THE RELATIONSHIP BETWEEN SACCADIC ADAPTATION AND PERCEPTION OF THE SACCADE TARGET OBJECT

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ABSTRACT

Saccades are the quick, ballistic eye movements that we make multiple times each second. Although their metrics, including amplitude, cannot be changed after they are initiated, these metrics can be altered through various methods. Saccadic adaptation is an effect resulting from one such alteration, namely, the repeated displacement of the saccade target during the saccade itself. During this process, the observer will typically make corrective saccades, but the initial saccade will gradually approach the target's final location, known as the adapted location. Previous studies have suggested that when the saccade landing point shifts, so does the pre-saccadic shift of attention. The pre-saccadic shift of attention is a well-documented process occurring just before saccade initiation, by which the visual system attends to the upcoming saccade target, and previous work has demonstrated that this shift can be altered through the induction of saccadic adaptation. In the current study, we investigated the effect of forward saccadic adaptation on color perception, hypothesizing that after saccadic adaptation has been established, color report will be biased toward the color displayed at the adapted location. We did not find this to be the case in our design. This result could likely be attributed to several weaknesses in the forward adaptation effect.

Keywords: Saccade, adaptation, visual attention

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CHAPTER ONE

INTRODUCTION AND LITERATURE REVIEW

In the field of vision research, much contention remains among researchers surrounding the mechanisms of visual perception before, during, and after saccades, the quick eye movements that enable us to efficiently search and process the visual environment. The workings behind the generation, programming, and control of saccades themselves are also of interest to many researchers. Despite some amount of mystery still surrounding these dynamics, several key properties of saccades have been identified. That saccades are ballistic is one of these crucial properties; once a saccade is initiated, its motor command cannot be updated, and it cannot change course. Instead, information about potential visual error can only be processed upon the landing of the saccade and used to inform the programming of subsequent saccades (Heins et al., 2019; Souto & Schütz, 2020).

Because saccades are executed exceptionally quickly, the movement spanning between 20 ms and 80 ms, the visual system does not have time to collect in-flight information about the features and location of the saccade target or to generate and process an internal proprioceptive report (Wolf & Lappe, 2021). By extension, there is not enough time for the visual system to use that information to reprogram the movement before the gaze lands (Chen-Harris et al., 2008; Garaas & Pomplun, 2011; Wolf & Lappe, 2021). However, despite the ballistic nature of saccades, their metrics can be altered in several ways through different experimental manipulations (Chen-Harris et al., 2008; Garaas & Pomplun, 2011; Heins et al., 2019; Heins & Lappe, 2022; Madelain et al.,

2011b). One way to systematically alter their amplitude, specifically, is through a phenomenon known as saccadic adaptation. This is an oculomotor learning process by which the visual system compensates for repeated landing-point errors by gradually adjusting saccade amplitude, allowing the gaze to land progressively closer to the saccade target object. The correction of these landing inaccuracies over time can be attributed to the visual system's calculation and tracking of visual error. Alternatively, adaptation can be induced artificially in experiments through the repeated displacement of a target stimulus in the same direction by the same magnitude each time. Over time, the observer's initial saccade typically begins to land closer to the final landing point of the displaced target. This phenomenon is known as saccadic adaptation.

The most studied and commonly used saccadic adaptation paradigm is the double-step design introduced by McLaughlin (1967). In this design, the observer fixates a designated starting point, after which a target object appears in the periphery. As soon as the observer initiates a saccade toward the target, the target moves a certain distance either in the direction of the saccade (forward adaptation) or in the opposite direction (backward adaptation). This manufactured error may lead the observer to make a second, corrective saccade (Bahcall & Kowler, 2000; Hopp & Fuchs, 2004). After between 50 and 100 identical trials, the visual system adapts to this repeated shift, and as a result, the initial saccade reliably lands closer to the adapted location, or the location to which the target moves, and farther from the non-adapted location, which is the target's starting point before saccade initiation (McLaughlin, 1967; Semmlow et al., 1989). This effect is the visuomotor system's effort to resolve a mismatch between the location of the target as

predicted by the pre-saccadic image and the target's actual location after the saccade has been completed (Aagten-Murphy & Bays, 2018; Bahcall & Kowler, 2000; Herman et al., 2013).

Research investigating the pre-saccadic shift of attention is crucial to determining what effect saccadic adaptation may have on visual perception. The pre-saccadic shift of attention is the mechanism by which the focus of visual attention moves toward the target object or saccade landing point prior to a saccade, and researchers have often investigated if this visuospatial attention is tied to motor preparation for a saccade, or if the two are interdependent in some way (Doré-Mazars & Collins, 2005; Hunt et al., 2019). Much support has been found for the former conclusion. For instance, previous studies have found that it is not possible for subjects to covertly attend one location while executing a saccade to a different location (Henderson et al., 1989; Hoffman & Subramaniam, 1995; Kowler et al., 1995). Further evidence of covert attention's close relationship with the saccade programming system comes from Born et al. (2014). These authors used a stop-signal paradigm to test the automatic covert shifts of attention prior to saccades. Participants prepared a saccade to designated target locations. On some trials, after saccade preparation they were cued to abort the saccade execution. The authors found that executing the saccade enhanced attention at the saccade target location, while simply preparing the movement did not. As a review from Hunt et al. (2019) has emphasized, the deployment of covert visual attention does not depend on the eventual execution of a saccade. However, carrying out a saccade does rely on the locus of covert attention, and saccade programming for an actual eye movement directs attention toward the saccade

target (Zhao et al., 2012). Still, despite general agreement that attention and visuomotor processes share close ties, researchers have debated where the shift of attention occurs. For example, in a study in which participants were directed to make saccades to designated targets while performing a discrimination task, Deubel and Schneider (1996) found evidence that visual attention and saccade preparation are necessarily tied to the same target object or location. While this is congruent with much research on the pre-saccadic shift of attention, the authors additionally emphasized that the object of the pre-saccadic shift of attention is the intended saccade target rather than the actual landing point, should the two locations differ (Deubel & Schneider, 1996) In contrast, Doré-Mazars et al. (2004) found that during a free-viewing task, attention was instead ultimately tied to the actual landing point However, these findings need not be mutually exclusive. Collins and Doré-Mazars (2006) explain that task differences could account for the different conclusions, as unlike Deubel and Schneider (1996), Doré-Mazars et al. (2004) did not use single, discrete saccade target objects, instead using a string of letters. Deubel and Schneider's (1996) post-hoc analysis of their own study also revealed that the actual landing point could still have exerted an influence (Collins & Doré-Mazars, 2006). Such questions notwithstanding, the above findings cumulatively, if indirectly, bolster the hypothesis that saccadic adaptation will impact color perception, because such an effect would rely heavily on a role of the pre-saccadic shift of attention.

The present study investigated the ways in which saccadic adaptation may influence the pre-saccadic shift of attention. Specifically, we wanted to test if and how changes in the pre-saccadic shift of attention through adaptation affect object

representations. To approach this question, it is first necessary to conceptualize the effect that the pre-saccadic shift of attention exerts on visual perception overall, and previous research into this has been largely consistent in its findings: when the pre-saccadic shift of attention moves to the saccade target, perception of that object or location is enhanced, to the detriment of objects that either are not the target or will not fall within the programmed saccade endpoint (Collins et al., 2010; Deubel, 2008; Doré-Mazars et al., 2004; Zhao et al., 2012). This shift is not only reliable and representative of a close tie between attentional allocation and saccade programming, but it also changes the way that the observer perceives different stimuli across the entire visual field, distributing attention and preferentially weighting objects and areas of interest (White et al., 2013). Although there is significant support for these conclusions in the literature, results from other studies appear to complicate the matter. Van der Stigchel and de Vries (2015), for instance, found that when a saccade lands between a target and a salient distractor, attention remains tied to those competing stimuli rather than to the space between them. In a similar vein, also suggesting to some extent a decoupling of pre-saccadic attention and eventual saccade landing point, Schut et al. (2018) concluded that deviating the saccade landing point from the saccade target did not affect the perception of transsaccadic integration (the proposed but still-debated perceptual merging of pre- and post-saccadic images). While these studies diverge from the aforementioned narrative of the role of the pre-saccadic shift of attention, they do not necessarily serve as decisive evidence against it. Rather, these discrepancies signal an ongoing conversation within the

field and indicate a need for continued investigation, which the present study aims to address.

If, after saccadic adaptation has been induced, the pre-saccadic shift of attention moves toward the adapted location along with the saccades, it is possible that saccadic adaptation is thus capable of altering perception of color at the non-adapted location. Past work has yielded mixed evidence of such an adaptation of pre-saccadic attentional shift. Ditterich et al. (2000a) used a discrimination task to test for this, and they did not find evidence for it, although it is possible that they incorporated too few adaptation trials for attention to have adapted (Pélisson et al., 2010). McFadden et al (2002), on the other hand, concluded that the pre-saccadic shift of attention does adapt along with the actual saccades. However, due to potential weaknesses in the experiment's design, it is possible that the effects they found were due to participant strategy (Hopp & Fuchs, 2004).

Dore-Mazars and Collins also offered further speculation that could account for previous work; along with likely insufficient adaptation, Ditterich et al.'s (2000a) design incorporated reactive saccades instead of voluntary saccades, which have distinct neural substrates (Doré-Mazars & Collins, 2005). In a discussion of the aforementioned seemingly conflicting results, Pélisson et al. suggest that a more robust body of evidence supports Doré-Mazars and Collins's (2005) conclusion: that the pre-saccadic shift of attention also moves toward the adapted location during saccadic adaptation. and that attention is likely tied to the actual saccade landing point, rather than to the original saccade goal. The proposed study would contribute to the ongoing gap in the research

regarding the effects of these adaptation-related dynamics on visual object representations.

Having established the above conceptual narrative, it stands to reason that the adaptation-induced change in the pre-saccadic shift of attention will likely change how the observer perceives the saccade landing point and the object or objects located at or near it. Previous research has indicated, for example, that saccadic adaptation affects visual perception in terms of localization: after saccadic adaptation, participants tend to be significantly more likely to mislocalize simple stimuli, such as dots (Awater et al., 2005; Bahcall & Kowler, 1999; Hernandez et al., 2008; Zimmermann & Lappe, 2009; Zimmermann & Lappe, 2016) However, this effect seems not to apply in the context of backward adaptation with reactive-type saccades when the eye is fixated (Pélisson et al., 2010). Admittedly, changes in localization form a substantial amount of the literature regarding altered perception through the implementation of saccadic adaptation. Less is known about how and whether other visual features and dimensions respond to saccadic adaptation, but some studies nevertheless offer compelling evidence suggesting that such responses do occur. A recent study found evidence supporting the authors' hypothesis that saccadic adaptation would affect size perception; specifically, after saccadic adaptation, perceived object size decreased. Importantly, argue the authors, this study is unique in that it tests a feature, size, that is not itself a part of the sensorimotor process underlying saccadic adaptation, as is perceived location (Pressigout et al., 2020). Thus, while investigations into saccadic adaptation's effects on localization perception have

supported the notion that adaptation indeed affects perception, there is a gap in the literature concerning this potential effect on features such as color, shape, and more.

Our present study's conceptual basis and experimental approach were inspired by a substantial body of previous research, but two studies were especially instrumental. One of these was the aforementioned 2005 study from Doré-Mazars and Collins. In light of previous research establishing a fundamental understanding of some kind of relationship between saccade planning and the locus of visual attention, the authors intended to determine the nature of this relationship. Specifically, they investigated whether this locus of visual attention changes obligatorily along with the saccade's landing point (as dictated by the saccade motor program) or if the two processes could be uncoupled. To address this question, the authors employed a task involving report of line orientation, using an adaptation block to dissociate the intended and actual saccade endpoints. In the task, participants reported the orientation of lines situated within frames in an array before, during, and after an adaptation block in which the set of stimuli shifted intrasaccadically by 1 dva to the left. The authors manipulated the saccade target location by instructing participants to make a saccade to either the third or fourth frame (ST3 or ST4) in the array. Just after the fixation cross offset, which cued participants to make the saccade, the previously-empty frames were each briefly filled with a short line, only one of which was oblique. The task was to report if the oblique line, which was considered the discrimination target (DT) and could be located in the second, third, or fourth frame, was slanted leftward or rightward. As noted in the paper, accuracy data can be interpreted as a reflection of attentional focus, with greater feature-report accuracy at a certain

location indicating greater deployment of attentional resources in that area. The time-course of response accuracy patterns in the pre-adaptation, adaptation, and post-adaptation blocks suggested that the pre-saccadic shift of attention adapted alongside the actual saccade landing point, as DT orientations were reported most accurately when they happened to be in the same location as that landing point (Doré-Mazars & Collins, 2005). We expect that similar logic will apply in our present study, which also aims to examine the consequences of dissociating the intended and actual saccade landing points. However, our results can extend the findings mentioned above by testing this effect with color, a higher-level visual feature.

A 2020 paper from Van der Stigchel et al. was similarly influential and extended the findings of Doré-Mazars and Collins (2005), this time using a color report paradigm. The current experiment is a modification of Van der Stigchel et al.'s (2020) design. Assuming that, based on previous work, the pre-saccadic shift of attention could be manipulated through the use of adaptation, Van der Stigchel et al. questioned if this phenomenon could be found in the context of transsaccadic color perception. In four conditions varying the timing of target color visibility (pre- or post-saccade) and color-change status (constant or change), participants reported the perceived stimulus color on a color wheel to establish a baseline estimate of report accuracy for each participant. These trials were followed by adaptation trials in which participants did not report stimulus color but instead followed the stimulus with their eyes as it underwent a backstep of 6 dva from a starting point of 16 dva from fixation (37.5% backstep). After these adaptation trials, participants completed a mixed block incorporating both trial

types to measure any changes in color report accuracy as a result of adaptation. The authors found that during color-change trials after adaptation, participants reported color values further away from the pre-saccadic color value, presumably due to a change in locus of pre-saccadic attention. Further, the standard deviation of the color reports increased after adaptation, showing that they were generally less precise than they had been before the adaptation trials (Van der Stigchel et al., 2020). Not only do these results bolster the idea that eye movements and attention are closely linked, but it also explores the implications of this relationship on color perception. They also validate the premise of the current study, which seeks to further investigate the influence of saccadic adaptation on color perception, this time when a distractor is introduced at the adapted location. Finally, these findings inform the current study's hypothesis that after an adaptation block, participants will report color values that skew towards those of the distractors, ultimately showing post-adaptation report to be both less accurate and less precise.

CHAPTER TWO

MATERIALS AND METHOD

Experiment 1

Participants

Participants were University of Tennessee graduate and undergraduate students who took part in the study as volunteers or for course credit. We determined that we needed a sample size of 26 participants through Bayesian tables and based on the sample size used by Van der Stigchel et al. (2020). The participants had normal vision or vision corrected-to-normal with contacts, and we screened each participant for red-green color deficiency using the Ishihara test. There were 26 participants. They ranged from 18 to 29 years old, with a mean age of 19 years. The Institutional Review Board at the University of Tennessee approved this study.

Apparatus and Stimuli

We used an ASUS VG248QE 3D Monitor, S/N H2LMQS031579, with dimensions 535 (width) x 304 (height) and resolution 1920 x 1080. An EyeLink eye tracker recorded eye movements.

Procedure

Data were collected in the Visual Perception and Cognition Lab at the University of Tennessee beginning in June 2023. Participants first verbally provided informed consent to participate in the study. They were then given scripted verbal instructions throughout the experiment. All participants were naïve to the study's aims and hypotheses until debriefing after the experiment.

This experiment is a modification of a design by Van der Stigchel et al. (2020). It included three successive blocks: Block 1 was the color report block, with 60 trials, Block 2 was the adaptation block, with 200 trials, and Block 3 was the mixed block, with 384 trials. In the color report block, participants first fixated a cross that appeared at either the left or the right side of the screen, counterbalanced evenly across participants. Then, two colored disks appeared on the other side of the screen side-by-side, with one disk at 4 degrees of visual angle (dva) away from fixation, and the other at 6 dva from fixation. The disks were thirty degrees apart in color space. Participants were instructed to report the color of the inner disk (the one closer to fixation), ignoring the outer disk. As soon as they initiated the saccade toward it (defined as the eye moving more than 1.5 dva from fixation), both disks disappeared and were replaced by a color wheel. The experimenter emphasized that the participants should not initiate an eye movement until the disks appeared. Participants then clicked the location on the color wheel that best matched, to their memory, the color of the inner disk.

Trials in the adaptation block also started with the participants fixating the cross on one side of the screen. In this block, however, only one colored disk appeared, at 4 dva from fixation. Upon initiation of the saccade, the disk moved an additional 2 dva away from fixation, landing at 6 dva before disappearing upon the initiation of the second saccade. The disk did not change color. The experimenter instructed participants simply to follow the disk as it “jumped.” The experimenter reiterated the instruction against making an anticipatory saccade. Participants did not make any other responses during this

block, which was implemented to induce the saccadic adaptation effect ahead of the color report trials in the mixed block.

The mixed block consisted of both color report and adaptation trials. This block presented the trials in a pattern of three adaptation trials (intended to maintain the saccadic adaptation effect), followed by one color report trial.

CHAPTER THREE

RESULTS AND DISCUSSION

Before analyzing color report responses, we excluded some participants and some individual trials from further analysis. For the former to be considered in subsequent stages, they needed to have demonstrated the adaptation effect, and to have done so in the correct direction. Trials were not considered in this preliminary analysis if that trial's initial saccade was less than 2.5 dva in the direction of the target, or, if the initial saccade was smaller than 0.5 dva, the second saccade did not reach 2.5 dva. For each participant, we compared mean saccade amplitude during the first versus the last thirds of the adaptation block as well as during the first versus the second halves. We subsequently excluded from further analysis those participants who did not demonstrate adaptation; adapted participants should display a longer average initial saccade amplitude in the earlier trials in the adaptation block than they do in the later trials. After making eliminations based on paired-samples t-tests, twenty out of the original thirty-three participants remained, and their color-report data were analyzed.

After narrowing the sample to include only adapted participants and their "good trials" as described above, we excluded some of those participants' trials in the baseline and mixed blocks as well. We used a similar strategy as we did when filtering trials in the adaptation block: we included trials in which the initial saccade was larger than 2.5 dva, as well as trials in which the initial saccade was less than 0.5 dva with a second saccade larger than 2.5 dva. We then used maximum likelihood estimation (MLE) in MATLAB

MemToolbox to examine the probability distributions of color report error for each subject and compare the accuracy of responses given in the baseline and mixed blocks.

After the MLE results were collected, a series of paired two-sample t-tests for means was performed to compare the participants' color report data in the baseline and mixed blocks. Most importantly, we wanted to determine if the standard deviation or the mean of the distribution changed across blocks, within participants. First, a paired two-sample t-test comparing the respective means of the response distributions in the baseline ($M = 0.43$) and mixed ($M = -0.33$) blocks revealed no significant difference between color report accuracy in the two conditions ($t(19) = 0.90$, $p = 0.190$). This is in contrast to the expectation of a decrease in accuracy in the mixed block, and this finding undermines our original hypothesis. Another paired two-sample t-test comparing the mean standard deviations in the baseline ($M = 11.25$) and mixed ($M = 10.45$) blocks also revealed a lack of significant difference between the two ($t(19) = 1.43$, $p = 0.084$). This finding contradicts our expectation of a larger mean standard deviation in the mixed block due to error induced by the altered presaccadic shift of attention after adaptation. No significant difference between the probability of selecting the target color (pt) in the baseline ($M = 0.98$) and the mixed ($M = 0.96$) conditions was found, either ($t(19) = 1.08$, $p = 0.146$), indicating that the target color was no more weakly represented after adaptation than it was before. Taken together, these results do not reflect our hypothesis that saccadic adaptation would influence color perception by moving the presaccadic shift of attention to the adapted location.

Our results diverged from those of the Van der Stigchel et al. (2020) study, which largely informed our study design and hypothesis. In the present study, the induction of saccadic adaptation did not influence color report by increasing the mean difference between the reported and actual target color value, by increasing the standard deviations of the response distributions, or by making participants more likely to report the color of the distractor and therefore less likely to report the color of the target.

Although these results were unexpected, an examination of the differences between the two studies' designs, especially with respect to the adaptation trials, could be illuminating. One major difference is that Van der Stigchel et al. employed backward adaptation, while we employed forward adaptation. Forward adaptation usually develops more slowly, at a rate of 200 to 400 trials, than does backward adaptation, which appears after about 100 trials (Hopp & Fuchs, 2004), possibly making the effect of forward adaptation weaker. Our current study's design took this into consideration by creating an adaptation block with 300 trials, reinforced by additional adaptation trials interspersed within the final mixed block. Also, a majority of our participants (60.6%) displayed adaptation even with the forward design. However, some evidence has suggested that the effects of backward adaptation are more fully realized than are the effects of forward adaptation. In other words, observers ultimately adapt to gain decrease to a higher degree than they do to gain increase (Miller et al., 1981).

Disparity in adaptation step size between the two studies also could have contributed to the different results. The difference between the 37.5% back-step in the experiment from Van der Stigchel et al. (2020) and our 50% forward step may have been

sufficient to cause differences in the allocation and adaptation of the pre-saccadic shift of attention. Some studies have suggested that the visuomotor system's responsiveness to adaptation increases up to a certain point, but when the step size becomes too large, the visual system begins to attribute the discrepancy to outward movement rather than to its own motor error, which may diminish the adaptation effect (Herman et al., 2013). Furthermore, a monkey study showed that gain changes larger than 25% yielded a weaker adaptation effect, although it is well-known that the characteristics and dynamics of saccadic adaptation often appear differently in monkeys than they do in humans (Robinson et al., 2003).

The fact that our study incorporated a second distractor disk in addition to the target disk in the color report trials should also be considered as a potential driver of the differences between our current findings and those of Van der Stigchel et al. (2020). A 2015 paper from Van der Stigchel and de Vries also examines the ties between the intended saccade target, the actual saccade landing point, and the allocation of the pre-saccadic shift of attention, and its experimental design incorporates a distractor. While the 2015 study does not employ saccadic adaptation, its findings may be relevant to the topic at hand, as participants were found to be able to attend to both competing stimuli (a target and a distractor) in a line-orientation discrimination task. This contrasts with the notion that even when the actual saccade landing point differs from the location of the intended saccade target, the pre-saccadic shift of attention will always necessarily follow the actual landing point. If that hypothesis were always the case, the authors of the 2015 study would have been more likely to find that participants perceived an average of the

competing stimuli instead of perceiving the target's orientation. Although adding the element of adaptation complicates a comparison between these experiments, the above findings help to legitimize the theory behind our current study's results.

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