adaptation was less effective and the novel distractor did not significantly increase amplitudes. We conclude that the discrepancy between the locus of attention and the landing position of the eye can act as an error signal for saccade adaptation.

Introduction

Saccades are the rapid eye movements that we use to explore the visual world. They typically last a few tens of milliseconds, so the ongoing movement cannot use visual feedback for guidance (Becker, 1989). This means that the size and direction of the saccade is planned...
before the eyes move and accuracy is maintained based on error signal(s) related to the consequence(s) of their movement.

An adaptive control mechanism ensures saccade accuracy in the face of changes in motor dynamics due to daily fatigue, aging, or pathology. When extraocular muscle impairment or weakness occurs, the initial large targeting errors diminish over time, meaning that the motor planning is able to adapt and restore saccade accuracy (Kommerell et al., 1976; Abel et al., 1978; Optican and Robinson, 1980; Snow et al., 1985). On a much more rapid time scale, in the laboratory surreptitiously displacing a target while the eye is in mid-flight with an intrasaccadic step (when vision is impaired) tricks the oculomotor system into thinking that the saccade had been inaccurate because when the saccade lands, the target is no longer on the fovea. If this occurs consistently, the oculomotor system gradually adjusts its saccade amplitude to partially compensate for the imposed error (McLaughlin, 1967). Despite the observer being unaware of the displacement, their saccades land progressively closer to the displaced position rather than the initial position of the target.

There are several possibilities as to what constitutes the error signal driving such saccade adaptation. Although a simple proposal would be for the oculomotor system to track the relative direction of the primary and the subsequent small corrective saccades needed to foveate the target (Albano and King, 1989), it appears that adaptation can still take place when there are very few corrective saccades made (Wallman and Fuchs, 1998), and saccades can be adapted in the opposite direction to the correctives (Bahcall and Kowler, 2000). Retinal error, which is the distance of the target from the fovea after each saccade, has also been proposed as an alternative error signal. Since saccade amplitude can be induced to decrease when the target is displaced backwards, and increase when the intrasaccadic step is forward, the direction and distance of the
target from the fovea when the saccade lands could provide a simple possible error signal to
guide saccade adaptation (Wallman and Fuchs, 1998; Noto and Robinson, 2001; reviewed in
Hopp and Fuchs, 2004; Havermann and Lappe, 2010). However, a direct test of the potency of
retinal error alone in driving saccade adaptation in the absence of actual intrasaccadic steps,
showed that it is much weaker than that provided when the predicted target position was changed
(Collins and Wallman, 2012). Earlier evidence that adaptation is not driven by the size of the
retinal error with respect to the target, but the retinal error with respect to the predicted location
was provided by Bahcall and Kowler (2000). They demonstrated that there was no saccade
adaptation when subjects were instructed to make saccades not to the target, but to a location that
was 75% of the distance to the target, showing that the retinal error at the end of the saccade to
the target alone was not sufficient to cause saccade adaptation. But with the same saccade goal of
75% of target distance, adaptation was seen when the target did make intra-saccadic steps
(despite the retinal error always remaining the same sign), suggesting it is the retinal error with
respect to the predicted location that is key. More remarkably, another experiment demonstrated
that the amplitudes of saccades could be adapted in the complete absence of any visual feedback
after the completion of the saccade (Madelain et al., 2011). Using auditory reinforcement to
reward certain ranges of saccades amplitudes, it was possible to induce saccade adaptation in
both the increasing and decreasing directions.

Attention is intimately linked to saccade targeting since it is required for object selection
and moves to the target location before every saccade (Hoffman and Subramaniam, 1995;
Kowler et al., 1995; Deubel and Schneider, 1996; Castet et al., 2006). These pre-saccadic covert
attentional shifts can be adapted in the absence of a saccade, by shifting a discrimination target
after the average time to shift attention, and following this attentional adaptation, saccades go to
the adapted location of attention (McFadden et al., 2002). We propose that attention may be a placeholder that allows the oculomotor system to keep track of the target across the saccade: If the locus of attention coincides with that of the fovea just after a saccade, the saccade is regarded as accurate; if the fovea is consistently on the far side of the locus of attention, the saccade is regarded as too large, and this error signal induces downward adjustment of subsequent saccade amplitudes. This placeholder role for attention was invoked to help explain the perceived stability of the world across saccades to stationary targets (Cavanagh et al., 2010).

To test this attentional signal in adaptation hypothesis, we performed an experiment that differed from the conventional saccade gain adaptation experiment in that, after each saccade, we moved not the target, but the locus of attention. Our experiments took advantage of the fact that exogenous attention shifts more quickly than the eyes, and we drew attention away from the target with a distracting stimulus during the time period just after saccades when saccade error would normally lead to a gain change (Shafer et al., 2000). This created a mismatch between the fovea and the locus of attention, even if the saccade had been accurate. We show that if a stimulus is sufficiently salient so as to attract attention away from the target while the eye is in flight, it can induce saccade adaptation in the direction of the attentional shift.

Methods

Subjects

Two experienced and twelve naïve subjects participated in Experiment 1 (7 female, 7 male) including two of the authors. Two experienced and eight naïve subjects participated in Experiment 2 (4 female, 6 male) including two of the authors. Naïve subjects were recruited from the City College Psychology Department and received course credit for their participation. All subjects had either normal or corrected vision. The Institutional Review Board of the City
College of NY approved the experimental protocol, and all subjects signed consent forms before participation.

**Equipment**

The stimuli were generated and under the control of an application written in LabView (National Instruments). Stimuli were displayed on a 22 inch Compaq color, CRT monitor with a vertical refresh rate of 160 Hz. For all experiments, luminance of the background and target was 14.9 cd/m² and 3.4 cd/m², respectively. Subjects observed the stimuli while seated 57 cm away from the monitor, in an otherwise darkened room.

**Eye Movement Recording and Analysis**

Eye movements were recorded using an infrared video eye-tracking system (EyeLink, SR Research Ltd, Mississauga, Ontario, Canada), which sampled pupil position at 1000 Hz. Calibration was based on having each subject fixate a 0.1° target at 9 locations near the corner and center locations of the screen immediately prior to the experimental session. During the experiments, the distractor onset was triggered when a saccade was detected based on a velocity threshold criterion of 30°/sec. During analysis, saccade start and endpoints were defined by a 10°/sec velocity threshold. Subjects’ head position was held steady during the experiment by use of a chin and forehead rest.

**Procedure**

Each subject’s task was to follow a target spot (0.1° in diameter), while they were tested consecutively in three phases. The first phase (“pre-adaptation”) and last phase (“post-adaptation”) were identical and each consisted of 100 trials to assess normal saccade gain to a target step under open-loop conditions. The intervening 2nd phase (“adaptation”) consisted of 250 trials in which attentional distractors were present.
In each trial during the pre-adaptation and post-adaptation phases, the target spot randomly stepped left or right, initially from a central fixation position and subsequently from its previous target location on successive trials. During every experiment, the target moved only along the horizontal meridian and never moved further than 13° from the center of the screen. The target step size was randomly varied between 7° to 9° and occurred 900-1400 ms after the end of the previous trial. As soon as a saccade was detected based on the velocity threshold, the target spot disappeared for 500 ms, and then reappeared in the same location until the end of the trial. The complete trial length was 1800 ms. In theory, this brief removal of the target once the saccade was underway should prevent any immediate postsaccadic visual error from mitigating any adaptation that had been previously established in the post-adapt phase. The change in saccade gain between the pre-adapt and the post-adapt phases was the primary measure used to determine the effect of the adaptation trials on saccade gain.

The adaptation phase consisted of 250 distractor trials in which the target spot stepped the same as in the other two phases, but when the saccade occurred, there were two differences: first, the target remained continuously on until the end of the trial (again trials were 1800 ms long); second, additional attentional distractors were presented either on the near side of the target (referred to as adapt-down condition) or the far side of the target (referred to as adapt-up condition) during and after the saccade in Experiment 1. In Experiment 2, the distractors were always presented on the near side of the target. The details of distractor type and location varied in both experiments as described below. In addition, there were 25 interleaved trials in which the target disappeared upon saccade detection similar to the pre- and post-adaptation trials.
**Experiment 1. The effect of visual distractors in the adapt-down and adapt-up condition.**

The aim in this experiment was to use novel visual stimuli to attract attention away from the target position during the postsaccadic window so that an attentional error signal might be generated. To do this, during the adaptation phase, when the subject made a saccade to the target (0.1° red spot on a white background which stepped 7-9° randomly to the left or the right), one of 35 different distractor images were randomly selected to appear consistently centered at 3° on the inner side of the target (i.e. at 62.5% of the initial target step, on average) for 300 ms. This timing was selected to allow sufficient time for attentional disengagement with the target and brief reallocation to the visual distractor. It should be noted that since the spot was left on, and the trial lasted for 1.8 sec, there were plenty of attentional resources allocated to the target location with which our early attentional disruption had to compete. The large number of possible distractors was in order for the distractors to remain novel and to prevent habituation to the distractors so that they might continue to draw attention over the 250 adaptation trials. Each image was presented no more than 8 times. Distractors consisted of birds, other animals, anime characters, recognizable objects, and popular cartoon characters. Each image was 2.1° in horizontal width and varied in height between 1.5° and 3.5° (an example is shown in Figure 3.1).

In the adapt-down condition of Experiment 1, we asked whether a strong visual attentional signal located on the near side of the target, might also be able to compete with the target to bias saccades to decrease their amplitudes. The adapt-up condition of this experiment was identical to the adapt-down condition, except that the visual distractors were centered 3° on the far side of the target spot. The same subjects were tested in both the adapt-down and adapt-up conditions, to compare the effectiveness of attentional location to cause amplitude decreases versus increases, respectively.
Figure 3.1. (A) Diagram of screen appearance and timing during the downward adaptation trials for the three experiments. Trials in all three experiments consisted of a fixation, which stepped to the left or right after a brief variable delay (900-1400 ms, of which only 400 ms was recorded). Diagram shows a rightward step example only. Upon saccade detection, a visual distractor was presented for 300 ms, after which it disappeared leaving only the target on the screen in the stepped location. An example of the three types of distractors used in the three experiments is shown (drawn approximately to scale). See text for a description of the full set of distractors used in each experiment. (B) A schematic of target, distractor, and eye position during an adaptation trial. After the target step, the eye follows with a saccade, upon which time a distractor is presented a short distance from the target, which remains at the stepped location for the remainder of the trial.
**Experiment 2. The effect of non-attention attracting distractors on the near side of the target.**

In Experiment 2, we asked whether a distractor that was less attention grabbing than those used in Experiment 1 would cause an equal or diminished magnitude of adaptation. This experiment was identical to the adapt-down condition of Experiment 1, except that the visual distractor used was a random noise pattern that was similarly 2.1° in horizontal width and also varied in height between 1.5° and 3.5°. This will be referred to as the “non-novel condition.” The same subjects also performed a task that was identical to the adapt-down condition of Experiment 1 (to be referred to as the “novel condition”) in order to compare the magnitude of adaptation to the novel distractor images with that of the non-novel, repetitive noise pattern.

**Data analysis**

The data presented here are the changes in the gain of the primary saccade during the pre- and post-adaptation phases, which were the open-loop saccade periods before and after the attention distractor trials. All trials were previewed in a custom graphical interface (Matlab, The Mathworks, Natick, MA). Statistical tests for individual experiments were based on paired t-tests. The raw data are shown together with a 20 point moving average calculated separately for each phase of the experiment. Saccade amplitudes elicited when the distractor was on the near or the far side of the target were compared using a Repeated Measures ANOVA.

**Results**

In brief, we found that a novel visual stimulus displayed on the near side of the target after the saccade was underway caused a decrease in saccade gain. The magnitude of adaptation was reduced when a non-novel, neutral distractor stimulus was used in all of the adapt trials instead of the novel visual images. The novel images in Experiment 1 were used to increase the
attraction of attention away from the continuously visible, unchanging target, and towards the locus of the distractor. These findings suggest that a discrepancy between the locus of attention and the fovea can provide an error signal to drive saccade adaptation. Moreover, when the distractor is not novel, the magnitude of adaptation that the distractor is able to induce is diminished.

**Experiment 1: Novel images can change the saccade gain**

Example of the raw data from one subject in both the adapt-down and adapt-up conditions of Experiment 1 is shown in Figure 3.2A. It is evident that in the adapt-down condition the saccade gain declined throughout the adaptation portion of the experiment. We found that when the visual distractor was on the near side of the target, the postsaccadic gain decreased significantly in 9 out of 14 subjects (p < 0.05 in all 9 cases), and was highly significant in seven of these subjects (p ≤ 0.01). We calculated the percentage adaptation, which was the difference in saccade gains between the pre- and post-adaptation phases divided by the maximum gain change possible (calculated as the difference between the pre- and post-adaptation phases relative to the percent distance of the distractor from the target). Across subjects, the average decrease was 11.5 ± 2.9% (One-way Anova (Repeated Measures), F=10.9, p=0.006) after 250 adaptation trials (Figure 3.2B).

In the adapt-up condition when the distractor was presented on the far side of the target, the distractors were less effective in increasing the gain than decreasing it (Figure 3.2). Gain increased significantly in only four subjects (one-tailed t-tests). Across subjects, the average increase in gain between the Pre- and Post-adapt gain was 0.6 ± 16.6% which was not significant (One-way ANOVA (Repeated Measures), F= 0.0876, p=0.77; Figure 3.2B). However, the
difference between the gain decrease and gain increase condition across all subjects was highly significantly different (Repeated Measures ANOVA, $F = 13.2$, $p = 0.003$).

Figure 3.2. (A) Saccade gain data of subject S1 during Experiment 1 in which distractors consisted of novel images. Gain decreased gradually in the adapt down condition (Experiment 1A, closed circles, black curves), and displayed a significant decrease in gain of the post-adaptation phase from the pre-adaptation phase. The adapt up condition did not demonstrate any significant change (Experiment 1B, open circles, gray curves). (B) Percentage adaptation (calculated as the difference between the pre- and post-adaptation phases relative to the percent distance of the distractor from the target) for each subject. Mean and standard error across all subjects is shown on the right.
**Experiment 2. Non-novel random noise on the near side of the target caused less of a decrease in saccade gain.**

A non-novel, random noise distractor alone was able to decrease saccade gain when presented on the near side of the target, as can be seen by the raw data from a sample subject in Figure 3.3A. Comparing the saccade gain during the pre-adaptation and post-adaptation phases, we found a significant decrease in eight out of the ten subjects in the non-novel condition. The overall decrease across subjects for the non-novel condition was $8.1 \pm 1.0\%$ (Repeated Measures One-Way ANOVA, $F = 60.9$, $p = 0.0003$, highly significant). The magnitude of this decrease was more modest than that of the novel condition performed by the same subjects as well as the adapt-down condition of Experiment 1. The overall decrease in gain after the adaptation for the novel condition was $14.4 \pm 2.9\%$ (Repeated Measures One-Way ANOVA, $F = 24.2$, $p = 0.0008$). Both the random noise and the novel distractors caused a gain decrease, and the interaction between the Pre- and Post-adaptation gain decrease and the distractor type was significant for 4 of the 10 subjects. The magnitude of this effect is not significant in most of the subjects, but the gain decrease was smaller for the non-novel condition compared to the novel condition in 8 of the 10 subjects. The effect of distractor-type, however, was significant when all the subjects were grouped together (Repeated Measures Two-Way ANOVA, $F = 4.99$, $p = 0.05$).
Figure 3.3. (A) Saccade gain data of subject S2 during Experiment 2 in which distractors consisted of a random noise patch (non-novel) in Experiment 2A and novel images in Experiment 2B. Gain decreased gradually in the presence of the random noise distractor (Experiment 2A, open circles, grey curves), and displayed a significant decrease in gain of the post-adaptation phase from the pre-adaptation phase. The novel distractors decreased gain even more rapidly and demonstrated a significant change (Experiment 2B, closed circles, black curves). (B) Percentage adaptation (calculated as the difference between the pre- and post-adaptation phases relative to the percent distance of the distractor from the target) for each subject. Mean and standard error across all subjects is shown on the right.

**Corrective saccades.**

Corrective saccades to the distractors cannot explain our observed gain changes. Because we are testing the hypothesis that the presumed change in the postsaccadic locus of attention is
responsible for the gain changes, we needed to assess whether we had inadvertently provided other cues, in particular, whether subjects made secondary saccades to the attentional distractor and then made a third saccade back to the target when the distractor disappeared. If this occurred during the adaptation phase, the direction of the secondary saccade might function as an error signal, as corrective saccades have been hypothesized to do during normal saccade adaptation. In our experiment, although hypothetical saccades to the distractors would be followed by ones in the opposite direction, this could still function as a motoric error signal, because the saccade toward the distractors would occur earlier within the postsaccadic window that is most responsive to error signals. To evaluate this possibility, we assessed the number of secondary saccades to the distractors made during the adaptation phase of the experiment. In the adapt down conditions of both experiments, corrective saccades made to the distractor were considered those that were downwards and that resulted in eye gaze landing closer to the distractor than the target. In the adapt-up condition of Experiment 1, the corrective saccades considered to the distractor were those that were forwards and that resulted in eye gaze landing closer to the distractor than the target. During the adaptation phase of Experiment 1, when the distractors were presented on the near side of the target (adapt-down condition), saccades were made to the distractor on average in 1.6% of the total number of valid trials. Similarly, on average, during the adapt phase of the adapt-up condition subjects made corrective saccades to the distractor in 7.3% of the total number of valid trials (Table 3.1). The correlation between the number of corrective saccades with the change in saccade gain for the adapt-down condition was -0.09 (p = 0.76) and was 0.24 (p = 0.40) for the adapt-up condition. Hence, we found that the number of secondary saccades to the distractor were not correlated with the change in saccade gain, suggesting that the error signal is more likely to be related to the shift of attention than to incidence of corrective
saccades. No correlation between the change in saccade gain and the number of correctives to the distractor was found for Experiment 2 either. The correlation between the adapt-down novel-distractor condition was 0.12 (p=0.73), and for the non-novel distractor condition the correlation was 0.30 (p=0.40) (in which on average 0.9% and 0.8% of the correctives were to the distractor in the adaptation phase, respectively) (Table 3.2).

Table 3.1. Corrective saccades in Experiment 1. The percentage of adapt trials with corrective saccades for the adapt-down and adapt-up condition respectively, and the percentage of those that were in the direction of the distractor and that landed nearer the distractor compared to the saccade target.

| Subject | Adapt-Down Condition |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |  |
|---------|----------------------|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|--|
|         | Trials with corrective (%) | Trials with backward correctives (%) | Trials with Correctives nearer distractor (%) | Trials with corrective (%) | Trials with forward corrective (%) | Trials with Correctives nearer distractor (%) |
| S1      | 86.0                 | 2.2                  | 0.0                  | 79.4                 | 70.9                  | 0.4                  |
| S2      | 87.2                 | 1.1                  | 0.0                  | 40.6                 | 37.6                  | 2.1                  |
| S3      | 86.2                 | 7.9                  | 0.0                  | 69.5                 | 56.8                  | 0.0                  |
| S4      | 76.8                 | 5.2                  | 2.4                  | 84.1                 | 80.2                  | 4.0                  |
| S5      | 78.3                 | 2.2                  | 0.0                  | 63.9                 | 59.0                  | 0.0                  |
| S6      | 84.3                 | 6.6                  | 5.4                  | 86.6                 | 86.1                  | 12.4                 |
| S7      | 95.0                 | 0.5                  | 0.0                  | 87.3                 | 83.5                  | 0.8                  |
| S8      | 90.1                 | 0.9                  | 0.9                  | 93.5                 | 92.9                  | 11.8                 |
| S9      | 50.0                 | 28.0                 | 11.9                 | 72.6                 | 64.2                  | 56.2                 |
| S10     | 13.5                 | 5.7                  | 0.0                  | 36.6                 | 19.8                  | 0.0                  |
| S11     | 79.6                 | 2.8                  | 0.0                  | 80.1                 | 70.2                  | 3.1                  |
| S12     | 49.3                 | 2.8                  | 0.9                  | 58.4                 | 57.9                  | 5.6                  |
| S13     | 79.1                 | 1.9                  | 0.0                  | 86.6                 | 83.1                  | 1.7                  |
| S14     | 75.8                 | 3.1                  | 0.6                  | 77.4                 | 74.9                  | 4.1                  |
| Mean    | 73.7                 | 5.1                  | 1.6                  | 72.6                 | 66.9                  | 7.3                  |
| Median  | 79.4                 | 2.8                  | 0.0                  | 78.4                 | 70.5                  | 2.6                  |
Table 3.2. Corrective saccades in Experiment 2. The percentage of adapt trials with corrective saccades for the novel-distractor and non-novel distractor condition respectively, and the percentage of those that were in the direction of the distractor and that landed nearer the distractor compared to the saccade target.

<table>
<thead>
<tr>
<th>Subject</th>
<th>Novel Distractor Condition</th>
<th>Non-novel Distractor Condition</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Trials with corrective (%)</td>
<td>Trials with backward correctives (%)</td>
</tr>
<tr>
<td>S1</td>
<td>86.0</td>
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<tr>
<td>S2</td>
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<td>S22</td>
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<tr>
<td>Mean</td>
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<tr>
<td>Median</td>
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<td>3.4</td>
</tr>
</tbody>
</table>

Discussion

We find that novel distractors appearing after a saccade can lead to saccade adaptation despite the target remaining visible and stationary. In both experiments, when distractors were consistently presented on the near side of the target during the adaptation phase, we found that saccade gain gradually decreased. As we changed the salience of the distractor, the magnitude of adaptation was affected (Figure 3.3), with the greatest magnitude of adaptation induced by the novel image distractors in Experiment 2. Even though the distance between the target and visual distractor was within the range of intrasaccadic step sizes shown to be most effective for saccade adaptation (Robinson et al., 2003), the adaptation that we observed was smaller than that typical in conventional saccade adaptation experiments (McLaughlin, 1967; reviewed in Hopp and
Fuchs, 2004; reviewed in Pelisson et al., 2010). The smaller magnitude of adaptation in our experiment however is not surprising considering that the target spot did not make any intrasaccadic movements and simply remained in its stepped location even after the saccade was made. Since a postsaccadic error must persist for >32 ms to affect adaptation (Shafer et al., 2000; Panouilleres et al., 2011), although we may have attracted attention away from the fovea, it was in competition with multiple veridical cues associated with the target being located on the fovea, and the attentional shift was presumably transient, as it had to be shared between the distractor location and the target location at the fovea. The adaptation we found was similar to conventional saccade adaptation, in terms of the asymmetry of larger gain changes for downward adaptation than for upward adaptation.

**Possible error signals for saccade adaptation**

We hypothesized that an error signal for saccade adaptation could be the difference between the locus of attention before the start of the saccade and after the eye lands. Previously, either the motor error (i.e. corrective saccades) or the visual error (difference between the target position and the eyes landing position) was thought to drive adaptation (Albano and King, 1989). We know now that corrective saccades are not necessary for saccade adaptation, suggesting that the error signal is visual (Wallman and Fuchs, 1998). However, it appears that it is not purely a sensory error, but possibly the difference between the actual retinal image of the target at the end of a saccade compared to the predicted retinal image after the saccade that primarily drives adaptation (Bahcall and Kowler, 2000; Ditterich et al., 2000; Wong and Shelhamer, 2011; Collins and Wallman, 2012), and yet visual feedback of the target is not even required for saccade adaptation to occur (Madelain et al., 2011). In addition to suggesting that prediction was required in saccade adaptation, Ditterich et al. (2000) invoked attention to explain some of their
data. They argued that a large scale of attention coded their background stimulus along with the saccade target, such that the background influenced adaptation, and a small scale did not code the background, which therefore had no influence on adaptation. Here, we tested the novel hypothesis that the locus of attention can act as the error signal for adaptation, by consistently directing attention to an attention grabbing, postsaccadic distractor located a few degrees from the target. In our experiment, the target was still present postsaccadically and in the predicted retinal location. The fact that neither retinal error nor predictive error can explain our findings presents a challenge to current ideas for the error signal guiding saccade adaptation.

**Ethology of saccade adaptation**

Attention is likely to be used to maintain the accuracy of saccades since in the visually complex natural world overt attention generally follows covert attention to objects that attract our attention. Most saccade adaptation experiments however rely on very sparse visual stimuli that rarely require any target selection. This fails to reflect the continuous competition in the natural world for our limited resources. In the natural world we utilize covert attention to select our next focus of gaze (Awh et al., 2006), therefore it is likely also involved in maintaining saccade accuracy as well. Although it has been shown that attention shifts and saccades can be dissociated (Juan et al., 2004; Belopolsky and Theeuwes, 2009), it is unlikely that a saccade would be judged inaccurate if it were made to what was being covertly attended in a crowded visual scene. It has been previously shown that only the attended visual information after a saccade is utilized in saccade adaptation (Ditterich et al., 2000). Therefore, we propose that the locus of attention after a saccade is also integrated to deem whether a saccade is accurate or not.

For the purposes of saccade adaptation the oculomotor system has demonstrated the ability to select the target over other distractors presented on the screen (Madelain et al., 2010),
however we demonstrated here that novel distractors are able to interfere with this target selection. The Madelain et al. (2010) experiment was similar to ours in that a distractor was presented after saccade initiation a short distance from the target (2° or 2.4°) (our distractor was presented for only 300 ms after the saccade while theirs remained for the rest of the trial). More importantly, unlike the array of possible distractors used in our experiment, the distractor that they used was not more salient than the target; indeed, the target and distractor were interchangeable between trials (the target was simply the first of the two colored spots to appear). Although we do not perform an explicit attentional task, we think that their distractors had a very weak attention attracting effect, while in Experiment 1 the visual distractors were more varied and novel so that they attracted attention more strongly, disrupting accurate target selection. Therefore, the mere presence of a visual stimulus on the screen along with the target by itself will not elicit saccade adaptation (Madelain et al., 2010) unless, as shown in our experiments, the distractor is novel enough to consistently attract attention.

To further test this novelty explanation for the differences between our data and that of Madelain et al. (2010), we compared novel and non-novel distractors in Experiment 2 and found that non-novel distractors (but ones larger and more salient than the target) gave some, but weaker adaptation than set of novel distractors. Thus, between our two experiments and those of Madelain and colleagues we observe a spectrum of decreasing novelty and decreasing salience of distractors leading to decreased levels of adaptation, with distractors of equal salience to the target being effectively ignored by the adaptation machinery (Madelain et al., 2010). In the absence of an explicit attentional task, we conjecture that the locus of attention after the saccade is more strongly drawn away from the saccade target by larger or more novel distractors, and that this directly caused the differences in adaptation that we have observed.
**Alternative Explanations**

One might argue that the gain change occurs because the oculomotor system does not distinguish between the saccade target and the attentional distractors, despite their diversity and dissimilarity to the target. That is, the center of gravity of all the stimuli on the screen might be used for computing an error signal, or adaptation occurs due to some averaging of the target and distractor locations such as in the global effect (Findlay and Gilchrist, 1997), albeit postsaccadically for our situation since the distractor was not present at the time of saccade onset. However, no global averaging of the target and distractor locations was found in a similar experiment where the distractor was similar in appearance to the target (Madelain et al., 2010). Under these conditions, despite a global stimulus configuration similar to ours, the oculomotor system effectively distinguished between the target and the distractor. Furthermore, if the purely visual signal of having more stimuli on one side of the fovea than on the other might act as an error signal to adjust the saccade gain in the directions shown here, it is surprising that such a small percentage of the secondary saccades (average of 7.2% for adapt-down condition in Experiment 1, and 16.3% for the adapt up condition) were made to the distractors, making it unlikely that they were regarded as the saccade target. Additionally, if the global effect were responsible for the saccade adaptation that we observe, we would expect that the magnitude of the adaptation might be similar between upward and downward adaptation, and between the novel and non-novel conditions of Experiments 2. But, we find that the non-novel distractors cue used in Experiment 2 produced a gain decrease that was about half of that produced in the novel condition (the only difference between the two conditions was the use of novel images compared to random noise distractors of the same size).
**Similar characteristics to conventional saccade adaptation**

The gradual adaptation in our distractor paradigm was similar to adaptation elicited in conventional intrasaccadic paradigms. In Experiment 1 there was the same asymmetry as found in conventional saccade adaptation between the magnitudes of saccade gain change in the adapt-up and adapt-down conditions (Figure 3.2). The adapt-down condition demonstrated a significant decrease while there was no significant change in the adapt up condition in Experiment 1. Conventionally, subjects frequently do not increase gain and an asymmetry in the degree of adaptation between the two directions has often been seen (reviewed in Miller et al., 1981; Semmlow et al., 1989; Hopp and Fuchs, 2004; Tian and Zee, 2010). Therefore it is unsurprising that we also did not find an increase in gain in the adapt-up novel distractor condition, possibly because the attentional error signal alone was too weak to induce saccade adaptation in a direction which is already difficult to adapt.

**Neural correlate of saccade adaptation**

Further support for our finding of attention-induced adaptation can be found by considering the possible neural basis of our protocol. Both the Superior Colliculus (SC) and the cerebellum have been shown to be involved in saccade adaptation (reviewed in Hopp and Fuchs, 2004). More recently, saccade adaptation, very similar in spatial and temporal dynamics to what can be produced by the McLaughlin method (1967), can be elicited by subthreshold microstimulation of the SC immediately after the saccade (Kaku et al., 2009; Soetedjo et al., 2009). Interestingly, it has also been found that subthreshold stimulation of the SC can cause shifts of attention (Cavanaugh and Wurtz, 2004; Müller et al., 2005). Hence, not only is it likely that the SC plays a major role in saccade adaptation, but the SC has an attentional role as well. Therefore, the distractors in our study might have acted as bottom-up visual transients on a SC.
map, producing adaptation by the same mechanism as these two recent studies. Because the target was always present, competing with these transients, any such attentional error signal originating in the SC would be expected to result in smaller magnitude effects compared to conventional saccade adaptation.

In conclusion, by using attention grabbing visual distractors suddenly appearing after a saccade, we have shown that adaptation can be induced even in the presence of an unambiguous target location. This supports the notion that consistent differences between the locus of attention and the landing position of the eye after a saccade can act as an error signal for saccade adaptation. This novel hypothesis challenges the current belief that retinal or predictive error is the error signal for saccade adaptation.
References

General Discussion

The goal of this research has been to look at the interactions between attention and eye movements in active vision. In this thesis, we have demonstrated the impact of visual attention on nearly every stage of saccades (Figure I.3). In Chapter 1, we have demonstrated that by changing the size of the target, we can rapidly change the timing of a saccade. In that experiment, we took advantage of the Size-Latency effect as a useful tool in measuring the dynamics of the changing scale of attention (Chapter 1). Not only is visual attention involved in saccade preparation, the decision to move, but also in the assessment of the accuracy of the saccade as well. In Chapter 2, we showed that the scale of attention can strongly influence the magnitude of saccade adaptation that we were able to induce. A large scale of attention surprisingly produced more saccade adaptation than a small scale. In Chapter 3 we also demonstrated that the locus of attention at the end of a saccade contributes to the error signal that leads to saccade adaptation. By consistently drawing attention away from a saccade target immediately after a saccade, which we believe creates to a mismatch between the locus of attention and gaze can induce saccade adaptation.

In natural viewing, we look at complicated visual scenes, and not simple spot targets. However, currently very little is known about how more complicated visual stimuli can influence saccades since most saccade experiments are performed using simple spot targets. Using paintings of scenes and portraits, Yarbus et al. (1967) also demonstrated the importance and use of active vision when free viewing. While studying scan paths, he highlighted that we change our fixation frequently in order to acquire more information about the image (Figure D.1). Yarbus demonstrated how the scan path of eye movements change depending on the demands of the task. In addition, microsaccades were shown to help subjects with fine spatial judgments in
the completion of a task requiring very fine visual acuity and a very small scale of attention similar to threading a needle (Ko et al., 2010). Here we can see the importance of the role that active vision can have on perception and everyday viewing.

Figure D.1. Example of a Navon stimulus, which consists of a composite letter composed of smaller (different) letters (Navon, 1977).

**Scale of attention**

Normally we do not exclusively look at a single fixed, small target size. With every eye movement or attention shift we could potentially change the scale of attention. Therefore, attention has been compared to a zoom lens (Eriksen and St James, 1986). The zoom lens of attention can be shifted, and the attentional resources can be distributed and scaled over a small or large area, for example. However, there has been some debate about whether attention actually changes scales, or that attention can be split into multiple spotlights, rather than expanding to include the entire area. An experiment that tested whether the attentional locus can be split found that two spatially separated areas could be attended, while the intermediate area between them was ignored, using a steady-state visual evoked potential (SSVEP), which is the electrophysiological response of the visual cortex to a rapidly flickering stimulus (Muller et al., 2003). However, in this experiment the attended targets in the noncontiguous condition were only presented in opposite hemifields. In another imaging experiment, an RSVP task demonstrated that attention could be split between hemispheres or the same hemisphere (McMains and Somers, 2004). Multiple, distinct areas of increased activity were found in the striate and extrastriate cortices when multiple lists were attended, compared to when one of the
lists were ignored. Similar pattern of increased activity was found when lists were presented in the opposite or the same hemifield. This suggests that attention can split into separate spotlights to attend to the lists separately.

There are conflicting results from behavioral experiments arguing either side of the debate on whether attention is split or the scale expanded. McCormick et al. (1998) found that the area between cued locations was attended, arguing for an expanded scale. While Awh and Pashler (2000) had the opposite results. It is unclear why these experiments had conflicting results, perhaps the multiple spotlight argument does not preclude the zoom lens argument. What is to be remembered is that the zoom lens model of attention is a simple analogy of a very dynamic process. Because the focus of attention can be split, does not mean that attention cannot be scaled as well.

**Scale of attention affects perception**

In this thesis we focus on the scale of attention in Chapters 1 and 2. This is because in normal viewing, the scale of attention is constantly changing, and because it has such a large impact on the perception of the visual world. This is demonstrated when viewing a Navon stimulus (Figure D.2), which on a global scale is a letter that is composed of smaller letters on the local scale, the perceived letter can be completely different depending on the scale of the target that is being attended (Navon, 1977). However, scaling attention alone is not sufficient to gain attention about the visual world, the necessity to change fixation using eye movements is also very important. The phenomenon of visual crowding demonstrates the importance of combining fixation changes and attentional scaling by highlighting the limits of what scaling attention alone can do for clarifying a visual scene (Pelli and Tillman, 2008). Perception of the
target is very difficult when many flanking distractor stimuli were presented near a target, but can become much easier if fixation were changed to a closer location (Figure D.3).

Figure D.2. If fixating on or near the green plus, the letter A is very visible. If fixating on red minus, the features are visible but due to crowding the A disappears (taken from Pelli and Tillman, 2008).

Figure D.3. Demonstrates the path of the eyes and fixations during (a) 3 min or (b) 1 min of free viewing without any instruction (taken from Tatler et al., 2010)

**Scale of attention affects the decision to make a saccade**

Not only can scale of attention alter perception, but it can alter saccade planning as well. As mentioned in the Introduction, pre-cuing a target location can speed saccade latencies while distractors could delay saccade latencies (Saslow, 1967; Kowler et al., 1995; Walker et al., 1997; Clark, 1999). The magnitude of these effects are generally up to approximately 50 ms. However,
we have demonstrated a very large and robust difference in saccade latencies based on the scale of attention. We observed a saccade latency difference of ~105 ms depending on the scale of attention that is consistent with the Size-Latency Effect (Madelain et al., 2005; Harwood et al., 2008).

In Chapter 1 we studied the temporal dynamics of the change in attention scale. We took advantage of the Size-Latency Effect and observed that the distribution of saccade latencies between a small and large scale of attention were so different that with 98% reliability, we could successfully categorize the scale of attention in any single trial in which the target size did not change. We demonstrated that the scale of attention changes very quickly. Expanding or contracting the scale of attention is completed within 32 ms. In this experiment we also showed that by changing the scale of attention, the decision to move, or when to initiate a saccade can still be modified up to 149 ms before the start of the saccade. In addition, we also found some differences in behavior between whether a target expanded or contracted. First, we found that the distribution of latencies were more bi-modal when the target changed from the small to the large target size, so that the change to programming of latencies was more sudden. Whereas, in the large-to-small condition we detected intermediate latencies between those we classified as having a saccade latency corresponding to either a small or large scale of attention. Second, the size change of the target caused either a saccadic inhibition (expanding) or facilitation (contracting) when the target size-change occurred near the start of the saccade.

Although we have shown that this scaling of attention is completed within a very short period of time, we would have liked to be more precise in this measurement. Since we know that scaling of attention is complete within 32 ms, by further narrowing the range of the size-change
times and reducing the size-change epochs, we could potentially increase the resolution of our measurements. Perhaps the change of scale even occurs instantaneously, especially with the small to large size-change? In addition, we can voluntarily modify the scale of attention (Stoffer, 1993). However, in the experiment in Chapter 1 we have investigated the dynamics of only reflexively changing the scale of attention. Therefore in the future we would also like to be able to study the dynamics of voluntarily changing the scale of attention. In the experiment described in Chapter 1, we presented a single ring target, causing subjects to involuntarily conform their scale of attention to that size. However, presenting a double ring stimulus with the instruction to attend to one or the other size would require subjects to voluntarily scale their attention. Additionally, by cueing a voluntary size change, we could similarly measure the dynamics of the voluntary scaling of attention by looking at its effects on saccade latencies. Similar to what Stoffer (1993) found, we expect that it would take longer to voluntarily scale attention. We also only tested two sizes of attention scale since they had previously been demonstrated to display a large difference in saccade latency. It would be interesting to also use other ring sizes in order to measure intermediate scaling of attention than what we originally studied. As would be to compare our results with saccade reaction times to a more conventional paradigm using the same stimuli in the absence of saccades, but relying on keypress reaction time and accuracy.

Children with the developmental reading disorder dyslexia have also demonstrated an impairment in their ability to change the scale of attention (Facoetti et al., 2003). It would be useful to test these children on our size-change paradigm as well since it varies from what has conventionally been used in the past. Subsequently, such subjects could potentially benefit from a training or rehabilitative procedure consisting of a slower stimulus size-change, especially since their brain is still developing.
We know that the scale of attention can be scaled very quickly with normal subjects. It would also be interesting to know how patients with cortical lesions or other disabilities would perform. Patients suffering from parietal lobe damage resulting in the condition simultanagnosia are unable to bind multiple objects to make a whole. Such patients’ attention would be drawn to the small elements of a stimulus instead of the global element, so that they would quite literally miss the forest for the trees. When tested on the global Navon stimuli, simultanagnosia patients perform better when the stimuli were small and densely packed (Dalrymple et al., 2007). Since we know how long it takes normal subjects to change their scale, perhaps we could use the ring stimulus that we employed in Chapter 1 to cue subjects to the global scale of a multiple-element target such as a Navon stimulus. Perhaps by having subjects first expand their attentional scale by using our large target, and then presenting the Navon stimulus could aid in rehabilitation so that they may be able to maintain a larger scales of attention and successfully combine more local stimulus elements into a whole global stimulus.

**Scale of attention and the assessment of accuracy**

Once a saccade is made, if an error signal is present, the properties of successive saccades will be modified. We showed that the amplitude and direction of saccades could be variably modified based on the scale of visual attention. The error signal for saccade amplitude is not completely known, but there are several different possibilities. Visual error has currently been described as the most likely source for saccade adaptation (Wallman and Fuchs, 1998), although other sources of error have also been demonstrated such as prediction error (Bahcall and Kowler, 2000; Wong and Shelhamer, 2011; Collins and Wallman, 2012), location reinforcement (Madelain et al., 2011), as well as attention (Ditterich et al., 2000; Madelain et al., 2010).
Does a large scale of attention lead to a variable magnitude of adaptation? This was the question we addressed in Chapter 2, and contrary to what we had hypothesized, the larger target demonstrated a greater magnitude of saccade adaptation in an orthogonal direction to the primary saccade. We find that this form of adaptation was very dynamic so that even non-fixed intrasaccadic steps were tracked very reliably. The question of the source or error signal of the variable magnitude of adaptation remains between the two sized targets and thus the scale of attention. On the surface, the task between the two conditions is identical. Subjects had to make the same sized primary saccade, as well as the same intrasaccadic steps, both to the central point of the target. As stated earlier, the scale of attention directly influences the latency of corrective saccades (so that corrective saccade latencies for a larger scale of attention were more than 100 ms longer than when attention scale was small). This most likely affected the cost-benefit analysis of making a corrective saccade (Downing, 1988; Harwood et al., 2008), and leaving gaze offset from the center of the target for a longer period of time for the large scale compared to the small scale of attention. We believe that the corrective saccades themselves were not driving adaptation, but this delay in foveating the center of the target that prolonged the visual or predicted error after the saccade. The longer corrective saccade latencies extended the duration of the error signal that possibly provided the oculomotor system with greater urgency for adaptation.

The influence of scale of attention on saccade adaptation has not been widely studied. Saccade adaptation studies generally utilize very small, sparse targets. But when we make saccades in the natural world, the scale and complexity of our targets are generally widely changing. A portion of one study has previously attempted to address this question, however Bahcall and Kowler (2000) concluded that there was no difference between the magnitude of
adaptation between a small and large target. But, upon reviewing their summary data figure visually, we found that their results were not as conclusive as they stated. It appeared that their results were consistent with our results in that the large target also demonstrated more adaptation than the smaller target. Therefore, their results do not actually contradict our findings in Chapter 2, and we conclude that the scale of attention plays an important role in both saccade adaptation for the primary saccade and the decision to move for the corrective saccades.

In the future, we would also like to study whether voluntarily scaling attention would similarly result in variable magnitudes of saccade adaptation. We expect to find a similar Size-Latency Effect in the corrective saccades, which would support our explanation if we similarly observe greater saccade adaptation with a larger scale of attention. In addition, the results of the experiment in Chapter 2 found no difference in the temporal dynamics of the adaptation to the two different sized targets, but by perhaps varying the cycle durations of the intra-saccadic steps we may be able to observe some variability.

**Locus of attention and the assessment of accuracy**

In addition to the scale of attention influencing adaptation, we showed that the locus of attention after the saccade contributes to the error signal for adaptation. There is much evidence that suggests that saccades are usually made to an attended location before a saccade (Hoffman and Subramaniam, 1995; Kowler et al., 1995; Deubel and Schneider, 1996). Building on this idea, in Chapter 3 we showed that the attended location immediately following a saccade also influences the amplitude of successive saccades. We show by consistently drawing attention away from a saccade target (either on the near side or the far side) that we can induce saccade adaptation in that direction. We used a novel, attention-attracting distractor presented upon saccade onset instead of an intra-saccadic step, and observed a gradual change in saccade
amplitude. In this experiment, the saccade target itself was not altered in any way intra-saccadically, therefore it could not be the source of the adaptation error signal. The target still remained at the expected location after the end of the saccade. Therefore there was no visual error, or other type of error from the expected location of the target. Also, the mere presence of a distractor alone does not drive adaptation (Madelain et al., 2010). The oculomotor system can distinguish between the distractor and the target. Therefore, the saccade adaptation that we observed cannot be attributed to the presentation of an additional stimulus, but we think by the distractor drawing the locus of attention after the saccade away from the target, which we believe creates an error signal driving adaptation. When we decreased the novelty of the distractors, thus decreasing the attention attracting influence of the distractor, we also observed a decrease in the magnitude of adaptation. This was an intermediate level of adaptation between our first experiment and that performed by Madelain et al. (2010). If the difference in saccade amplitudes were caused by some averaging of the locations of the target and distractor consistent with the global effect (Findlay and Gilchrist, 1997), we would not have seen differences in the magnitude of adaptation in these different conditions that directly relate to how much attention is drawn to the distractor. Even though the magnitude of adaptation that we observed was very small compared to what is normally observed in conventional saccade adaptation experiments, this was not surprising considering that the actual saccade target was unaltered intra-saccadically. We believe that the saccade adaptation that we observe in Chapter 3 is due to the distance of the locus of attention and the foveated location at the end of the saccade. One thing we would like to do in the future would be to directly measure the attention attracting ability of the distractors used, and compare them to the magnitude of adaptation that was induced. Also, we would like to vary the properties of the distractor. For example, we would like to test whether adding auditory
distractors would increase the magnitude of adaptation since multisensory cues have been shown to be more effective in attracting attention (reviewed in Spence and Santangelo, 2009).

**Conclusion**

Even though active vision is very dynamic and unconstrained, most saccade experiments and saccade adaptation experiments are performed using very simple stimuli. Although these experiments provide vital insight into the oculomotor system, they cannot form a complete picture of the mechanisms of normal viewing and can miss some of the behavior of more complicated stimuli. We demonstrate in Chapter 1 how quickly the scale of attention can be modified in active vision. Importantly, when we tested the scale of attention and saccade adaptation, our results were very different than what we had predicted based on past experiments (Chapter 2). Also, we demonstrated the involvement of the locus of attention on the error signal by using an attention attracting distractor in order to induce saccade adaptation even in the presence of the saccade target (Chapter 3). These experiments demonstrate how behavior can change when the target is slightly modified. In addition, both of these experiments indicate that visual attention after the saccade has been made can influence successive saccades and not just the upcoming saccade.

The experiments in this thesis highlight the importance of testing larger, more complicated targets instead of simply sparse spots, since results can be so different and contrary from what experiments using sparse stimuli would lead us to predict. Upon reflection, the assumption that performance of various oculomotor tasks would be identical between small, simple stimuli and large, more complicated stimuli is unreasonable. As mentioned earlier, perception of stimuli can change, therefore would strategy and motivation in different tasks not be affected as well? We observed how a large scale of attention could lead to a larger magnitude
of saccade adaptation, which opens the question of how larger, complicated stimuli could affect other oculomotor tasks as well. For example, in the double-step paradigm in which the target steps a second time before the first saccade is initiated, both saccades are programmed “in parallel” (Becker and Jurgens, 1979). It would be interesting to see whether a large-scale target would demonstrate a similar double-saccade behavior as well. Alternatively, would a diminished urgency to make a movement also change the observed oculomotor behavior. Also, how would countermanding tasks and gap tasks, in which the urgency to start the movement is manipulated, be affected by having larger, more complicated stimuli? There are potentially many different behaviors that could be affected by a different scale of attention. Studying active vision in this way would lead to a greater understanding of how we look at the world around us.
Gain adaptation of exogenous shifts of visual attention

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Abstract

Gain adaptation of saccadic eye movements is the process whereby the size of the saccade is gradually modified if the target is consistently and surreptitiously displaced during the saccade. Because one attends to the saccade target before each saccade, we asked whether covert shifts of exogenous attention might themselves be adaptable. We did this by presenting a peripheral cue and then displacing it by 3 deg after an interval equal to the average time required for attention to shift from a central to a peripheral cue. This interval, as well as the location at which attention landed, was determined by a modification of the line-motion illusion, in which a line appears to shoot from a previously cued location. We found that this adaptation paradigm produced consistent gradual reductions (for back-steps) or increases (for forward-steps) in the magnitude of the shifts of attention. Like saccadic adaptation, adaptation of shifts of attention could be manipulated independently for rightward and leftward shifts. Furthermore, the backward adaptation paradigm also decreased the magnitude of subsequent saccades, even though no saccades had been made during the attentional adaptation. This argues that saccades are targeted to the locus of attention, and when this locus is systematically shifted, so too are subsequent saccades. In conclusion, the adaptability of shifts of attention suggests that attentional shifts, like saccades, are recalibrated using a spatial error signal.

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1. Introduction

Shifts of attention are similar to eye movements in a number of ways: First, both attention and the eyes appear to move in two distinct modes. Like the eyes during saccadic eye movements, attention may, after a delay, shift suddenly and at high speed to the location of a visual object or a visual transient (Yantis, 1988); like the eyes during smooth pursuit, attention can also pursue a moving object, matching its velocity to that of the target (Cavanagh, 1992). Second, when the brain moves the eyes to pursue an object, it produces an efference copy signal, which when added to the visual motion signal results in a veridical assessment of the object’s speed, whether the eye is still (so all the motion is on the retina) or is tracking the object (so there is little motion on the retina). Tracking an object with attention can greatly facilitate measuring the speed of a moving object amidst other moving objects, suggesting that an attentional efference copy signal also exists (Cavanagh, 1992). Third, eye movements can be summoned either by a visual transient such as an object suddenly appearing or moving (exogenous saccades) or by an act of will, as during search or reading (endogenous saccades). Similarly, the locus of attention can be shifted by exogenous or endogenous cues (Yantis & Jonides, 1990). Fourth, the time to initiate saccades or to shift attention can be reduced if the fixation point is extinguished some time before the stimulus is presented (Fischer & Weber, 1993; Mackeben & Nakayama, 1993). Fifth, during search tasks, the size of the attentional field and the average saccade size are similar (Motter & Belky, 1998), and there is a similar effect of priming on saccade latency and focal attentional deployment in visual search tasks (McPeek, Maljkovic, & Nakayama, 1999).

These similarities between shifts of attention and eye movements, especially saccades, are probably not fortuitous. When a change occurs somewhere in the visual field, it attracts first one’s attention, and, a bit later, one’s gaze. Because of this attentional shift, discrimination is better and faster at the saccade target (and elsewhere in the target hemifield, Crovitz & Davies, 1962),
even if one is instructed to make a different discrimination elsewhere (Chelazzi et al., 1995; Posner, Snyder, & Davidson, 1980; Shepherd, Findlay, & Hockey, 1986). Indeed, saccades cannot be made without attention at the target location, and, conversely, one generally cannot attend elsewhere just before making a saccade (Deubel & Schneider, 1996; Kowler, Anderson, Dosher, & Blaser, 1995).

There are two distinct ways that this obligatory coupling might work: Attention might simply alight on visual features and thereby select them for the oculomotor system, which would calculate their location independently. Alternatively, saccades might be targeted specifically to the locus of attention. In this case any errors in the position of attention would produce corresponding errors in saccadic targeting. There is little evidence that bears on which of these two views is correct.

If the saccade targeting is derived from the locus of attention, one can interpret this tight coupling between the attentional and oculomotor systems in several ways. The most extreme one holds that shifts of attention are outcomes of the programming of saccades, even when the eyes do not move (Rizzolatti, Riggio, Dascola, & Umiltà, 1987). A difficulty with any model that makes attentional shifts an epiphenomenon of saccadic programming, is that it leaves unexplained why attention should possess the attribute of spatial extent as well as location, while saccades are only location based. A more moderate position holds that attention is manifested as a peak of activation on a saliency map. Competition among neurons in this map gives rise to a single winning location that corresponds to the most salient object, which then becomes the input to the saccade generator (Clark, 1999; Koch & Ullman, 1985).

How attention shifts is controversial. One view is that attention moves in a continuous (“analog”) fashion, as do the eyes, that is, moving at a finite velocity and passing over intermediate points (Shulman, Remington, & McLean, 1979). Early studies using the Posner (1980) paradigm of comparing reaction time or discrimination enhancement between a previously cued versus non-cued location supported the notion of analog shifts (Tsai, 1983), at speeds of 125 deg/s. An alternative view, based on experiments with better control of the cuing and the effects of stimulus eccentricity, is that attention moves in discrete, abrupt steps, such that shifts of various magnitudes take the same amount of time (Henderson & Macquistan, 1993; Kwak, Dagenbach, & Egeth, 1991; Remington & Pierce, 1984; Sagi & Julesz, 1985). Shifts of auditory attention have also been found to be distance invariant (Mondor & Zatorre, 1995). A third view of attentional shifts considers that attention does not shift from one point to another, but zooms in on one locus and then zooms back out before going on to another (Eriksen & St. James, 1986). Finally, one might view the “movement” of attention as illusory, being a manifestation of different points on a map gaining ascendancy over the other points. This would be true whether selective attention is an interaction among feature maps, each of which implicitly encode stimulus saliency (Desimone & Duncan, 1995), or if saliency is encoded in separate topographic maps (Itti & Koch, 2000). Whether attentional ascendancy emerges through binding or saliency, clearly the locus of attention can change. We refer to such changes in spatial locus as “shifts” of attention. Our interest in this paper is whether these “shifts” are adaptable. In particular, we demonstrate that a salient feature of the motor programming of saccades—gain adaptation—also applies to shifts of attention.

In the case of saccades, it is clear that visual information present after the saccade can influence the size of subsequent saccades. This is evident from a long line of experiments starting with those of McLaughlin (1967), in which the experimenter surreptitiously moves the target back towards its previous location while the eye is in mid-flight with vision impaired. As a result, the brain is fooled into thinking that an accurate saccade had been too large. Over many saccades this results in the saccade amplitude being gradually reduced so that the saccades land progressively closer to the displaced position rather than the initial position of the target. By similar procedures, one can cause the saccade amplitude to be increased (Albano, 1996; Semmlow, Gauthier, & Vercher, 1989; Straube, Fuchs, Usher, & Robinson, 1997) or the saccade vector to be rotated (Deubel, 1987; Noto, Watanabe, & Fuchs, 1999). Saccade adaptation is specific to the particular directions (Deubel, 1991; Semmlow et al., 1989) or amplitudes (Miller, Anstis, & Templeton, 1981; Noto et al., 1999; Straube et al., 1997). Furthermore, adaptation is specific to the type of saccade (Deubel, 1999; Erkelens & Hulleman, 1993, but see Fuchs, Reiner, & Pong, 1996), that is, adaptation of exogenous saccades does not transfer to endogenous (scanning or memory guided) saccades, perhaps because adaptation can take place in any of several saccade-generating brain pathways (Deubel, 1999; Ganvarz & Grossberg, 1999).

To look for a similar adaptational change in shifts of attention, we examined whether the magnitude of shifts of attention could be changed by a method similar to that used to demonstrate saccade adaptation. To do this, we presented to subjects, whose eyes stayed on a fixation point, a peripheral cue and then, when we estimated that their attention was shifting, we moved the cue back by 30% so that the attentional shift would appear to have been too large. Using this back-step paradigm, we examined the magnitudes of the attentional shifts to see whether the size of the attentional shift changed gradually over many trials. Furthermore, if saccades were made to the locus of attention, one might expect that if
the attentional shifts were smaller after adaptation, then subsequent saccades would also be smaller.

Because we cannot continuously measure the location of attention, as we can measure eye position, we needed to use indirect methods to determine (a) the time when attention shifts and (b) the spatial (landing) location of attention after an attentional shift. We addressed both of these needs by using different variants on the line-motion illusion of Hikosaka, Miyachi, and Shimojo (1993), which is strongly influenced by the locus of attention. In this illusion, if attention is drawn or directed to a cue, and a line is then presented adjacent to the cue, the line appears to grow (or “shoot”) from the end nearest the cue; if the line is centered on a previous cue, the line appears to shoot outwards in both directions from the cue location. This illusory motion is seen whether attention is drawn to the cue through visual, auditory or tactile means (Shimojo, Miyachi, & Hikosaka, 1997). This illusion has been explained as a result of attention speeding the processing of visual information, so that the attended part of the line is perceived first (Hikosaka et al., 1993). We found that a psychophysical paradigm using the line-motion illusion gives reliable estimates of both the latency to shift attention and the location of attention. Using this paradigm, we were able to track the magnitude of shifts of attention over time.

Our principal results are, first, that by utilizing the back-step paradigm, we gradually reduced the magnitude of attentional shifts and, second, that this adaptation reduced the size of subsequent saccades. By stepping the cue forward, instead of back, we increased the size of attentional shifts. Finally, we adapted shifts to the right without affecting those to the left. All of these characteristics have been also observed in saccadic adaptation.

2. Methods

2.1. Subjects

The subjects were 21 naive volunteers (City College students of both sexes) and one of the authors (AK). Self-selection eliminated those who were not of a patient disposition. In addition, we discarded the data of subjects whose performance on the line-motion task during the pre-adaptation phase did not pass a criterion (line-motion origin reported as more than 0.5 deg from the actual cue location or standard deviation greater than 0.5 deg). Fourteen subjects participated in Experiment 1; three of these were in both Experiments 2 and 3; and seven subjects participated in Experiment 4.

2.2. Stimuli and apparatus

Stimuli were displayed on a 21 in. green monochrome monitor at 200 frames/s and were viewed at 51 cm by subjects using a chin-rest in a dimly lit room. The fixation spot and cue were 0.33 deg in diameter; all the stimuli were light green (≈37 cd/m²) on a darker green background (≈3 cd/m²) and were generated by a computer running VisionWorks (Vision Research Graphics Inc., Durham, NH). The timing of the stimuli and the collection of the subjects’ keyboard responses were controlled by a second computer using routines written under SuperScope (GW Instruments, Somerville, MA, USA). Display timing was accurate to within 10 ms. A foot pedal was used by some subjects to initiate a trial sequence or to temporarily halt the task for brief rest periods.

2.3. Monitoring eye movements

To monitor fixation and to assess whether the adaptation of attentional shifts also affects saccadic gain (Experiment 4), we measured eye movements with an infrared limbus tracker (Model 5400, Microguide Inc., Downers Grove, Illinois, USA). The eye tracker was mounted on a frame, and head stabilisation was aided with a chin and forehead rest. Data acquisition was controlled by a SuperScope program on a Macintosh computer. The output of the eye tracker was linearized by having the subject pursue a spot moving through one cycle of a sinusoid with an amplitude of 34 deg and a frequency of 0.04 Hz. This method of calibration minimized the number and size of saccades that the subject made, thereby permitting us to recalibrate the eye movement apparatus after the lengthy attention adaptation procedure, without introducing more than a few saccades that might reverse the effects of any saccadic adaptation that had occurred.

The amplitude of each saccade was measured by the experimenter, using a computer-assisted data analysis program. Each trial was calibrated by measuring the eye position before the target step and after the eye reached its eventual stable position near the end of the 1.6-s trial. We regarded this distance as equal to the distance that the target moved. The saccadic gain was calculated as the amplitude of the saccade divided by this estimate of change in target position.

On five subjects (three of whom are included here), we monitored the eye movements during the attention adaptation experiments, to see whether fixation was maintained. We found that the subjects did not make any saccades during the adaptation experiment.

2.4. Determining time required to shift attention

To determine for each subject the time required for a shift in attention, we used a two-alternative forced-choice discrimination task using the line-motion illusion. With the subject fixating on the centrally located
fixation point, a cue stimulus identical to that used during the adaptation experiment was displayed at 10 deg randomly to the right or left. After a randomly selected delay of 60–200 ms, the cue was followed by a horizontal rectangular line stimulus (10 deg wide by 0.3 deg high), which spanned the distance between the cue and the fixation point.

If the stimulus onset asynchrony (SOA) between the cue and the line was sufficiently long for the subject to shift attention from the fixation to the cue location, the line would appear to shoot from the end located at the cue position. If the SOA was briefer, the line would appear to originate from the fixation point or would appear, veridically, to come on simultaneously across its length. The subject was instructed to identify the origin of the line-motion as either from the inner end (near the fixation point) or from the outer end (near the cue location) by selecting one of two keys on a standard keyboard. If the motion did not appear to originate from near the line’s extremities, subjects were instructed to select the key associated with the inner position, since attention had not yet shifted to the outer cued location.

The psychometric functions of the probability of the perceived line-motion origin being at the outer end of the line vs. the SOA were plotted and the raw responses were fitted with a sigmoidal curve (see example subjects in Fig. 1). The average steepness of these functions was 44 ms between the 20% and 80% points and was quite consistent (SD = 15 ms, n = 10). These results support the validity of using the line-motion illusion to determine the latency of shifts of attention, as has been previously reported (Hikosaka et al., 1993).

Approximately one day before each adaptation experiment, we calculated the attentional shift latency by an approximate psychometric function obtained by fitting the raw data with a Lowess non-linear smoother (see Section 2.7). An individual subjects’ shift time (that is, the time taken for attention to be changed from the fixation point to the target cue location) was obtained by locating the SOA equivalent to the 50% inward line-motion on this function. The mean attentional shift time was 116 ms.

2.5. Experimental design

In saccadic adaptation experiments, the target is surreptitiously and consistently displaced during the saccade, causing the eye to land beyond or short of the target. We used a similar experimental design to determine whether the magnitude of shifts in visual attention can also adapt to visual feedback. However, in our experiments the subject maintained fixation on a central 0.33 deg fixation spot while tracking an identical cue spot with covert attention. In brief, the cue stepped to the right or left of the fixation spot, and then, after the average latency for that subject to shift attention, the cue briefly turned into a grating of the same size and then returned to being a spot. The subject’s task was to identify the orientation of this grating which briefly replaced the cue. This task was designed to ensure focal attention at the cue location. During adaptation, the cue either stepped back (e.g., leftward after a rightward step) or stepped forwards by 3 deg at the moment it became the grating. Thus in this situation the cue could be described as signalling the appearance of the grating 3 deg away.

Interleaved with these grating trials (usually making up 87% of the trials) were line-motion trials (usually 13%) in which a modification of the line-motion illusion was used to identify where attention landed after a shift of attention. The trials are described in detailed in Section 2.6.

We conducted four experiments, each of which required multiple sessions: a series of training sessions (see Appendix A), a session measuring an individual subject’s attentional shift time (as described in Section 2.4) and finally the experimental session.

2.5.1. Experimental session

The experimental session of each of the 4 experiments consisted of three phases (Fig. 2): (I) a pre-adaptation baseline phase (mean across subjects = 277 trials, SD = 88 trials); (II) the adaptation phase (mean = 734 trials, SD = 142 trials); and (III) a post-adaptation recovery phase (mean = 367 trials, SD = 117 trials). These three consecutive phases were identical except that during phase II the cue stepped back or forward, after an interval corresponding to the subject’s latency to shift attention, whereas in the pre- and post-adaptation phases the cue remained at the location where it first appeared (i.e., either 9 deg or, in Experiment 3, 7 deg).
2.5.2. Experiment 1: Adaptation to back-steps in both directions

During the adaptation phase of this experiment we stepped the cue 9 deg either to the right or left of the fixation spot and then, at a time corresponding to the subject’s latency to shift attention, stepped it backwards by 3 deg. At the moment of the step-back, the cue was briefly replaced by a grating, before returning to a spot. We tested whether the magnitude of the attention shift decreased over time.

2.5.3. Experiments 2 and 3: Directional specificity of adaptation

In Experiment 2, we examined the directional specificity of the adaptation by stepping back the cue only during trials in which it had initially stepped to the right. In Experiment 3, we tested whether the magnitude of the shifts of attention could be increased (instead of decreased) by presenting the cue at 7 deg right or left and then stepping the cue forward by 3 deg only during the rightward trials.

2.5.4. Experiment 4: Effect of adaptation of attention on saccade adaptation

In this experiment we measured the gain of saccades before the pre-adaptation phase and again after the adaptation phase of an attention adaptation experiment like Experiment 1, except that the frequency of line trials was reduced to 5% to minimise their possible attenuation effect on the adaptation. To assess the gain of saccades, targets were stepped across the screen in 9–11 deg steps for 100–150 trials. When the computer detected the start of a saccade (based on a velocity criterion), the target was extinguished for 300 ms, so that the oculomotor system received minimal feedback as to the accuracy of the saccades. We chose this interval because saccadic adaptation is reduced by two-thirds if the target is not present for 300 ms after the saccade (Fujita, Amagai, Minakawa, & Aoki, 2002).

2.6. Trial descriptions

2.6.1. Grating trials

During these trials, the cue appeared randomly either 9 deg to the right or left of the continuously available fixation point (Fig. 3). After an interval corresponding to the previously determined attentional shift time (see Section 2.4), the cue was replaced for 50–100 ms with a square-wave grating, (Fig. 3, frame 3b; diameter = 0.3 deg, spatial frequency = 6 cpd) randomly chosen from one of four orientations. The Michaelson contrast (0.3–0.4 for the two oblique orientations and 0.2–0.3 for horizontal and vertical orientations) was established for each subject during a training session to yield 75%

Fig. 2. Cue position during the different phases of each experiment. Subjects fixated a 0.33 deg diameter circular fixation point (A), and were instructed to shift their attention (but not their eyes) to an identical cue stimulus when it appeared at position B. B was located at 9 deg (randomly to the right or left) in all phases of Experiments 1, 2 and 4, or at 7 deg in all phases of Experiment 3. During the adaptation phase only, after a predetermined interval (the attention shift latency), the cue was displaced by −3 deg to position C (6 deg from A) either on both sides (Experiment 1) or one side (Experiment 2) or stepped forward by +3 deg to position D (Experiment 3). The cue briefly changed into a small grating upon reaching its final position (position B in phases I and III or at C or D during phase II).

Fig. 3. Sequence and timing of events. Frames indicate the sequence for the two types of trials, those used to assess the location of attention (line-motion task, frames 3a–5) and those used to hold attention on the cue (grating task, frames 3b–5) during the adaptation phase in Experiments 1 and 2.
accuracy. This level of performance was maintained during the experiment by modifying the grating duration and contrast. After the grating intervals, the cue, now acting as a mask, returned for 200 ms. Subjects selected the grating orientation with a keyboard response.

It is worth noting that in addition to requiring our subjects to maintain fixation, our experimental protocol would have discouraged saccades because the grating to be discriminated appeared about 100 ms after the target step and was masked 100 ms later. Thus most saccades would not reach the grating cue while it was present, and the grating would not have been discriminable during the saccade. Indeed, no saccades were detected on those subjects whose eye movements were monitored. Thus, the task involved covert attentional shifts only.

The grating and mask were at the initial cue location of 9 deg to the right or left of the fixation spot (7 deg in Experiment 3) during the pre-adaptation and post-adaptation phases, but were displaced by 3 deg during the adaptation phase, either back towards the fixation point (Experiments 1, 2 and 4) or forward (Experiment 3).

2.6.2. Line-motion trials

The principal innovation in these experiments is the use of a modification of the line-motion illusion to track where attention landed after attention shifted from the fixation spot to the cue. To do this we expanded the response to the line from being a two-alternative forced-choice (“from which end did the line grow?”) to being a nine-alternative forced-choice by having the “line” be a row of nine adjacent filled circles, each 0.33 deg in diameter, and having the subject judge from which of the filled circles the line appeared to originate (examples of stimulus conditions from different experiments are shown in Fig. 4). This procedure yielded a consistent percept in trained subjects that the line originated from the perceived location of a previously flashed cue, and thus, we infer, from the location to which exogenous attention had been drawn.

Like the grating trials, the line trials began with the cue appearing 9 deg (7 deg in Experiment 3) randomly either to the right or left of the fixation point. After an interval corresponding to the attentional shift time for that subject, the cue was replaced for approximately 600 ms by the line stimulus, which spanned 3 deg (Fig. 3, frame 3a).

In Experiment 1, for the first half of the subjects the line was positioned so that the outermost filled circle was aligned with the initial cue location (9 deg right or left), thus spanning the 3 deg between the initial and step-back cue locations (Fig. 4A). In the second half of the subjects and in Experiments 2 and 4, the third circle from the outer end was aligned with the cue location, so that changes in response variability would not cause shifts in response position because of truncation (Fig. 4B). In Experiment 3, in which the cue stepped forward, the cue started at 7 deg and stepped to 10 deg, a position chosen because the cue’s stepping forward from 9 to 12 deg made the grating discrimination too difficult. In this experiment, the third circle from the inner end of the line was aligned with the cue location (Fig. 4C).

2.6.3. Catch trials

In contrast to the training on the line-motion task, in which each of the 9 circles that made up the line was cued with equal probability, during the experiment the line origin remained constant over many consecutive trials (e.g., at position 9). Thus, subjects might bias their responding to the expected cue location. To minimize this effect, which would cause the degree of adaptation to be underestimated, we interleaved an equal number of catch trials with the line-motion trials. These catch trials lacked predictability about the location of the apparent line origin because the line was offset with respect to the cue by a random amount, so that the line-motion appeared to originate with equal probability from each of the eight circle positions other than the actual cue position. The responses on these catch trials were not used in our estimates of adaptation, but were used to ascertain the accuracy of the line-motion task during the experiment.

Fig. 4. Modified line-motion illusion. (A) If a single cue (at position 9) precedes a line (composed of a 3 deg row of 9 identical circles), the line appears to shoot from the cue location in the direction of the arrows. (B) If the cue preceding the line is at a position within the line (here position 7, as used in Experiments 1, 2 and 4) the illusory motion flows in two directions but is strongest for the longer line segment (here to the left). (C) If the cue is located at position 3 (as in Experiment 3 in which forward-steps from 7 to 10 deg were used during adaptation), line-motion is seen mostly to the right. In all cases subjects were trained to locate accurately the origin of line-motion to one of the 9 circles.
2.6.4. Frequency of line-motion, catch and grating trials

Because the line was present for much longer than the attentional shift time, each shift to it tends to counter the adaptation produced by the grating trials. Thus, if the frequency of the line trials is higher, our ability to track the locus of attention is better, but the adaptation is weaker. In Experiment 1, the correlation (r) between the degree of adaptation and the frequency of line trials experienced by each subject was 0.82. For this reason, we varied the proportion of line and grating trials in different experiments.

The frequency of the line trials (half of which were normal line-motion trials and half of which were catch trials) was 25% for the first 7 subjects in Experiment 1, after which it was decreased to 13% (for the remaining 7 subjects and for Experiments 2 and 3) to minimize interference of the line trials with the adaptation. In order to maximise the degree of adaptation in Experiment 4, in which the primary measurement was saccadic gain, the number of line-motion and catch trials was further decreased to 5%. Therefore, the ratio of the percentage of line-motion:catch trials of all trials was 25:0% for the first 7 subjects of Experiment 1; 6.5:6.5% for the remaining subjects in Experiments 1 and 2; and 2.5:2.5% in Experiment 4.

2.7. Data presentation

The principal data presented here are the changes in the location of attention immediately after a shift of attention in response to steps of the cue. On each line trial, the subject reported the circle from which the motion appeared to originate. We converted these responses into a percentage of the 3-deg step-back or step-forward. Thus a reported origin of line-motion of 0% corresponded to the actual cue location (B in Fig. 2), −100% corresponded to the backward step location (C in Fig. 2) and +100% corresponded to the forward-step location (D in Fig. 2). The raw data were smoothed using a Lowess smoother as implemented in Sigma-Plot® (SPSS Inc., Chicago) or Data Desk® (Data Description Inc., Ithaca, NY). This non-linear iterative fitting function involves computing a regression line within a window around each y-value and assigning each point a weight inversely proportional to its distance from the fitted line. Because the line-motion trials occurred at only occasional and random trial numbers in each subject, to average across subjects, we interpolated the smoothed data for each subject to yield data at each trial number. The number of trials was not the same for each subject, so for statistical purposes we compared individual trials during the first 180 trials of the pre- and post-adaptation phases and the first three consecutive blocks of 180 trials during the adaptation phase.

3. Results

Because our results rely on the use of the line-motion illusion to determine the location of the focus of attention, we first present results which demonstrate the accuracy of this method. We then show that the shifts of attention measured in this way can be adapted if the target is systematically displaced to a new spatial location at the time of the initial attentional shift. Finally we explore the directional specificity of such attentional adaptation and its effect on subsequent saccadic eye movements.

3.1. Accuracy and reliability of assessments of locus of attention

Our assessments of the adaptation of shifts of attention rely on the accuracy and reliability with which subjects correctly identify the location from which the line-motion originates. Our subjects were able to locate the origin of the line-motion to less than 0.57 deg during training, during which correction trials were given. Furthermore, we tested one of the authors (AK) under extended conditions for 1794 consecutive trials on the line-motion task with the cue randomly presented at all possible positions on the line. We found that the slope of the line relating the perceived locus of line initiation to the actual cue location was very close to 1. After removing the correction trials, r = 0.83 (Fig. 5A) and the mean accuracy was 0.76 deg (SD = 0.18 deg).

Over the 2 h time-course of this experiment, we found that the error (the absolute value of the deviation of the reported line origin from the cue location) was stable. This indicates that the repeated use of the line-motion illusion without adaptation does not by itself appreciably change the apparent origin of line-motion. So too in our experimental subjects, as will be seen, we also find that the locus of attention is relatively stable in the long series of over 1000 baseline trials in Experiments 2 and 3, and during the shorter pre-adapt baseline phase in Experiment 1.

To assess the reliability of the line-motion trials during the experimental conditions, in which the task demands were much greater because the line-motion trials occurred infrequently and without warning, we looked at the performance on the catch trials (in which every position on the line was cued) for subjects in Experiment 1 (Fig. 5B). Even under these conditions, the mean accuracy was quite high at 0.72 deg (SD = 0.4 deg).

A curiosity of our origin of line-motion data is the slight displacement in the direction of the line-motion, resulting in the baseline measures being slightly less than zero. This might be a manifestation of the Frohlich illusion, in which one sees the origin of motion of a
moving stimulus displaced in the direction of the motion (Kirschfeld & Kammer, 1999).

3.2. Experiment 1: Adaptation to back-steps in both directions

3.2.1. Example of raw data

The general result of the adaptation experiment was that once each step of the cue was followed by a back-step at the attention-shift-latency, the magnitude of the shift of attention gradually decreased. Thus the location where attention landed (as measured by the origin of line-motion) became closer to the point to which the cue back stepped. An example of the raw data and its Lowess smoothed function from one subject is shown in Fig. 6. The subject’s judgement of the apparent line origin was fairly stable during the pre-adaptation baseline period. During the adaptation phase, the apparent line origin shifted over several hundreds of trials in the direction of the back-stepped location with a clear downward trend to a maximum of approximately 40% of the size of the 3 deg back-step. Once the adaptation was discontinued in the post-adaptation phase, the apparent line origin shifted substantially back toward the original cue location (0%).

3.2.2. Magnitude and consistency of adaptation

Every one of our 14 subjects significantly decreased the size of their attentional shifts by the third block of 180 adaptation trials compared to the first 180 pre-adaptation trials (Fig. 7A and Table 1; mean shift = −16.6%, SD = 8.9; Kruskal–Wallis ANOVA and Dunn’s Comparison, \( p < 0.01 \) for each subject; 12 of these subjects showed a significant shift using \( t \)-test comparisons of raw responses during these periods: in 9 subjects \( p < 0.001 \) and in 3 subjects \( p < 0.05 \)). Both the mean and the mode of the magnitude of the shifts of attention changed with adaptation. Thus the adaptation was not a consequence simply of an increase in the frequency of the subject selecting the adapted position with a concordant decrease in the frequency of selecting the unadapted position (Fig. 8). Notice that the principal difference between the first (Adapt 1) and third (Adapt 3) blocks of the adaptation was the decrease in the frequency of selecting the unadapted position (0%) and the increase in the frequency with which the circles three (-33%) and four (-44%) positions away were chosen. It is important to note that even after adaptation our subjects never reported that the line started at the position representing full adaptation (~100%).
Averaging across subjects as above underestimates the degree of adaptation because of individual differences in time course. Therefore we also show the greatest degree of adaptation shown by each subject (in the third block of 180 adaptation trials) relative to the average of the pre-adaptation phase (Fig. 7B). The median amount of adaptation some measured was 22.5%. Furthermore, all but three of our subjects shifted in the opposite direction during the first 180 trials of the post-adaptation phase after subtracting the mean of the third block of adaptation trials. The x-axis is expressed as a percentage of the size of the step-back. The arrows show the median of each distribution.

Fig. 7. Distribution of the degree of adaptation in individual subjects in Experiment 1. (A) The mean origin of line-motion over the third block of 180 adaptation trials after subtracting the mean of the pre-adaptation phase. (B) The greatest adaptation as shown by the minimum point on the smoothed curve of responses minus the average of the pre-adaptation phase. (C) The mean origin of line-motion during the first 180 trials of the post-adaptation phase after subtracting the mean of the third block of adaptation trials. Averaging across all 14 subjects (Fig. 9), the magnitude of attentional shifts clearly decreased during the adaptation phase of the experiment compared to the pre-adaptation baseline phase (by 17.5% of the backstep size during the third block of 180 adaptation trials) and then increased again (by 11.4%) during the post-adaptation phase (Fig. 9 insert). Subjects who had catch trials but fewer line trials showed slightly greater amounts of adaptation than those subjects who did not have catch trials, but not significantly so (difference between the adaptation phase III and pre-adaptation was −13.5% for subjects A–G and −19.8% for subjects H–N, Table 1, p > 0.05). Statistically, the averaged magnitude of attentional shifts across all subjects differed significantly among the three experimental phases (Kruskal–Wallis ANOVA, $H = 794.5$, df = 4, $p < 0.001$) and was significantly different between the pre-adaptation and the adaptation or each of the three blocks of the adaptation phase (Dunn’s Comparisons, $p < 0.01$ in all cases).

3.2.3. Time-course of adaptation

An important attribute of saccadic gain adaptation is that it is gradual. We find this is also true of adaptation of shifts of attention. From the averaged change in the perceived origin of the line-motion across all subjects (Fig. 9), the regression of apparent line origin on trial number during the adaptation phase shows a significant downward linear trend (slope = −2.19% per 100 trials; $r = 0.99$, $p < 0.001$) and a reversal of that trend when the adaptation trials were discontinued in the post-adaptation phase (slope = +2.81% per 100 trials; $r = 0.77$, $p < 0.001$). These changes from the pre-adaptation baseline were not due to variability during the pre-adaptation control period, because performance was relatively stable (slope = −0.64% per 100 trials) and accuracy during this period was high—the average perceived position of the origin of the line-motion was 0.25 deg away from the actual cue location. Although Fig. 9 shows that the average adaptation is progressive, this does not necessarily imply that adaptation in individual subjects is progressive; the same curves could have resulted from each subject suddenly adapting but after different numbers of trials. The full adaptation curves of each subject (Fig. 10) show that adaptation is not sudden. Rather, the adaptation curve of most subjects proceeds more or less steadily downward, and regression fits give negative slopes in all but one case (Subject N in Fig. 10). Additionally, the mean level of adaptation relative to the pre-adaptation period in individual subjects does not differ significantly during the first block of the adaptation period, but does by the second and third blocks (ANOVA, Tukey comparison, $p < 0.001$). Eleven of the 14 subjects significantly decreased further between the first 180 trials and the third block of 180 trials (Kruskal–Wallis ANOVA and Pairwise Dunn’s Comparisons, $p < 0.001$ for $n = 11$, Table 1). When the adaptation trials were discontinued during the post-adaptation phase, slopes were positive in 10 of 14 subjects.
3.2.4. Coupling between leftward and rightward adaptation steps

Because the time-course of adaptation differs among individuals (or among experiments), we looked to see whether, in individual subjects, the course of adaptation to rightward and leftward steps of the cue was similar. In 9 subjects, the linear regressions of the smoothed interpolated values in the two directions were well correlated (mean $r = 0.77$, $SD = 0.2$), while the remaining subjects had weak or no coupling (mean $r = 0.22$, $SD = 0.04$). The degree of correlation between the left and right sides was not related to the magnitude of the mean adaptation in individual subjects.

3.3. Experiments 2 and 3: Directional specificity of adaptation

A salient feature of saccadic adaptation is that adaptation to rightward steps does not transfer to leftward steps. To see whether the rightward and leftward shifts of attention could also be adapted independently, for 3 subjects we had the cue step either backward (Experiment 2) or forward (Experiment 3) during the adaptation phase, but only during trials in which the initial step was to the right. When the cue appeared on the left side, there was no displacement, with the grating and the cue remaining in their initial location for the duration of the trial.

We found that rightward attentional shifts can be adapted without affecting leftward shifts. Furthermore, it is clear that the magnitude of attentional shifts can be increased as well as decreased by our adaptation paradigm. These unidirectional effects are evident both in the time-course of adaptation averaged over the three subjects (Fig. 11) and the differences between the means of the entire adaptation period for leftward and rightward steps in individual subjects (Fig. 12; ANOVA and Tukey comparisons, $p < 0.001$ in all cases).

Specifically, highly significant shifts of attention were observed for the rightward direction for the averaged performance during the adaptation phase when compared with either the rightward baseline trials during the pre-adaptation phase or with the leftward (non-adapting) trials during the adaptation phase (Dunn’s Pairwise Multiple Comparison after Kruskal–Wallis ANOVA; backward steps, $Q = 20.1$ and 23.2, forward-steps, $Q = 6.1$ and 28.6 respectively, $p < 0.01$ in all cases). No adaptation occurs in the leftward (non-adapting direction) (Dunn’s Pairwise Multiple Comparison after Kruskal–Wallis ANOVA; backward steps, $Q = 1.34$, forward-steps, $Q = 1.39$, not significant in both cases). This finding confirms that the change shown in Fig. 9 during the adaptation phase of Experiment 1 is specific to the adaptation condition, rather than being one that would be observed for any long series of attentional steps. Like saccadic gain, the magnitude of attentional shifts may be decreased more easily than increased, as the mean change during the adaptation phase relative to the pre-adaptation baseline phase was greater for backward shifts (mean $= -19.1$,

### Table 1

<table>
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<tr>
<th>Subject</th>
<th>Shift time (ms)</th>
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<th>Adapt phase II</th>
<th>Post-adapt phase III</th>
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<tr>
<td></td>
<td></td>
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<td>Mean% SD</td>
<td>Mean% SD</td>
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<td>-15.71 0.62</td>
<td>-19.84 2.27</td>
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<tr>
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<tr>
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<td>-12.40 0.60</td>
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<tr>
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<tr>
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<td>-4.84 0.58</td>
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</tr>
<tr>
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<td>-15.54 2.65</td>
<td>-17.45 1.74</td>
</tr>
<tr>
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<tr>
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<tr>
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<tr>
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<td>-15.31 1.98</td>
<td>-19.92 2.13</td>
</tr>
<tr>
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<td>22</td>
<td>6.25 1.67</td>
<td>8.90 2.32</td>
<td>10.47 1.20</td>
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</table>

The upper group of subjects (A–G) were those with 25% line-motion trials and with position 9 of the line aligned with the cue, while the lower group (H–N) had 6.5% line-motion trials and position 7 was aligned with the cue (see Section 2). Data are expressed as the percentage of the 3 deg back-step. Full adaptation would be $-100\%$. Shift time is the estimated time taken by each subject to shift attention to a brief peripheral cue (see Section 2.4).
Fig. 8. Mean frequency distribution for the origin of line-motion during the adaptation phase for the first seven subjects in Experiment 1 (for whom the line spanned the cue (0%) and back-step (~100%) locations). (A) First 180 trials of the adaptation phase and (B) last 180 trials of the adaptation phase. The circle location numbers (as in Fig. 4A) are shown at the bottom of each bar. Notice that adaptation did not arise because of a change in the relative ratio in which only the cue and back-stepped locations were selected. Instead there was a shift in preference away from the initial cue location towards (but never at) the back-stepped location.

Fig. 9. Average changes in the locus of attention during Experiment 1. The location of attention, as measured with the line-motion illusion, was averaged for all 14 subjects during the first 180 trials of the pre- and post-adaptation phases and for the first 540 trials of the adaptation phase of Experiment 1. The inset shows the mean position for each 180 trial block.

Fig. 10. Smoothed adaptation curves during the adaptation phase for each subject in Experiment 1. The numbers at the end of each curve show the amount of adaptation (in terms of the percentage of the backstep) at the last point on the curve. A–N labels refer to the subject number as listed in Table 1.

A. Backward Adapt Steps Drive Attention Gain Down

B. Forward Adapt Steps Drive Attention Gain Up

Fig. 11. Unidirectional adaptation of shifts of attention. Line origin reported during experiments in which the cue stepped backward (A—Experiment 2) or forward (B—Experiment 3) only on trials in which the cue stepped to the right (solid lines). Adaptation occurred in both cases. On trials in which the cue stepped first to the left and remained in its new position for the rest of the trial (dashed lines), responses were similar during the pre-adaptation (left curves), adaptation (middle curves) and post-adaptation (right curves) phases. Data averaged across 3 subjects.
SD = 9.5, \( n = 3 \) than for forward shifts (mean = +11.4, SD = 6.1, \( n = 3 \)).

3.4. Experiment 4: Effect of adaptation of attention on saccade size

Because attention shifts to the saccade target before the eye moves, it is possible that the location of attention defines the saccade target. If this were so, adapting attention so that a target at 9 deg causes attention to move 8 deg might cause saccades to that target to be 8 deg as well, even though during the adaptation no saccades took place (the eyes were always on the central fixation point). We found that in 5 out of 7 cases of adaptation of the shifts of attention similar to Experiment 1 there was subsequently a statistically significant reduction in the saccadic gain (0.064 ± 0.026 s.e.m., \( p < 0.05 \); two-sample paired \( t \)-test; Fig. 13). We are uncertain, however, whether there was a relationship between the magnitude of adaptation of attention and the size of the subsequent saccades (\( r = 0.54 \)), because to maximize attentional adaptation, very few line-motion trials were included during the adaptation. It is also likely that during the measurement of the saccade gain, the attentional shifts gradually disadapted back toward their original value because we left the target on for about 200 ms (until the saccade was initiated). As a consequence, once attention had shifted to the adapted location the target would have remained on at the original location for an additional 100 ms before the saccade. If adaptation of attentional shifts is like saccadic adaptation, having the stimulus at the unadapted location just after the attentional shift would reverse the effects of the adaptation. A more definitive test of the relation between adaptation of attention and saccades would be to interleave attentional adaptation trials with trials requiring a saccade to a briefly flashed target (suggested by Laurence Harris, York University).

4. Discussion

We have shown that when a subject views a cue that steps back (or forward) around the time that the subject usually shifts his or her attention, the amplitude of the attentional shift gradually decreases (or increases). As such, these adaptational changes resemble those that take place in saccadic eye movements during experiments in which a target is stepped backwards or forwards during a saccade. To evaluate the similarity of these two adaptational phenomena, we will consider first the differences in methods of producing these two forms of adaptation and then the differences in the magnitude of adaptation obtained. Finally, we will discuss the implications of adaptation of attentional shifts for understanding saccades and for understanding how the locus of attention shifts.

4.1. Appropriateness of the line-motion illusion for measurement of the location of attention and of the time to shift attention

Our results rest on our use of a modification of the line-motion illusion to evaluate where visual attention is at a particular point in time. It has been proposed that non-attentional visual factors may contribute to the shooting line illusion (Downing & Treisman, 1997; but see Schmidt, 2000). However, the fact that the direction
of the illusory line-motion can be determined by which end of the line attention has been drawn to, whether by visual, auditory or tactile stimuli or by verbal instructions (Shimojo et al., 1997) suggests that the attentional component of this illusion is at least strong enough to warrant its use in our task.

In particular, we find that the line-motion illusion has four properties that are useful for our purposes: (a) It locates attention with considerable precision. Using our 9-circle line, our subjects could be trained to identify the origin of the line-motion to less than 0.5 deg. (b) The long-term accuracy of the apparent line origin was stable. When we gave a subject nearly 1800 line-trials over 2 h, the origin of the line-motion was discriminable to within 0.68 deg of the actual cue position over the whole period. (c) The shifting of “attention” from one location to another, as assessed by the line-motion, is rapid and orderly. We find that the standard deviation (across subjects) of the SOA that elicits 50% inward line-motion is 22 ms. (d) The latencies that we measure are similar to other reports on the exogenous shifting of attention (Eriksen, Webb, & Fournier, 1990; Remington, 1980; Yantis & Jonides, 1990).

Because of the limitation that we have only one method for measuring the locus of attention with the precision we require, we cannot be entirely sure that non-attentional factors might not participate in the adaption we report. If our judgement is incorrect with respect to the line-motion illusion being predominantly determined by the locus of attention, one would have to look elsewhere for the cause of the adaptation we report.

4.2. Alternative explanations of attentional adaptation

We find that our adaptation situation results in a change in the magnitude of the attentional shift to the onset of a cue at an eccentric location. Is it reasonable to consider this an adaptation like that of saccades subjected to a somewhat similar stimulus situation? We will consider several alternative explanations.

First, one might attribute the changes we observe to a voluntary reallocation of attention, rather than an adaptation of the attentional shifts. Because attention can be voluntarily directed, might not the onset of the cue be taken as a signal to attend to the stepped-back or stepped-forward location, rather than to the cue location? If so, what we are calling “adaptation” would not be a modification of the magnitude of the shift of attention to the cue location, but rather would entail a shift in strategy such that the subject would cancel the shift of attention to the primary cue location and attend directly to the expected location of the grat ing. In general, our evidence does not support this explanation. Subjects do not suddenly change their locus of attention during the course of adaptation. Rather, it is evident that the changes are generally progressive, both across subjects (Fig. 9) and in each individual subject (Figs. 8 and 10), as would be expected of an adaptational change, even though some subjects do quickly reduce the size of their attentional shifts at the start the adaptation.

Furthermore, none of our subjects adapted fully to the back-step (or forward-step) of the cue (Fig. 8). If a cognitive strategy had been employed, one might expect that any such endogenous attentional mechanism would have shifted the locus of attention directly to the cue. Instead, it appears that even after hundreds of nearly identical trials, the endogenous attentional mechanism cannot cancel the exogenous shifts of attention. It has been explicitly shown that when conflicting endogenous and exogenous cues are presented, the demands of the exogenous cues cannot be denied (Muller & Rabbitt, 1989; Remington, 1980). The reason for this lack of interaction may be that the exogenous attentional latency is much shorter than the endogenous (less than 100 vs. 300 ms or more—see Eriksen et al., 1990; Hikosaka, Miyachi, & Shimojo, 1996; Remington, 1980; Yantis & Jonides, 1990). The forms of attention also differ in that exogenous attention does not linger long in one place, whereas endogenous attention can be sustained (Muller & Rabbitt, 1989; Nakayama & Mackeben, 1989; Remington, Johnston & Yantis, 1992). It would be interesting to know how sensitive the adaptation is to the timing of the step-back.

Second, we will consider whether there might be a false impression of adaptation because the cue location is at or close to one end of the line or the other, so that a large increase in the variability of the responses during the adaptation phase of the experiment might cause the mean perceived line origin to shift towards the center of the line (because responses can be much further from the starting point in the direction of the near end of the line than in the direction of the far end of the line). We can exclude increased variability as an explanation for our results for two reasons: (a) The magnitude of adaptation of the 7 subjects for whom the cue location was at the third outermost circle on the line (Fig. 4B) was the same as, or even slightly greater than, that of the 7 subjects for whom the cue location was at the end of the line (Fig. 4A) (mean over 540 trials of −20.4% vs. −18.9% respectively, p = 0.8). (b) The variability during the adaptation phase was not correlated with the degree of adaptation. We computed the square of the residuals of the fit to the Lowess function for each subject and correlated this variance-like measure to the amount of adaptation. The correlation coefficients had an average value of −0.09 (SD = 0.17, n = 14).

Third, the adaptation is not a consequence of progressive changes in the apparent line origin that would have occurred even if the cue had not stepped backwards or forwards. In Experiments 2 and 3 where adaptation occurred only for rightward steps, the shifts of attention to leftward steps did not differ from the
pre-adaptation baseline phase and were relatively stable throughout all phases. Also, the single experiment with 1794 consecutive line-trials showed no tendency of a progressive shift in line-origin that could account for the adaptation that we have observed.

4.3. What is necessary to produce adaptation?

In our experiments we required an explicit orientation task of our subjects. Thus, although the unpredictable appearance of the cue summoned attention exogenously, the task also would have been aided by an endogenous shift of attention to the back- (or forward-) stepped location. As just discussed, the adaptation measured reflected changes in the exogenous shift of attention, because the endogenous shift would not have occurred by the time that the line was presented. One can ask therefore whether the discrimination task was necessary at all. We speculate that the adaptation could have occurred without the discrimination task, but that the discrimination task served to keep the spatial scale of attention narrow, so that all attentional resources were deployed in the small region of the cue and grating. Without this endogenous signalling of the appropriate scale of attention, the attentional focus might have been so broad that both the original cue location and the stepped back location would have been encompassed by a single broad focus of attention. We have evidence that saccade adaptation is sensitive to the size of the attentional field (Wallman, Khan, Yun, & McFadden, 2001).

4.4. Does adaptation of attention require that attention actually moves?

Our interpretation of both the latency and the adaptation of the attentional shift was motivated by the supposition that attention does in fact shift, but the results we have obtained and the conclusions we have drawn from these results do not rest on this supposition. One can take the alternative view that attention does not move in the sense of a spotlight moving, but rather that at the start of each trial attention is diffuse and then after the cue is presented it becomes focused in one region (that is, it zooms in to the cued location) (Eriksen & St. James, 1986; Shepherd & Muller, 1989). This view does not demand a change in our interpretation of our results. Rather, we would say that our results imply that after attention is focused, some process assesses whether it zoomed accurately to the cue location, and, if not, the zoomed location is altered over hundreds of trials. Similarly, our finding of an orderly sigmoidal curve when we assessed the time to shift attention could be interpreted as the time necessary to focus attention to the cued location. This interpretation would, however, require that, before the cue is presented, attention is somewhat more intense at the fixation point than it is elsewhere in order to account for the illusory line-motion being in the direction away from the fixation point. Indeed, the fact that the line-motion does shift in direction with time after moving the cue argues that at least the centroid of attention must move from one spot to another, an interpretation that borders on saying the locus of attention itself moves.

4.5. Comparison of the magnitude of attentional adaptation with that of saccadic adaptation

The adaptation we measure in the magnitude of shifts of attention is similar to saccadic adaptation in three respects: It is gradual, it is specific to the direction of target step (right vs. left), and it is specific to the sign of the subsequent target shift (backwards vs. forwards). However, the adaptation seems to differ from saccadic adaptation in being slower or smaller in magnitude. During saccadic adaptation in humans, the system adapts from 20% to 25% (Straube & Deubel, 1995) up to 90% (McLaughlin, 1967). In our attentional adaptation experiments, we found that on average, the amount of adaptation was about 20%, although individual subjects adapted up to 35%.

There are several possible explanations for why our attention adaptation values are towards the lower range found in saccadic adaptation experiments. First, our method of assessing the location of attention itself interferes with the degree of attentional adaptation. That is, we found that the mean amount of adaptation increased as the proportion of line-motion trials decreased. If we extrapolate this function to 0% line-motion trials then the amount of attentional adaptation would be on average approximately 30% of the back-step size. The reason for this interference may be that during the line-motion trials, the visual stimuli are on the screen for longer than the attention shift-time and attention is free to move about, so that these shifts are not adapted. Furthermore, if the subjects had a tendency to persist in responding to the key representing the cue-location, this might bias their responses in the direction opposite to adaptation. However, we did not find any difference in degree of adaptation between subjects who had catch trials and those who did not. More generally, unlike saccade adaptation experiments, in which one can instruct the subjects not to make extraneous eye movements and one can monitor their compliance, in attention adaptation experiments this is, of course, not possible. Second, if one views the attention adaptation procedure like that of a saccade adaption experiment, the deficiency in the shift-of-attention adaptation procedure is that we cannot tell when the attention shifts during a given trial and then step the target forward or back at that time. Instead, we must step the target at the average attention-shift-latency, meaning that in most cases we shift the target either
before or after the attention shifts. Presumably this causes a smaller adaptational change than would have been the case if we shifted the target at just the right moment, as can be easily done with saccades by monitoring the eye movements continuously. Third, in saccade experiments one typically measures the eye position at the moment when it comes to rest at the end of the saccade. In the case of our attention experiments we measure the location of attention (on our line-motion trials) at a fixed time after the target step, the same time we use to step back the target during the adaptation phase. If attention moves continuously across the visual field (Shulman et al., 1979) at a finite velocity (e.g., 125 deg/s; Tsal, 1983), as proposed by some authors, we may have assessed the location of attention while it was still moving, at least in some proportion of trials. Whether attention moves at a finite velocity is, however, a matter of some debate (Yantis, 1988). The magnitude of this underestimation would depend on unknown aspects of the dynamics of the line-motion illusion.

Whether the degree of attentional adaptation is small for fundamental or methodological reasons, it should be noted that the degree of saccadic adaptation in humans, even after many trials, also is typically considerably less than that which would bring the eye directly onto the displaced target. Miller et al. (1981) have suggested that there are fast and slow adaptive processes, of which only the fast process is adapted during these experiments.

4.6. Implications for saccade targeting and adaptation

Our finding that adaptation of shifts of attention transfers to saccades implies that saccades are directed specifically to the locus of attention, rather than to stimuli identified by attention but targeted by independent means. This in turn implies that saccadic adaptation, as it is usually defined, could result from either adaptation of attentional shifts or from saccadic adaptation at the motoric level, or both. We conjecture that these two levels of adaptation are independent, because the brain would need a way to compensate for specific changes in the strength of the eye muscles without affecting covert shifts of attention.

Does this mean that saccade adaptation experiments might actually be adapting the shifts of attention that precede saccades? We think not. Our experiment was unusual in that the cue remained in its initial location only long enough for attention to move there, whereupon the back-step occurred. In normal saccade adaptation experiments the target spot is on for approximately twice as long, allowing time for an attentional shift to the target and a corrective step before the saccade occurs. Therefore the fact that the target subsequently steps back during the saccade should not stimulate adaptation of attentional shifts. Recently, an explicit study of the locus of attention before saccades showed that it was not shifted by saccadic adaptation (Ditterich, Eggert, & Straube, 2000). Indeed, the step-back during the saccade may well be registered by the attentional system as simply another target step, not signalling an error in attentional localization. In other situations, however, either attentional or saccadic adaptation might take place. For example, in memory guided saccades to briefly presented targets, adaptation might be either at the attentional or motoric level. This possibility extends the view that saccadic adaptation can take place at several different levels of the visual and oculomotor systems (Deubel, 1999).

4.7. At what level might adaptation of exogenous shifts of attention occur?

As mentioned in the Introduction, exogenous spatial attention has been characterized in several ways, including being the peak on a map of perceptual saliency and being an intrinsic component of saccadic eye movements (although the eye movement itself may be cancelled after the shift of attention). At first glance, it might appear that the finding that the magnitude of shifts of attention can be adapted argues that attention lies clearly on the motoric side of the continuum, because it is easy to see the adaptation in terms of changing a motoric gain term, as in saccadic adaptation. However, in both the cases of saccades and attention, there are at least four levels at which adaptation might occur. We will consider the possibilities for saccadic adaptation and then consider which might apply to adaptation of attention.

First, the adaptation could involve a warping of the visual map, so that stimuli at 10 deg right are mapped at 8 deg right. Presumably such a remapping would not affect all visual maps. If it did, the perceived geometry of the visual world would be influenced by saccadic gain adaptation provoked by such things as weakness of an eye muscle. There is evidence against visual remapping being the basis of saccadic adaptation (Wallman & Fuchs, 1998). Second, the transformation between the visual map and the premotor spatial map used in selection of the saccadic target might be altered. In the case of neurons with large motoric fields, such as those in the superior colliculus, a simple spatial gradient of modulatory input across the map could cause a consistent shift in the location of the peaks of activity. Such gain modulation effects (gain fields) have been proposed to account for the effect of attention on cortical areas (Connor, Preddie, Gallant, & Van Essen, 1997; Salinas & Abbott, 1997). Third, saccadic eye movements involve a transformation from a spatial coordinate scheme, in which the saccade is planned, to a temporal coordinate scheme, in which the amplitude of the saccade is coded in the duration of the burst of firing of the ocular motor neurons that will get the eye to the desired target. Saccadic adaptation might be manifested by a change in
the duration of this burst. There is evidence of changes in the dynamics of saccades as a result of adaptation (Abrams, Dobkin, & Helfrich, 1992; Straube & Deubel, 1995) as well as evidence that the fastigial nucleus might produce saccadic adaptation by changing the duration of saccades (Scudder, 1998). Fourth, although in one sense saccades are entirely pre-programmed in that the saccadic endpoint cannot be influenced by visual signals acquired en route, in another sense the eyes’ path can be considered to be guided by internal feedback in that the oculomotor system is thought to keep track of where it calculates the eye is during the saccade and to terminate the saccade when it estimates that the target has been reached (Van Gisbergen, Robinson, & Gielen, 1981). Saccadic adaptation might act at the level of this efference feedback calculation.

By similar reasoning we can consider the possibility that adaptation of shifts of attention might occur at the same four steps. First, if saccadic alternations can be remappings at the level of visual maps, surely this would affect shifts of attention as well. Second, if one views spatial attention as peaks on a saliency map achieved by a winner-take-all process, one would have to accept that there is some process that transforms the raw visual map into this saliency map. Alterations of this transformation could constitute adaptation. The third possibility of temporal changes in the motoric signal is least likely to apply to attention, in that we have no evidence for such a spatial-to-temporal transformation in the case of shifts of attention. In the case of the fourth possibility, there is evidence of something like an efference feedback pathway for attention (Cavanagh, 1992); this might be involved in adaptation both of saccades and of shifts of attention.

5. Conclusions

We have shown that shifts of attention, like saccades, can be adapted if the target is spatially displaced during the time of the initial attentional shift. This finding can be added to the list of similarities between attention and saccades presented in the Introduction. The fact that the targeting of attention is plastic suggests that it represents the output of on-going spatial computations, rather than being an inherent attribute of the visual image in the brain. The fact that this targeting appears to be linked to saccadic targeting suggests that saccades may be directed to the locus of attention, rather than to targets identified by attention. In some situations adaptation might be effected by changes at the level of either attention or saccades or both.

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Appendix A

We trained subjects on the grating identification task and the line-motion task in separate sessions 1–3 days before the experiment. Subjects required approximately 550 line-motion training trials and 150 grating training trials.

A.1. Training for line-motion trials

In order to effectively discriminate the location of the origin of the shooting line, subjects required three types of training. First, they were trained to type a key corresponding to particular circles on the line. For this phase, the cue appeared at a random position between 2 and 5 deg right or left of the fixation point, and stayed on for 320 ms, after which it was replaced (for 600 ms) by the row of circles, spanning the distance from 2 to 5 deg from the fixation point. At first the subject was told in advance which circle would be turned on until 10 consecutive correct responses had been made. Thereafter, correct responses were signalled by a beep, and errors caused the subsequent trials to have the cue appear in the same location until the correct response was made (correction trials).

In the second training phase, this task was made more difficult by first moving the range of cue-locations to span 4–7 deg from the fixation point and then 6–9 deg. Finally, in the third training stage, the duration of the cue (the SOA) was reduced from 320 to 100 ms in 2 steps. Each change in eccentricity and reduction in duration occurred once the 10-point running average of the difference in the number of circles between the reported origin and the actual cued location fell below 0.7 circles (0.57 deg), including the correction trials. The line training was concluded when the subject maintained this criterion for approximately 40 trials, with the final stimulus location (spanning 6–9 deg) and final SOA (100 ms; Fig. 3, frame 3a). In practice, most subjects achieved an accuracy less than 0.57 deg. On the day of the experiment, immediately before the experiment began, the subject was given brief refresher training on the line-motion illusion. This training began with the 6–9 deg line span with a 320 ms cue duration which, once criterion was passed, was decreased to 100 ms.

At the end of the training on the line-motion illusion, subjects were able to accurately locate the origin of line-motion, the locus of which could not be predicted since each cued position appeared randomly and with equal probability. During the actual experiments, the same line-motion task was used to assess the perceived origin of line-motion, except that the line-motion trials oc-
curred only occasionally rather than on each successive trial as in training. When a line-motion trial did occur during the experiment, subjects were unable to predict the cue location as it occurred at a random position on the catch trials, and the catch trials were themselves randomly interspersed with the normal line-motion trials.

A.2. Training for grating trials

The grating trials were introduced so that focal attention was required at the cue location. These trials required the subject to identify the orientation of a small briefly presented grating. To perform this task required some training and required setting the grating parameters for a criterion level of performance for each subject.

Training trials presented stimuli like those in the grating trials described in Section 2.6.1, except that the difficulty of the task was increased in several steps. At the beginning of the training, the grating stimulus was 1.0 deg in diameter (9.0 mm), with a contrast of 1.0, a duration of 250 ms and a spatial frequency of 6.0 cpd. These stimulus parameters were used until the subject made 20 consecutive correct responses. During successive steps in the training the duration was decreased to 100 ms, the diameter was decreased to 0.33 deg (the same size as the cue), and the contrast was reduced to 0.3–0.4 for the oblique orientations and 0.2–0.3 for the vertical and horizontal orientations until performance was stable at approximately 75% (over 20 trials for an individual subject). The grating properties at this performance level were used at the start of the experiment for that subject.

References


References


