

Visual continuity across saccades is influenced by expectations

Hrishikesh M. Rao

Department of Biomedical Engineering, Pratt School of Engineering, Duke University, Durham, NC, USA



Zachary M. Abzug

Department of Biomedical Engineering, Pratt School of Engineering, Duke University, Durham, NC, USA



Marc A. Sommer

Department of Biomedical Engineering, Pratt School of Engineering, Duke University, Durham, NC, USA
 Department of Neurobiology, Duke School of Medicine, Duke University, Durham, NC, USA
 Center for Cognitive Neuroscience, Duke University, Durham, NC, USA



As we make saccades, the image on each retina is displaced, yet our visual perception is uninterrupted. This is commonly referred to as *transsaccadic perceptual stability*, but such a description is inadequate. Some visual objects are stable (e.g., rocks) and should be perceived as such across saccades, but other objects may move at any time (e.g., birds). Stability is *probabilistic* in natural scenes. Here we extend the common notion of transsaccadic visual stability to a more general, ecologically based hypothesis of transsaccadic visual continuity in which postsaccadic percepts of objects depend on expectations about their probability of movement. Subjects made a saccade to a target and reported whether it seemed displaced after the saccade. Targets had varying probabilities of movement (ranging from 0.1–0.9) that corresponded to their color (spectrum from blue to red). Performance was compared before and after subjects were told about the color-probability pairings (“uninformed” vs. “informed” conditions). Analyses focused on signal detection and psychometric threshold measures. We found that in the uninformed condition, performance was similar across color-probability pairings, but in the informed condition, response biases varied with probability of movement, and movement-detection sensitivities were higher for rarely moving targets. We conclude that subjects incorporate priors about object movement into their judgments of visual continuity across saccades.

Introduction

Every eye movement introduces sensory ambiguity for the brain. Did objects in the world move, or did they just

appear to move as a result of the eye movement? The visual system resolves this ambiguity with mechanisms that are not fully understood but seem to involve internal signals of eye movements called *corollary discharge* (Sperry, 1950; Von Helmholtz, 1925; Von Holst & Mittelstaedt, 1950). These signals influence visual processing (Duhamel, Colby, & Goldberg, 1992; Sommer & Wurtz, 2006) and are thought to aid in the disambiguation of external from self-induced motion of visual stimuli (for review, see Sommer & Wurtz, 2008). Visual responses of single neurons in many brain areas can distinguish whether a stimulus moves or remains still when saccades are made (Crapse & Sommer, 2012; Robinson & Wurtz, 1976; Troncoso et al., 2015), and the brain as a network is exquisitely adept at such transsaccadic judgments (for review, see Melcher & Colby, 2008).

A classic paradigm for studying visual perception across eye movements is the saccadic suppression of displacement (SSD) task (Bridgeman, Hendry, & Stark, 1975). Subjects make a saccade to a peripheral target that is displaced during the saccade and report the direction of the target movement. Small target movements often go unnoticed (Bridgeman et al., 1975; Deubel, Schneider, & Bridgeman, 1996; Müsseler, Van Der Heijden, Mahmud, Deubel, & Ertsey, 1999), apparently because the brain attributes the retinal discrepancy to oculomotor error rather than object motion (Collins, Rolfs, Deubel, & Cavanagh, 2009). That is, subjects in these experiments have a bias toward expecting visual stimuli to remain unchanged across saccades (Niemeier, Crawford, & Tweed, 2003; Read, 2002; Weiss, Simoncelli, & Adelson, 2002). When this

Citation: Rao, H. M., Abzug, Z. M., & Sommer, M. A. (2016). Visual continuity across saccades is influenced by expectations. *Journal of Vision*, 16(5):7, 1–18, doi:10.1167/16.5.7.

doi: 10.1167/16.5.7

Received October 23, 2015; published March 10, 2016.

ISSN 1534-7362



expectation is violated through manipulation of the stimulus, such as postsaccadic disappearance (Deubel et al., 1996; Deubel, Schneider, & Bridgeman, 2002), change in form (Demeyer, De Graef, Wagemans, & Verfaillie, 2010), or movement (Gysen, De Graef, & Verfaillie, 2002; Gysen, Verfaillie, & De Graef, 2002), the percepts of the subjects change: SSD diminishes such that smaller displacements are more readily detected.

Outside of the laboratory, it would be erroneous to expect uniform visual stability, because much of the world is animate. Some objects move rarely, such as rocks, but others move frequently and rapidly, such as birds. All kinds of objects fall in between. Through experience, we develop priors, or expectations, about classes of objects in natural visual scenes (Eckstein, Drescher, & Shimozaki, 2006). When these expectations are violated, it is important to react. Sudden movement at a location expected to be stable, for example, could signal a camouflaged predator.

Motivated by these ecological considerations, the overall goal of this study is to move past the idea of studying visual stability across saccades and instead study *visual continuity*: our facility at predicting the postsaccadic state of each visual image as a function of its movement statistics. Studying visual continuity across saccades expands on traditional assessments of visual stability and provides a more general framework for understanding visual perception that could facilitate the design of more naturalistic experiments.

Here we tested the fundamental hypothesis of this framework, that perceiving object instability across saccades depends not only on visuomotor factors (e.g., corollary discharge and the size of object movement) but also on *expectation*, a cognitive factor. In our case, expectation is a prior about the probability of movement given the object's features. We designed a variant of the SSD task in which the movement probability of a stimulus was signaled by its color. Subjects were tested before and after learning the relationship between color and jump probability. In support of our hypothesis, we found that expectations influenced the ability to detect whether a stimulus moved across saccades. Response bias, sensitivity to displacement, and psychometric thresholds were all affected by expectations. The results suggest a tight interplay between priors about objects and the percept of visual continuity across saccades.

Methods

Subjects and overview

Twenty-four naive human subjects (16 women), with normal or corrected-to normal vision, were recruited

from the Duke University community. All individuals were older than 18 years and gave informed consent through protocols approved by the Duke Institutional Review Board. Subjects performed a novel SSD task in two experiments. Twelve of the subjects participated in Experiment 1, which tested our primary hypothesis about the effect of priors on visual continuity. In a follow-up study, 12 other subjects participated in Experiment 2, to examine the potential influence of implicit learning on performance.

Data collection

Subjects sat in a dark room with their heads supported by a chin rest and a forehead strap. All subjects reported their responses using their right hand on the number pad on a standard keyboard. Stimulus delivery was accomplished using Presentation software (Version 0.70, www.neurobs.com) and custom-written code available upon request. Visual stimuli were displayed on an LED monitor using a refresh rate of 60 Hz at $1,920 \times 1,080$ resolution. The monitor was positioned 60 cm in front of the subject and centered relative to the head. All saccadic targets were $1^\circ \times 1^\circ$ squares. Monocular eye position was recorded at 333 Hz with the eye-tracking system developed by Matsuda et al. (Matsuda, Nagami, Kawano, & Yamane, 2000; Matsuda, Takemura, Miura, Ogawa, & Kawano, 2014). Using a position threshold of 2° , we detected saccades online at $3.15^\circ \pm 1.23^\circ$ (average \pm SD) from the fixation point or, as evaluated offline, 19.1 ± 14.7 ms after saccade initiation. Saccade detection triggered a software command to refresh the target at its new location. This command took 1 to 16 ms to execute (confirmed trial-by-trial in Presentation). We used a photodiode to measure the delay between execution of the screen refresh command and the actual time that the target appeared at its new location on the screen (11.6 ± 0.3 ms). Hence, the total average lag from saccade initiation to target jump was $19.1 + 16$ (max) $+ 11.6 = 46.7$ ms, compared with the average saccade duration (determined offline) of 71 ms, or about 66% of the way into the saccade, similar to previous target presentation timings in our laboratory (68.9% in Crapse & Sommer, 2012). No trials had to be excluded because of target jumps occurring after saccade termination. Some trials were excluded for other reasons, however, as described below in the Psychometric Curves section. Offline, eye position traces were low-pass filtered at 50 Hz before saccade onset and completion calculations and related analyses.

Experiment 1

Subjects performed a novel variation of the SSD task in which targets had different probabilities of moving

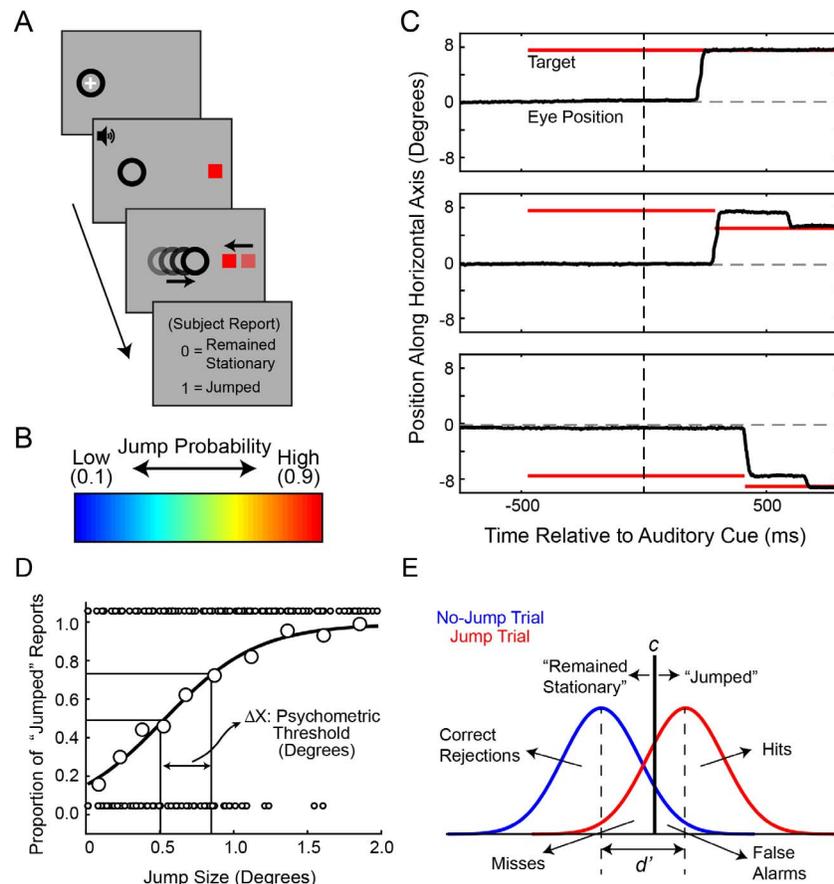


Figure 1. Methods and data analysis. (A) Schematic of a single trial. Eye position is represented by the black circle. After foveation of a fixation spot (white crosshair), a saccadic target (red square) appeared in the periphery and the fixation spot disappeared. An auditory cue provided the go signal for subjects to make a saccade to the target. On some trials, the target jumped rightward or leftward during the saccade (as shown), but on other trials, the target remained stationary. Subjects reported their percept that the target “jumped” or “remained stationary” with a key press to end the trial. (B) From trial to trial, the target color was uniformly drawn from a gradient of colors that was associated with linearly varying likelihoods that the target would jump during the saccade. (C) Example eye position traces (black traces) from one trial in which the target (red traces) remained stationary (top) and two trials in which the targets jumped during the saccade (middle and bottom). Dashed lines are referenced to fixation spot location. (D) Example psychometric curve. Each small circle represents the average binary decision of the subject (proportion of “jumped” reports) for trials within an equal-number bin of jump sizes. This binning is just for illustration; the psychometric curves were fit using logistic regression across all jump sizes (although fitting logistic curves to the binned jump sizes yields similar results). We computed threshold as the difference in jump size (ΔX) that corresponded to a rise in the proportion of “jumped” reports from 0.5 to 0.75. (E) Schematic of signal detection theory analysis of the two trial types (jump vs. no jump), the two response types (“jumped” vs. “remained stationary”), and the four classifications of trial (Hits, Misses, False Alarms, and Correct Rejections). d' represents the separability of the two Gaussian curves and the criterion, c , represents the response bias of the subject.

depending on their color. Expectations about target movement were manipulated by withholding or providing information about these color-probability assignments. The visual display, the task, and the underlying probabilities of movement assigned to each color were the same for both conditions; only expectations about target properties varied. The purpose was to see if changes in expectation affected reports of transsaccadic stimulus displacement.

At the start of every trial, a fixation point (crosshair) appeared in the center of the screen (Figure 1A). Upon

acquisition of the fixation point, the crosshair disappeared but the subject had to continue to maintain fixation. After 500 ms, a saccadic target appeared on the horizontal plane at an average eccentricity of 8° (uniform distribution from 7.5° to 8.5° , pseudorandomized in position and hemifield to avoid spatial cues or biases). The trial-by-trial randomization of position helped to ensure that subjects used internal estimates of target position and eye position rather than relying on external spatial cues and biases (Bansal, Bray, Peterson, & Joiner, 2015; Joiner, Cavanaugh,

FitzGibbon, & Wurtz, 2013; Joiner, FitzGibbon, & Wurtz, 2010). After target onset, the subject was required to maintain fixation for an additional 450–650 ms until an auditory signal (single beep) cued the subject to make a saccade to the target. This delay period was enforced to allow for ample time to build a spatiotopic representation of the target (Zimmermann, Morrone, & Burr, 2013). During the saccade, the target could either remain stationary or jump to the left or right. On trials in which the target jumped, the amplitude of the displacement was drawn from a modified standard Gaussian distribution (minimum amplitude was 0.05° to maximum amplitude 4°). Postsaccadically, subjects were required to fixate on the stimulus for 500 ms before it disappeared. Subjects then reported, using a keyboard press, whether the target was perceived to have jumped or remained stationary. There was no required distinction between a leftward or rightward jump; both were reported as “jumped.” If a subject broke fixation before the auditory cue to saccade, the trial was immediately aborted and three rapid beeps provided an error signal.

The task differed from standard SSD paradigms in two ways. First, subjects assessed whether or not the target jumped or remained stationary as compared with the traditional “left/right” reports for targets that were known to jump on every single trial. Second, targets varied in color, and these colors symbolized the probability that a target would jump. In each trial, the color of the target was chosen from a gradient from cold colors (bluer) to warm colors (redder; Figure 1B). Fifty discrete colors along the gradient were mapped linearly to the probability of jumping, from very low (probability of 0.1) to high (probability of 0.9). For half of the subjects, the probability assignments were from blue (lowest) to red (highest) and for the other half, from red (lowest) to blue (highest). We chose to use a gradient with many steps (rather than a reduced set of colors) to encourage participants to use a behavioral rule rather than relying on simple stimulus-response associations. Furthermore, using a warm-to-cool or cool-to-warm gradient requires many intermediate steps to convey the gradient properly; otherwise, it may appear as a disparate collection of individual colors. Determination of whether a target would jump on a particular trial was calculated according to these probabilities, selected with replacement. If a target was to jump on a particular trial, the size of the jump was drawn from the same modified Gaussian distribution regardless of the color of the target. Thus, a target’s color indicated the likelihood that it would jump on a given trial but not the size (or direction) of the displacement.

Each subject performed three blocks of trials. The first was a *Control* block for which the targets were always white with a 0.5 chance of jumping on each trial,

although that probability was unknown to the subject. The second was an *Uninformed* block that used the color-probability SSD task described above, but subjects remained naïve about the existence or identity of any color-probability assignments. After that block, we queried each subject to find out their subjective opinion about how the colored targets differed, and then we informed them of the true relationship between colors and probabilities of movement. The subjects then performed an *Informed* block that, except for their new knowledge about the color-probability assignments, was exactly the same as the Uninformed block. The experiment was split into two sessions (one session per day). The Control block lasted approximately 1 hr, and the Uninformed block lasted approximately 2 hr, and both were performed in the first session. The Informed block also lasted approximately 2 hr and was performed in the second session.

Between the Uninformed and Informed blocks (at the start of the second day), the information given to the subjects followed this script: “The color gradient corresponds to a probability of jump where the coldest color jumps 10% of the time and the warmest color jumps 90% of the time. The cold-to-warm gradient represents a linearly varying jump probability.” This description was modified appropriately for subjects tested on the opposite assignment (red-low probability, blue-high probability). The investigator answered any questions the subject had to ensure that the meaning of the colors, and their corresponding jump probabilities, was clear and understood.

In addition to the reasons discussed above, the large number of colors (50 from blue to red) was chosen to mitigate implicit learning of the color-probability assignments in the Uninformed block. During that block, we wanted the subjects to have no expectations about whether a particular target would move in a trial. The goal was for subjects’ expectations about the targets to change in a stepwise manner, due to the instructed information, to optimize identification of any resulting changes in task performance. To test whether implicit learning of color-probability assignments occurred in the Uninformed block without explicit instruction, we compared performance early and late in the block as described in the Results section. In addition, we ran a follow-up study, Experiment 2, as described next.

Experiment 2

The purpose of this experiment was to amplify the possibility of implicit learning in the Uninformed block, to determine the extent to which subjects might, within the 2-hr block of trials, develop expectations about target movement based on inferred color-

probability assignments. If subjects did develop expectations, we could examine how the behavior differs as a result of explicit instruction as opposed to implicit learning. Experiment 2 was the same as Experiment 1 except that only three colors from the blue-red gradient were used: the two extremes and the central color (light green). With only three unique targets instead of 50, subjects had about 17 times as much exposure to each color. In Experiment 2, just as in Experiment 1, subjects performed a Control block, an Uninformed block, and then an Informed block. Twelve new subjects were recruited. For half of them, the color-probability assignment was blue-low to red-high, and for the other two, this assignment was reversed.

Data analysis

The data sets included eye movement traces and binary reports that the target jumped or remained stationary during the saccade. Eye movement traces were used for offline confirmation of steady fixation and, thorough comparison with target jump times, to ensure that target motion occurred during the saccade, not before or after (Figure 1C). From the reports of the subjects, we evaluated performance using psychometric curves and signal detection theory. Statistical tests were parametric (analyses of variance [ANOVAs], t tests, and Pearson correlation tests) and evaluated at a significance criterion of $p < 0.05$ with Bonferroni correction for multiple comparisons as appropriate.

Psychometric curves

The data set from each subject consisted of binary reports that the target jumped or remained stationary during the saccade. The main measure was the “Proportion of ‘jumped’ reports” for each color (or bin of colors) and jump size. As discussed at the end of this section, “jumped” reports were further classified into Hits and False Alarms, and “stationary” reports into Correct Rejections and Misses, for signal detection (response bias c and sensitivity d') analyses. 9.8% of all the trials were aborted online when presaccadic fixation was broken before the auditory cue was delivered. Of the successfully completed trials, we excluded trials in which the first saccade landed more than 5° from the target’s presaccadic location (3.35%) and trials in which saccadic reaction times were greater than 1 s (4.1%). This time value was selected as a balance between using comparably quick responses across trials and allowing ample time for subjects to build an internal representation of the spatiotopic position of the targets (Zimmermann et al., 2013). The average presaccadic viewing duration of our subjects was 680 ± 99 ms (measured as time from target onset to saccade

initiation). All the data presented in this report were also split by inward/outward as well as leftward/rightward target jumps. All results and interpretations were nearly identical across these subgroups. Thus, we pooled the data across directions of target jumps as well as direction of saccades.

Psychometric curves were fit to the proportions of “jumped” responses using logistic regression,

$$y = \frac{1}{1 + e^{-z_i}} \quad (1)$$

$$z_1 = b_0 + b_1 \mathbf{j} \quad (2)$$

$$z_2 = b_0 + b_1 \mathbf{c} + b_2 \mathbf{j} + b_3 \mathbf{c} \mathbf{j} \quad (3)$$

where \mathbf{j} represents the vector of jump size and \mathbf{c} represents the corresponding vector of colors. The logistic regression was either applied to individual bins of adjacent colors as a function of jump size only (vector of exponents z_i in Equation 1 equaling z_1 from Equation 2) or incorporated both color and jump size simultaneously and thereby using all trials in a given block (vector of exponents z_i in Equation 1 equaling z_2 from Equation 3). For the former method, five equal bins were formed by partitioning the full range of 50 colors into five bins of 10 adjacent colors. Figure 2 shows the qualitative difference between these two methods. For the purposes of this article, all analyses and statistics were performed by fitting the psychometric curves across jump sizes only (Equation 1 and Equation 2; Figure 2, top row), for each of the five color bins, as this provided results closer to the raw data. All conclusions were unchanged, however, using the color and jump size double-fitted regressions (Equation 1 and Equation 3; Figure 2, bottom row). Psychometric thresholds were measured as the change in jump size corresponding to a rise in the proportion of “jumped” responses from 0.5 to 0.75 (Figure 1D). In a few cases, the entire psychometric curve exceeded the 0.5 level (although never the 0.75 level). For such data, we extrapolated the curve to negative jump sizes for calculating the threshold.

Signal detection techniques

There were four main types of trial results. A trial was a “Hit” when the target jumped and the subject reported that it jumped, a “Correct Rejection” when the target remained stationary and the subject reported that correctly, a “Miss” when the target jumped but the subjects did not report it, and a “False Alarm” when the target remained stationary but the subject reported movement. Psychometric curves provide a useful overview of performance, but they poorly take into account false alarms and correct rejections. We performed a more thorough assessment of transsacca-

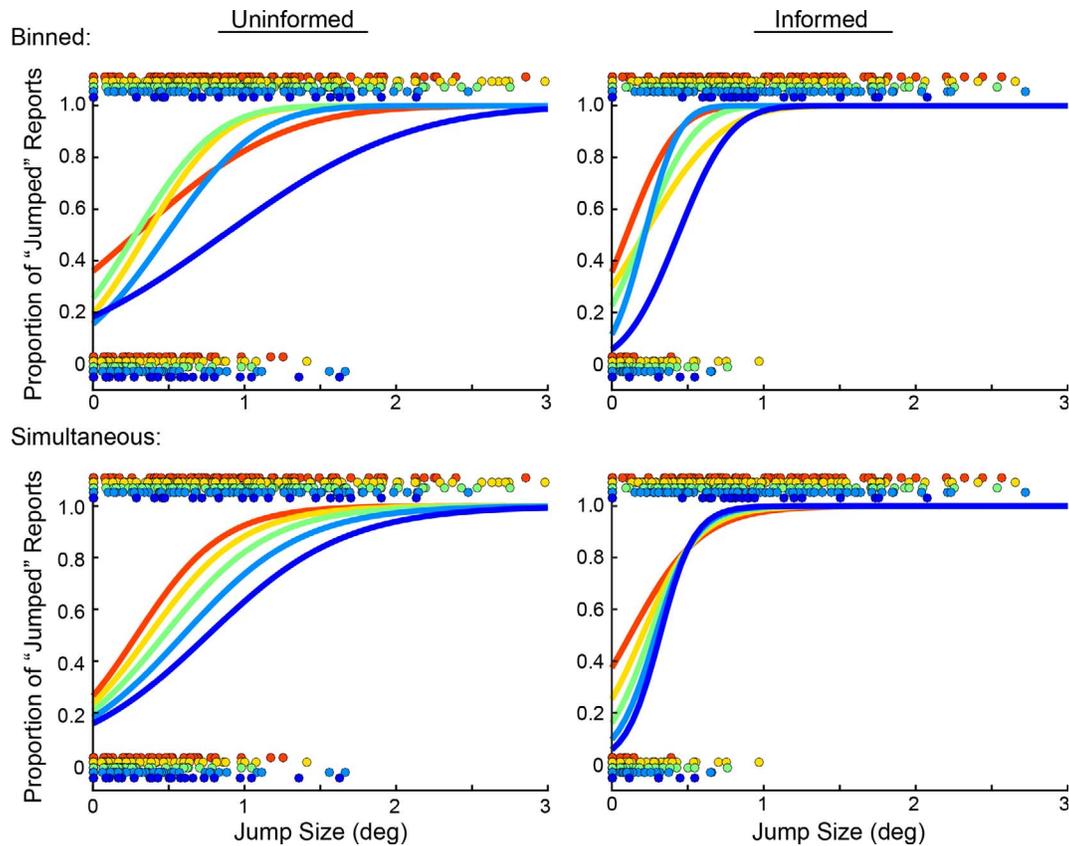


Figure 2. Single-subject behavior. Data from the Uninformed block are shown in the left column, and data from the Informed block are shown in the right column. Filled circles represent the binary responses on individual trials across the binned color spectrum, vertically spaced for viewing clarity. Top row: Psychometric curves computed by fitting to jump sizes for each bin of colors individually. Bottom row: Curves computed by fitting to all colors and all jump sizes simultaneously without any binning (for viewing comparison, only five color values, i.e., every 10th color, are shown).

dic change detectability using signal detection techniques that took into account all four trial outcomes (Figure 1E; Macmillan & Creelman, 2004). Specifically, we calculated the sensitivity index, d' , and a response bias term called criterion, c ,

$$d' = z(H) - z(FA) \quad (4)$$

$$c = -0.5 \times [z(H) + z(FA)] \quad (5)$$

where H is Hit Rate = Hits/(Hits + Misses), FA is False Alarm Rate = False Alarms/(False Alarms + Correct Rejections), and $z(*)$ denotes the inverse Gaussian cumulative distribution function. A d' value of zero corresponds to performance at the level of chance. The more positive the value of d' , the better the sensitivity of the subject to transsaccadic target displacement. The response bias c reports the behavioral preference of a subject. For an ideal observer, c would be zero. A positive value of c (rightward shifts) indicates that a subject was biased toward reporting that the target remained stationary. Conversely, a negative value of c (leftward shifts) would mean a bias towards reporting “jumped.”

Just as the colors were binned into five equally sized groups to construct the psychometric curves, the same color bins were used for calculating d' and c . For both metrics, data from representative subjects are shown as well as population averages across subjects for the Uninformed and Informed blocks. Differences in c and d' as a function of color were assessed with linear regression over the five groups of colors. Negative c slopes would indicate a preference for reporting “Jumped” for the targets that jump frequently and “Remained Stationary” for those that rarely jump. For d' , the sign of the slope indicates whether transsaccadic change detection was better for targets that jumped with low probability (negative d' slopes) or high probability (positive d' slopes).

Results

We used a modified SSD task, in which the color of a saccade target signified its probability of jumping, to test the hypothesis that expectations about object

movement influence the percept of visual stability across saccades. Subjects performed the same task in *Uninformed*, then *Informed*, conditions. Just before starting the Informed condition, subjects were told the color-probability relationships. A Control condition established baseline performance with no colors. In Experiment 1, we used a spectrum of color-probability assignments during the Uninformed and Informed conditions. In Experiment 2, we used a reduced set of colors, mapped to the extremes and middle of the probability range.

Experiment 1

The twelve subjects performed an average of 360 ± 130 trials in the Control block, 705 ± 95 trials in the Uninformed block, and 652 ± 114 in the Informed block.

Single-subject example

Data from a representative subject, for qualitative assessment, are shown in Figure 2. The subject's detection of the jump increased with jump size and seemed to vary by color (probability of jumping). The main point of our analysis was to quantify performance as a function of color and how this relationship changes from the Uninformed to the Informed condition.

We summarized performance with logistic functions fit individually for bins of color as a function of jump size (Figure 2, upper panels; shown are curves for the 50 colors binned into five equal groups) or fit simultaneously as a function of both color and jump size (Figure 2, lower panels; shown are the curves evaluated at every 10th color). The simultaneously fit logistic curves are shown for purpose of illustration, because they depict the pattern of effects more clearly, but for all quantitative analyses, we used the individual color bin curves that were fit to jump size only, as they involved less “smoothing.” The study's results and conclusions were the same using either method.

For the subject in Figure 2, the color-probability assignments were blue-low to red-high. In other words, blue targets rarely jumped, $P(\text{jump}) = 0.1$, whereas red targets jumped frequently, $P(\text{jump}) = 0.9$. During the Uninformed condition (Figure 2, left), psychometric thresholds varied by color, but no clear pattern was apparent in the color-binned, jump-size fit logistic curves (Figure 2, upper left). When color and jump size were fit simultaneously (Figure 2, lower left), a clearer pattern was seen in which “jumped” was reported more often for the redder colors compared with the bluer ones. Further, fits for the redder colors had a smaller threshold. False alarm rates, corresponding to the y-intercepts of the psychometric curves, ranged from 0.2 to 0.4 depending

on the logistic fit method. We will take false alarms into account quantitatively with c and d' measures.

In the Informed block (Figure 2, right), behavior changed in two main ways. First, the thresholds decreased for all colors, but this effect was especially pronounced for the bluer colors (lower probability of movement during the saccade). Second, the false alarm rates diverged, dropping for the bluer colors for both logistic fit methods (Figure 2, upper and lower right) and increasing for the redder colors in the double-fit logistic curves (Figure 2, lower right). Both measures suggest that introducing an expectation that some targets are more stable than others changed performance. In particular, expectation that a target will be relatively stable (here, the bluer targets) seemed to increase both the accuracy of detecting when it was actually stable (lower false alarm rates) and the ability to notice when it moved (smaller thresholds).

To determine if these single-subject trends were significant, we calculated signal detection theory measures of behavioral response bias c and perceptual sensitivity d' for each subject and analyzed the overall changes in these measures across the group data.

Response bias

The response bias criterion c represents the influence of subject behavior on performance, regardless of underlying signal/noise distributions (see the Methods section). If a subject exhibits no bias and uses a strategy based only on signal/noise distribution separation, then $c = 0$. If a subject favors “jumped” responses, relative to what is optimal based on objective evidence, then $c < 0$. If a subject is more conservative and favors “remained stationary” responses, then $c > 0$. The response biases as a function of color bins for four typical subjects, including the subject in Figure 2, are shown in Figure 3A for the Uninformed trials and in Figure 3B for the Informed trials.

The pooled response bias data for all 12 subjects are shown in Figure 3C and 3D for Uninformed and Informed conditions, respectively ($M \pm SD$ for each color bin). In the Uninformed condition (Figure 3B), response bias did not change significantly across color bins (slope = -0.05 ± 0.06 ; one-sample t test, $p = 0.17$) and remained, on average, around $c = 0$ for all. That is, on average, the subjects responded in a relatively unbiased way to all targets regardless of color and underlying jump probability. In the Informed condition, however, subjects showed a striking and systematic change in behavior: The response bias decreased significantly with jump probability (slope = -0.14 ± 0.05 ; one-sample t test, $p = 0.0069$). In addition, mean response biases are >1 for rarely jumping targets and <1 for commonly jumping targets. This means that they alter their behavior to favor reports of “jumped” for targets that they expect to jump more frequently

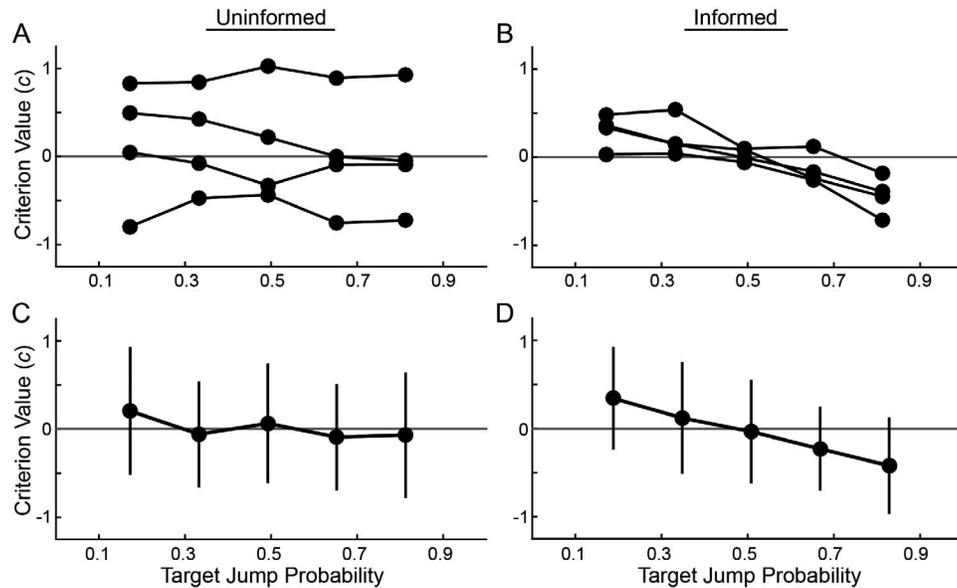


Figure 3. Response bias. The top row shows the criterion c for four typical subjects, and the bottom row shows the population criterion values. Uninformed blocks are on the left, and Informed blocks are on the right. (A) In the Uninformed condition, the criterion values remained relatively unchanged across the color spectrum (i.e., target jump probability). (B) In the Informed condition, criterion values decreased systematically from positive values for low-probability jump targets to negative values for high-probability jump targets. (C) As a population, c stayed near zero in the Uninformed condition across the spectrum of colors. (D) In the Informed condition, c increased for targets with low jump probability and decreased for targets with high jump probability.

and reports of “not jumped” for targets that they expect to remain stable.

Sensitivity

The change in response bias confirmed that subjects took into account priors about stimulus movement, but one could argue that this change in behavior was not altogether surprising. More compelling would be a change at the perceptual level, as quantified by the sensitivity measure d' . Recall that $d' = 0$ indicates random responses with no perceptual detection of stimulus movement regardless of jump size. The larger the d' value, the better the transsaccadic change detection as determined by aggregate analysis of Hits, Misses, False Alarms, and Correct Rejections. In Figure 4, results of d' calculations as a function of jump probability are shown for the same four subjects depicted in Figure 3A and B. Each row corresponds to a single subject. Consider first the data in the top row of Figure 4, which are from the subject of Figure 2. In the Uninformed block, this subject performed about the same across the color/probability spectrum, with slightly higher sensitivity for redder colors (higher probability of jumping), as indicated by the positive slope of d' versus jump probability (slope value shown in upper right of each plot). In the Informed block, the d' values for bluer colors (lower jump probabilities) increased while d' for redder colors stayed about the same. The overall result

was a strongly negative slope of d' versus color after instruction.

Examining the results of the other subjects in Figure 4, the slopes of d' versus jump probability varied in the Uninformed condition (Figure 4, left column), with two subjects exhibiting positive slopes and two subjects negative slopes. Overall, six of the 12 subjects showed positive slopes in the Uninformed condition. In the Informed condition, however (Figure 4, right column), the results were uniform: all 12 subjects showed negative slopes of d' versus jump probability.

These slope data (d' vs. jump probability) are compiled for all 12 subjects in Figure 5A. Individual slopes are shown with black circles and average slopes with open circles for the Uninformed and Informed data sets. The average slope in the Uninformed condition was not significantly different from zero (0.09 ± 0.45 ; one-sample t test, $p = 0.53$) but, in the Informed condition, the average slope was significantly below zero (-0.68 ± 0.47 ; one-sample t -test, $p = 4.17 \times 10^{-4}$). Overall, there was a significant decrease in d' slopes from the Uninformed to the Informed condition (paired t test, $p = 0.0046$).

The data in Figure 5A were calculated from binned color data for each subject. A complementary way to evaluate the data, shown in Figure 5B and C, is simply to plot the average d' value across subjects for each of the 50 probability levels. The conclusions were the same: The slope of average d' versus jump probability was not significantly different from zero in the

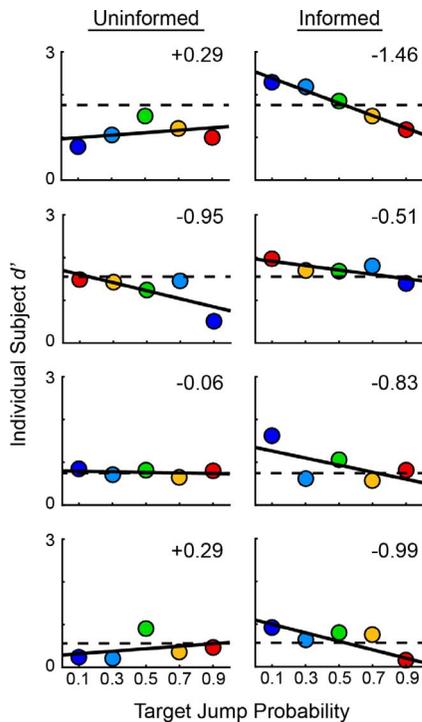


Figure 4. Individual subject d' values. Data from the Uninformed (left column) and Informed (right column) blocks are shown for the same four subjects (rows) of Figure 3. Also, the top row is from the subject of Figure 2. Dashed lines indicate d' in the Control blocks (constant jump probability). Solid lines are linear fits to the d' data, and numbers at the upper right of each plot are the slopes of those fits. Symbol colors depict the direction of the color gradients used for each subject (blue to red, or red to blue).

Uninformed block (slope = 0.10 ± 0.17 ; one-sample t test, $p = 0.54$), but it was significantly less than zero in the Informed block (slope = -0.69 ± 0.14 ; one-sample t test, $p = 5.0 \times 10^{-6}$). This pooled method provided insight into the reason for the drop in slope. Primarily, it seemed to be due to an elevation in d' values for

targets with low jump probabilities after instruction (compare bluer targets in Figure 5B vs. Figure 5C). In contrast, d' values for targets that jumped frequently stayed about the same after instruction (compare redder targets in Figure 5B vs. Figure 5C). Finally, note that d' for targets that were expected to move about half of the time (green colors in Figure 5B, C) aligned well with the average d' from earlier Control blocks in which only white targets were used that moved 50% of the time (dashed lines), confirming that, on average, SSD performance for “movement-neutral” targets was the same throughout the experiment. This suggests that temporal factors that could decrease average d' over time, such as fatigue, had little impact on the results.

A spatial factor that can influence the perception of displacement across saccades is the point of subjective stationarity (PSS), or perceptual null location (Bansal et al., 2015; Boi, Öğmen, Krummenacher, Otto, & Herzog, 2009; Collins et al., 2009; Öğmen, Agaoglu, & Herzog, 2015). Ideally, the PSS is at the presaccadic target location. If it is offset, it causes directional differences: The perception of displacement varies with target jump direction. To assess whether a nonzero PSS may have affected our data, we tested whether the effects of expectation varied with target jump direction. We split all trials into two groups, “Inward” and “Outward” target jumps, and computed d' as a function of target jump probability in the Uninformed and Informed blocks just as done before (as in Figure 5B and C). Because the calculation of d' requires trials in which the target does not move, we randomly distributed no-jump trials between the Inward and Outward groups. We found that in the Uninformed block, the d' slopes for both groups were not significantly different from zero (Inward: slope = 0.19, $p = 0.29$; Outward: slope = -0.11 , $p = 0.61$; one-sample t tests), whereas in the Informed block, the d' slopes for both groups were significantly negative (Inward: slope = -0.75 , $p = 1.9 \times 10^{-4}$; Outward: slope = -0.73 , $p = 3.3 \times 10^{-4}$; one-sample t tests), nearly identical to each

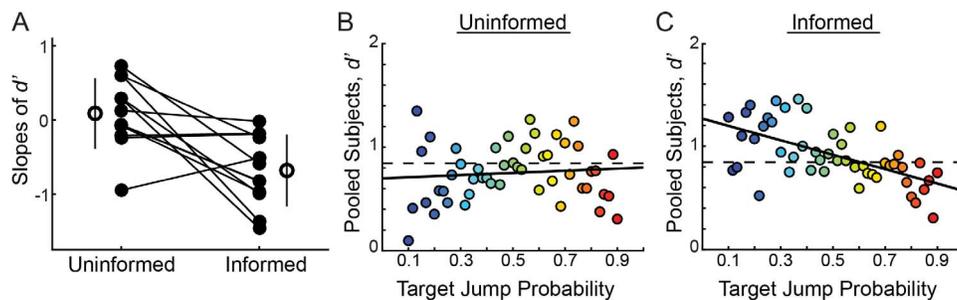


Figure 5. Population d' results. (A) Slopes of d' data comparing the Uninformed block with the Informed block. Mean \pm standard deviation (open circles) are plotted next to corresponding sets of individual data points (black circles). In a second analysis, average d' values from all 12 subjects for each of the 50 target colors were plotted against target jump probability for the (B) Uninformed and (C) Informed blocks. Solid lines are linear fits to the d' data. The slope was not significant in the Uninformed condition but significantly negative in the Informed condition (see text). Dashed lines represent the population d' from the Control blocks.

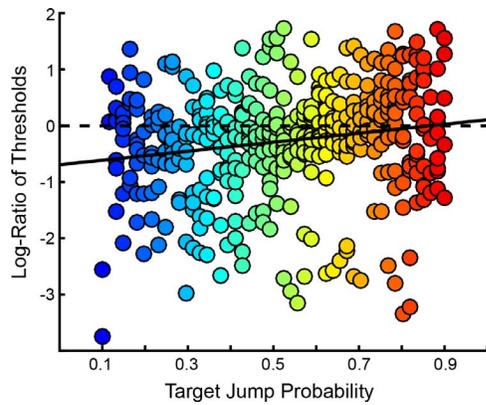


Figure 6. Population psychometric threshold results. The thresholds from psychometric functions for data collected in the Informed block were expressed relative to thresholds calculated for corresponding data in the Uninformed block. Each circle represents these “normalized threshold” data from an individual subject, based on psychometric curves fit for each color independently. To correct for the skewed ratio data, we log-transformed them. A linear fit to the pooled log-ratio data (solid black line) was mostly below the zero line with a significant positive slope. Therefore, the lower the probability of target movement, the greater the reduction in threshold.

other and close to the slope of the pooled data (-0.69 ; cf. Figure 5C). Because the d' results did not vary with target jump direction, an influence of PSS on our data seems unlikely.

Psychometric thresholds

For each of the 50 jump probabilities, a psychometric curve can be computed independently. This curve is not as precise a measure of performance as d' or c , as it includes false alarms that influence the y-intercept. Thresholds derived from the curve, measured as the jump distance corresponding to a rise in the proportion of “jumped” responses from 0.5 to 0.75,

nevertheless provide a straightforward and commonly used assay of sensitivity (Bansal et al., 2015; Deubel, Bridgeman, & Schneider, 1998; Joiner et al., 2013). Smaller thresholds indicate better performance in that smaller changes in jump sizes are detected. We analyzed thresholds to determine if they yielded results consistent with those found using signal detection theory.

In Figure 6, we plot normalized thresholds for all of the 12 subjects. The normalization provided the ratio of the threshold in the Informed block relative to that in the Uninformed block. Taking the ratio yielded skewed data with median <1 but a long tail >1 (skewness = 4.63). We log-transformed the ratios to work with a representation of the data that was much closer to a normal distribution (skewness = 0.75). Each data point indicates whether information about color-probability assignments caused a subject’s threshold for detecting target movement, for each jump probability, to decrease (log-ratio <0), increase (>0), or stay the same ($=0$). To determine if the log-ratios varied across the color-probability spectrum, we computed a linear fit to the data. The fit rose significantly from <0 at lower probabilities to ~ 0 at higher probabilities (slope of linear fit = 0.80; $R^2 = 0.183$; one-sample t test, $p < 1.40 \times 10^{-4}$). Hence, psychometric threshold data were consistent with the d' results, indicating that when subjects received explicit information that certain stimuli were relatively unlikely to move, they exhibited a lower threshold (heightened ability) to perceive the movement of those stimuli across saccades but experienced little to no perceptual change for targets that were likely to move.

Effects of saccade parameters

Differences in saccadic latency or accuracy from trial to trial can affect perceptual judgments (e.g., Bansal et al., 2015; Collins et al., 2009; Zimmerman et al., 2013), so we analyzed those saccade parameters and their possible effects on our data. Saccadic latencies are

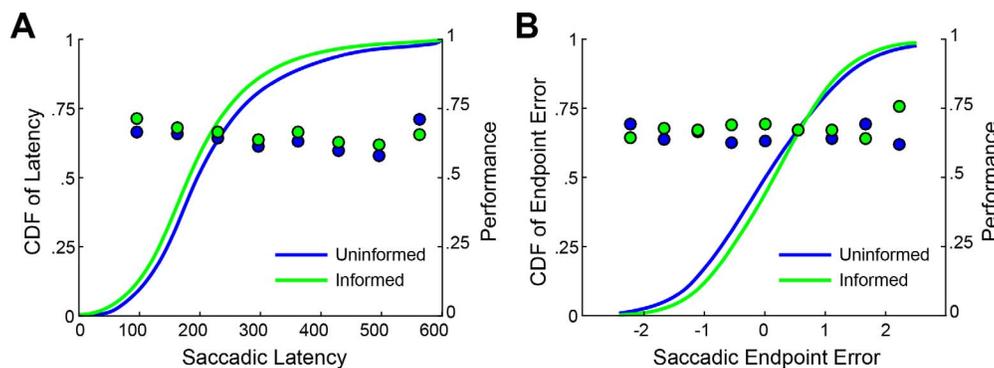


Figure 7. Comparison of saccadic (A) latency and (B) endpoint error between blocks. Curves show the cumulative distribution functions of each saccade parameter for Uninformed and Informed blocks. Dots show the fraction of correct trials across the ranges of saccade parameters, calculated in 60-ms bins for latency and 0.5° bins for endpoint error.

	b_0 (Intercept)	b_1 (Latency)	b_2 (Endpt)	b_3 (Block)	b_4 (Latency × Endpt)	b_5 (Latency × Block)	b_6 (Endpt × Block)	b_7 (Latency × Endpt × Block)
Coefficients	0.70	−0.0005	0.119	0.211	−0.0002	−0.057	−0.001	0.0007
p values	<0.001	0.056	0.112	0.017	0.585	0.288	0.102	0.072

Table 1. Values and significance of each coefficient for the regression analysis of performance as a function of latency, endpoint error, and block. Note: Significant results ($p < 0.05$) are in bold.

plotted as cumulative distributions in Figure 7A for the Uninformed (blue) and Informed (green) conditions. In most trials, the latencies ranged from 100 to 300 ms, and there was no significant difference in the distribution of latencies between the Uninformed and Informed conditions (medians 199 ms and 180 ms, respectively; Wilcoxon rank sum test, $p = 0.421$). Saccade accuracy was determined by measuring trial-by-trial endpoint error, the magnitude of the difference between the saccadic landing point and the presaccadic position of the target. Most endpoint errors were $<1^\circ$ (Figure 7B), and there was no significant difference in the distribution of endpoint errors between the Uninformed and Informed conditions (medians -0.06 and 0.08 , respectively; Wilcoxon rank sum test, $p = 0.869$).

Although neither the saccadic latency nor accuracy varied significantly between Uninformed and Informed blocks, it was possible that performance might have been affected by the variations in saccade parameters. To examine this, we plotted the average performance (fraction of correct responses) in Uninformed (blue dots) and Informed (green dots) blocks across latency (Figure 7A) and endpoint accuracy (Figure 7B). We quantified whether performance depended on latency, endpoint error, block, or their interactions using a logistic regression that included all three variables:

$$\mathbf{z}_3 = b_0 + b_1\mathbf{l} + b_2\mathbf{e} + b_3\mathbf{b} + b_4\mathbf{le} + b_5\mathbf{lb} + b_6\mathbf{eb} + b_7\mathbf{leb} \quad (6)$$

Vector \mathbf{z}_3 was used by Equation 1 to calculate the dependent variable y , the trial-by-trial performance denoted as correct ($y = 1$) or incorrect ($y = 0$). The independent variable vectors were \mathbf{l} , latency; \mathbf{e} , absolute value of endpoint error; and \mathbf{b} , block (Uninformed: 0, Informed: 1). Results are listed in Table 1. Aside from the intercept b_0 , the only significant term was coefficient b_3 , representing an effect of block. Its positive sign meant that performance was better in the Informed than in the Uninformed blocks, as expected from the subjects' exploitation of color-probability information (see the Response Bias and Sensitivity sections). With regard to saccade parameters, performance did not depend

significantly on latency, endpoint, or any interactions involving them (b_1 , b_2 , and b_4 – b_7).

Implicit learning

We have assumed that subjects changed their expectations in a stepwise manner, when they received information about the underlying probabilities of target movement at the start of the Informed condition. After every Uninformed block, subjects were questioned about whether they inferred the roles of the colors and the links to the jump probabilities. None of the subjects reported that they noticed the relationship. It is possible, however, that they may have detected color/probability associations during the Uninformed block and acted on them unknowingly. To test the hypothesis that subjects learned color-probability associations implicitly during the Uninformed condition, we examined the time course of effects during this condition. We did this by splitting the data from this condition into the first two-thirds and last one-third of trials (finer time-course analyses yielded noisier data because of the many trials needed to calculate stable signal detection theory measures). As in our d' analysis, we calculated the slopes of d' versus jump probability for each of these two time ranges separately. Implicit learning should be evidenced as a significant drop in the d' slope late in the Uninformed condition (last one-third of trials) relative to earlier (first two-thirds of trials). Further, to test any systematic changes that could have occurred in the Informed block, we performed the same split analyses on data from the Informed condition. As shown in Figure 8, the only effect was at the juncture between conditions, when information about color-probability assignments was provided explicitly. A one-way ANOVA with Bonferroni-corrected post hoc tests showed no significant differences between the first two-thirds and last one-third of d' slopes within the *Uninformed* block ($p = 0.44$) or within the *Informed* block ($p = 0.53$). In contrast, there was a significant decrease in d' slopes from the last one-third of the *Uninformed* block to the first two-thirds of the *Informed* block ($p = 9.0 \times 10^{-5}$). In these data, then, there is no

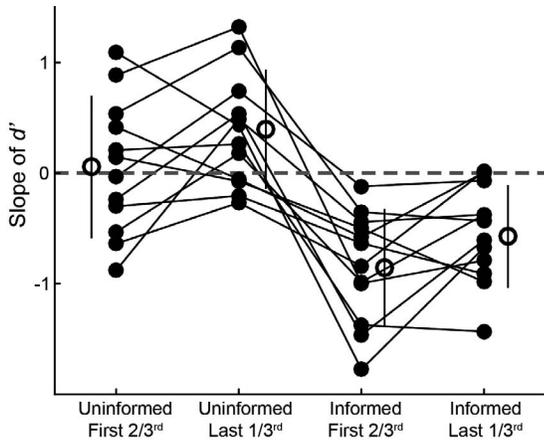


Figure 8. Lack of evidence for implicit learning of color-probability pairings. Each block, for each of the 12 subjects, was split into the first two-thirds and last one-third (black circles). d' values and slopes were computed individually for each of the four segments. Across-subjects, mean \pm standard deviation are plotted next to individual-subject data within each subset of trials (white circles). There was no significant change between the first and last segments within either the Uninformed or Informed blocks. Explicit information about color-probability associations, provided between the Uninformed and Informed blocks, caused the only significant and systematic shift in all subjects' behaviors, and that change lasted through the entire Informed block.

evidence for implicit learning; Effects on performance were attributable only to the explicit instruction provided in between conditions.

Experiment 2

Within the Uninformed block in Experiment 1, we found no evidence that subjects implicitly learned the rule linking the colors of the targets with jump probability. Experiment 1 may have discouraged implicit learning, however, because of the many colors involved. To test this, we modified the paradigm such that the targets had only three possible colors: blue, green, and red. All other facets of Experiment 1 were maintained in Experiment 2. This simplification of this experiment led to a better chance to answer two questions. Is instruction necessary to set up the expectations about target movement in subjects, or could they derive their own expectations from repeated exposure to a limited number of stochastically different stimuli? If subjects could learn the task implicitly, would the resulting signal detection and psychometric effects be different from those introduced by explicit instruction?

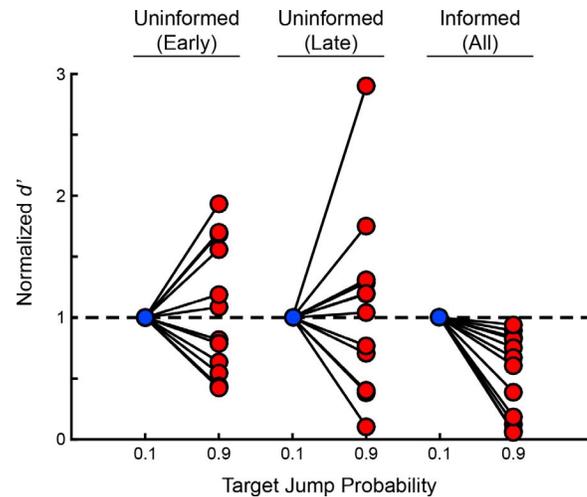


Figure 9. Experiment 2 results: Implicit learning compared with explicit instruction for 12 subjects. The Uninformed block was split into two halves (early and late) and d' computed independently. Data were normalized to the d' of the low-probability targets, to focus on whether d' for the corresponding high-probability targets was relatively higher or lower. The latter would correspond to a negative d' slope, the main signature of expectation effects in Experiment 1.

In 12 new subjects, we repeated the study of Experiment 1 but with the more limited color set. Just as was done in Experiment 1, subjects were questioned after the Uninformed block to determine whether they noticed the link between color and likelihood of jump. Again, none of the subjects reported an understanding of the underlying rules. To test whether there was a more subconscious effect or pattern recognition, we calculated d' for each jump probability, with a focus on the Uninformed block in which we expected to find implicit learning, if it occurred. For simplicity, we compared d' for the extreme probability targets (10% probability of jumping vs. 90% probability) within the first half of the Uninformed condition, the second half, and the entire Informed condition (Figure 9). We were interested primarily in the difference in d' between the high and low jump probability targets, so for viewing clarity, we normalize the d' value for each high jump probability target to that of its paired low jump probability target d' value.

We found, first, in the Informed block (Figure 9, rightmost data set), that all 12 subjects showed lower d' for high jump probability than for low jump probability targets, analogous to negative d' slopes. This result replicates the basic d' findings from Experiment 1. Second, we found that early in the Uninformed session (Figure 9, leftmost data set), the ratio of d' values seemed to be random, with d' larger for the high probability target than the low probability target for six of 12 subjects. This again was similar to the findings in

Experiment 1. The critical data set was late in the Uninformed block (Figure 9, central data set). If subjects implicitly learned the task through the course of Uninformed block, we should expect to see the patterns of d' in the second half of the Uninformed block resembling those of the Informed block. However, this was not the case; seven of the 12 subjects had larger d' for the high probability target late in the Uninformed block. Therefore, even in this version of the task in which we tried to optimize the chance of implicit learning prior to instruction, we found no evidence for it. We conclude that our modified SSD task seems to be successful at introducing expectations abruptly at the time when information about color-probability associations is explicitly provided to the subjects. Before that information is revealed, there seems to be little if any contamination by implicit learning.

Discussion

These results suggest that expectations about object motion influence transsaccadic visual perception. We found a general change in response bias toward more frequent reporting of movement for presumed animate objects than for presumed stable objects. At the same time, there was an increase in perceptual sensitivity for detecting the movement of presumed stable objects. The differences between these effects may seem subtle, and we will discuss them first.

Expectations about object stability lead to both perceptual and behavioral changes

Techniques in signal detection theory allow us to measure both the behavioral (c) and perceptual (d') changes that occur due to the incorporation of priors about object stability. The c and d' measures are orthogonal to each other, such that evidence for changes in one does not imply that there should be evidence for changes in the other (Golomb, Kupitz, & Thiemann, 2014; Macmillan & Creelman, 2004). Humans are not ideal observers, so it is unsurprising that manipulating priors leads to a behavioral bias (Beck, Ma, Pitkow, Latham, & Pouget, 2012; Gold, Bennett, & Sekuler, 1999; Green & Swets, 1966). The bias varied with the priors in a logical way (Figure 3D): Subjects favored “remained stationary” responses (positive c) for targets they knew had low probability of jumping and “jumped” responses (negative c) for targets they knew had high probability of jumping, with a smooth, significant transition in between. This is evidence that subjects did in fact pay attention to the

information about color-probability relationships and adjusted their behavior accordingly.

Perceptual changes as measured by consistent changes in d' were found as well, in that subjects became more sensitive to target motion when they expected targets to remain stationary. In other words, jumps are detected at a higher acuity when they are rare and unexpected. This finding was bolstered by an identical result from analysis of psychometric thresholds. These effects complement research demonstrating that rare distractors are more salient (i.e., more distracting) than common ones (Geyer, Müller, & Krummenacher, 2008; Sayim, Grubert, Herzog, & Krummenacher, 2010). At first glance, these findings seem to contradict the standard Bayesian model, which would predict that our perception is biased toward our expectations, meaning that jump detection should be better for *expected* jumps. However, recent computational work has shown that under assumptions of efficient coding, rare events can be and are detected disproportionately often even in a Bayesian framework (Wei & Stocker, 2015). Such effects are not explainable as a change in behavioral strategy. Rather, they suggest covert alterations in visual processing. We do not know how priors affected the visual system to yield these results, but the underlying neural mechanism could be studied with neuroimaging or neurophysiology. The simplest hypothesis about mechanism is a top-down influence in cognitive terms (Li, Piëch, & Gilbert, 2004; Supèr, Spekreijse, & Lamme, 2001) or a frontal to parietal-occipital influence in circuit terms (Bressler Tang, Sylvester, Shulman, & Corbetta, 2008; Desimone & Duncan, 1995; Miller & Cohen, 2001; Stocker & Simoncelli, 2006).

Because subjects are more sensitive to unexpected jumps, it is only natural to ask if the converse is true: Are subjects also more sensitive to unexpected *non-jumps*? This complementary effect would lead to elevated d' for high jump probability targets because of improved detection of unexpected stability. However, we did not find any evidence for such an increase in d' for targets that were expected to jump. This could be attributed to the fact that improved detection of nonmovement across saccades seems especially challenging because of the various sources of noise inherent in the system, including visual acuity (poorer spatial localization in the periphery), motor variability (scatter of saccade endpoints), and unknown levels of precision between movements and internal records—corollary discharge—of the movements. In other words, there are no obvious nonjumps in the same way that there can be obvious (i.e., large amplitude) jumps. From an ecological or evolutionary perspective, it may be that violations of expected stability are especially salient because they could represent the presence of a

living entity in our environment of which we were not initially aware, such as a predator hiding in tall grass. As primates, most of our natural predators rely on stealth while hunting: Being able to pick up on surprising movement may be more important to survival than detection of stability of known animate objects.

d' and c are agnostic to jump size

Prior belief (expectation) is combined with evidence (extent of target jump) to yield a posterior (perception of “jumped” or “remained stationary”). However, the interplay between priors and evidence in our task is nontrivial. When evidence is strong (e.g., a 3° jump), there is little chance that a subject will report anything other than “jumped” regardless of what the prior expectation is. When evidence is weak (e.g., a 0.25° jump), a subject is likely to base the decision primarily on the prior, while downplaying the evidence. Given the signal detection analysis presented in this article, we are unable to tease apart the relationship between jump size and the weight placed on a prior. Both d' and c are computed on a collection of data involving instances when the target jumps and when it remains stationary. Further, the metrics are agnostic to the actual jump sizes itself because all that is factored in is whether there was a jump or not (Green & Swets, 1966; Macmillan & Creelman, 2004). Additional studies are needed to quantify how the weight placed on a prior changes on a trial-by-trial basis.

Color gradient as a proxy for different types of targets in the world

Real scenes consist of a great variety of objects with varying probabilities of movement, but as a first approximation to this natural arrangement of stimuli, we used targets with features that were constant except along two dimensions, color and probability of movement. This is an extremely reduced preparation, but it allowed for collection of large amounts of systematically analyzable data. The concept of a thermal scale of colors, from blue (cooler) to red (warmer), is familiar to subjects, and the discrete set of 50 colors along that “heat” range provided a useful means of assigning the distribution of probabilities from 0.1 to 0.9. It may be that a more optimal number of colors could be found, but this would need to be experimentally determined and could vary by individual. Our basic goal was to introduce color-probability assignments that subjects could follow at some reasonable level of difficulty.

Importance of including a delay period in the task

Most previous studies of SSD required subjects to make a saccade reactively to a target that appears suddenly. We diverged from that standard procedure for two reasons. First, Zimmermann et al. (2013, their figure 3) indicated that we might expect a nonlinear relationship between viewing duration and accuracy of reports. Their results suggested that for shorter viewing durations (approximately 100–500 ms), the threshold for transsaccadic change detection is higher, and for viewing durations greater than 600–700 ms, it begins to plateau. On every trial of our task, the stimulus was present for about 500 ms before the auditory cue was delivered, and this time window was followed by additional saccade latencies of ~ 200 ms (Figure 7A). Thus, our subjects were operating in the long viewing duration regime in which performance was stable (Table 1, nonsignificant b_1). We wished to focus specifically on the effect of prior information without having viewing duration as a confounding variable. Second, we wanted to allow ample duration for the subjects to detect the color of the peripheral target and incorporate the prior belief into the transsaccadic expectation. Little is known about the time course of these cognitive factors influencing transsaccadic perception, and we did not want to limit the processing times that could potentially be needed.

Implicit learning versus explicit instruction

Through experience, we build a representation of the things around us, and with that representation comes an expectation about how things behave. For example, we know that rocks and sticks seldom move whereas birds and insects may move quickly and frequently. These priors are not instructed to us but, rather, they are learned gradually over time. To see clear, steplike changes in behavior, we chose to instruct the subjects about what their priors should be. One limitation of our study from an ecological perspective is that expectations induced by explicit instructions might be different from those arrived at during long periods of implicit learning. We found no evidence for implicit learning in either our main experiment or in a follow-up experiment with a more reduced stimulus set meant to encourage implicit learning of priors within a single experimental run. Therefore, we cannot answer the question of potential differences between implicitly learned and explicitly provided expectations, and it appears that much longer exposure to the natural statistics of target movements will be needed to examine such implicit factors.

One motivation for testing whether our results generalize from explicit instruction to implicit learning is to set the stage for neurophysiological studies. The use of nonhuman animals (e.g., rhesus monkeys) would seem to preclude explicit instruction. It may be that the only way to incorporate priors into such subjects is through implicit learning. If the d' and c effects we find here carry over to the use of priors learned implicitly, neurophysiological study of underlying mechanisms would be plausible.

Neural mechanisms of remapping and the roles of prediction

Neural evidence for the incorporation of saccadic corollary discharge into visual analysis has been shown in the form of presaccadic remapping (Duhamel et al., 1992; Sommer & Wurtz, 2006; Umeno & Goldberg, 1997; Walker, Fitzgibbon, & Goldberg, 1995). The direction of this remapping is a point of some controversy, with some evidence for a bias toward the saccade target (Tolias et al., 2001; Zirnsak, Steinmetz, Noudoost, Xu, & Moore, 2014; but see DiTomasso, Mayo, & Smith, 2013; Neupane, Guitton, & Pack, 2014; Neupane, Pack, & Guitton, 2013; figure S5 of Sommer & Wurtz, 2006). Neurons that shift their visual sensitivity parallel to the saccade may achieve a presaccadic sample of the region of visual space that will be occupied by the receptive field after the saccade. The classical view is that this “snapshot” of the presaccadic scene provides a prediction of the post-saccadic scene (Higgins & Rayner, 2015; Melcher & Colby, 2008; Wurtz, Joiner, & Berman, 2011). Our present results and data from previous studies suggest, however, that visual continuity operations access more than just discrete snapshots of the world (Cheng, Shettleworth, Huttenlocher, & Rieser, 2007; Griffiths & Tenenbaum, 2006; Niemeier et al., 2003; Vaziri, Diedrichsen, & Shadmehr, 2006). They must take into account probabilistic information and learned context to fully explain visual perception and behavior as we move our eyes (Pouget, Beck, Ma, & Latham, 2013). The frontal eye fields may contribute to such mechanisms (Crapse & Sommer, 2008; Ostendorf, Kiliyas, & Ploner, 2012; Ostendorf, Liebermann, & Ploner, 2010) and are a candidate area (perhaps among many) for representing priors, working with them and distributing them to earlier visual areas.

Conclusions

In this study, subjects performed a modified SSD task in which the color of the saccadic target cued the

subject as to the likelihood that the target would jump during the saccade. We found that expectations about a target’s stability influenced both behavior and perception. The response bias became coupled to the probability of target movement in the Informed trials, whereas it was independent of the probability of target movement in the Uninformed trials. Subjects also exhibited an increase in perceptual sensitivity to the movement of targets that were presumed to remain stable. Movement perception was unchanged, in contrast, for targets that were expected to shift transsaccadically. The results indicate that our perception depends not just on the visual information gathered before and after the eye movement but also on the prior belief about the behavior of the objects. Violations to transsaccadic visual continuity occur when objects behave in a way that is contrary to our expectations.

Keywords: eye movements, perceptual continuity, active vision

Acknowledgments

Dr. Jeff Beck contributed helpful discussions and guidance. This research was supported by the National Science Foundation (NSF) through a Graduate Research Fellowship (GRFP) and IGERT (DGE-1068871) fellowship to H. M. R.

Commercial relationships: none.

Corresponding author: Hrishikesh M. Rao.

Email: hrishikesh.rao@duke.edu.

Address: Department of Biomedical Engineering, Pratt School of Engineering, Duke University, Durham, NC, USA.

References

- Bansal, S., Bray, L. C. J., Peterson, M. S., & Joiner, W. M. (2015). The effect of saccade metrics on the corollary discharge contribution to perceived eye location. *Journal of Neurophysiology*, *113*, 3312–3322.
- Beck, J. M., Ma, W. J., Pitkow, X., Latham, P. E., & Pouget, A. (2012). Not noisy, just wrong: The role of suboptimal inference in behavioral variability. *Neuron*, *74*, 30–39.
- Boi, M., Ögmen, H., Krummenacher, J., Otto, T. U., & Herzog, M. H. (2009). A (fascinating) litmus test for human retino- vs. non-retinotopic processing. *Journal of Vision*, *9*(13):5, 1–11, doi:10.1167/9.13.5. [PubMed] [Article]

- Bressler, S. L., Tang, W., Sylvester, C. M., Shulman, G. L., & Corbetta, M. (2008). Top-down control of human visual cortex by frontal and parietal cortex in anticipatory visual spatial attention. *Journal of Neuroscience*, *28*, 10056–10061.
- Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, *15*, 719–722.
- Cheng, K., Shettleworth, S. J., Huttenlocher, J., & Rieser, J. J. (2007). Bayesian integration of spatial information. *Psychological Bulletin*, *133*, 625–637.
- Collins, T., Rolfs, M., Deubel, H., & Cavanagh, P. (2009). Post-saccadic location judgments reveal remapping of saccade targets to non-foveal locations. *Journal of Vision*, *9*(5):29, 1–9, doi:10.1167/9.5.29. [PubMed] [Article]
- Crapse, T. B., & Sommer, M. A. (2008). The frontal eye field as a prediction map. *Progress in Brain Research*, *171*, 383–390.
- Crapse, T. B., & Sommer, M. A. (2012). Frontal eye field neurons assess visual stability across saccades. *Journal of Neuroscience*, *32*, 2835–2845.
- Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2010). Object form discontinuity facilitates displacement discrimination across saccades. *Journal of Vision*, *10*(6):17, 1–14, doi:10.1167/10.6.17. [PubMed] [Article]
- Desimone, R., & Duncan, J. (1995). Neural mechanisms of selective visual attention. *Annual Review of Neuroscience*, *18*, 193–222.
- Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates space constancy. *Vision Research*, *38*, 3147–3159.
- Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic suppression of image displacement. *Vision Research*, *36*, 985–996.
- Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form. *Progress in Brain Research*, *140*, 165–180.
- DiTomasso, A., Mayo, J., & Smith, M. (2013). Probabilistic maps of peri-saccadic receptive fields in the frontal eye fields. Program No. 826.21 [online]. *2013 Neuroscience Meeting Planner*. San Diego, CA: Society for Neuroscience 2013.
- Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science*, *255*, 90–92.
- Eckstein, M. P., Drescher, B. A., & Shimozaki, S. S. (2006). Attentional cues in real scenes, saccadic targeting, and Bayesian priors. *Psychological Science*, *17*, 973–980.
- Geyer, T., Müller, H. J., & Krummenacher, J. (2008). Expectancies modulate attentional capture by salient color singletons. *Vision Research*, *48*, 1315–1326.
- Gold, J., Bennett, P. J., & Sekuler, A. B. (1999). Signal but not noise changes with perceptual learning. *Nature*, *402*, 176–178.
- Golomb, J. D., Kupitz, C. N., & Thiemann, C. T. (2014). The influence of object location on identity: A “spatial congruency bias.” *Journal of Experimental Psychology: General*, *143*, 2262–2278.
- Green, D. M., & Swets, J. A. (1966). *Signal detection theory and psychophysics*. New York; John Wiley & Sons.
- Griffiths, T. L., & Tenenbaum, J. B. (2006). Optimal predictions in everyday cognition. *Psychological Science*, *17*, 767–773.
- Gysen, V., De Graef, P., & Verfaillie, K. (2002). Detection of intrasaccadic displacements and depth rotations of moving objects. *Vision Research*, *42*, 379–391.
- Gysen, V., Verfaillie, K., & De Graef, P. (2002). The effect of stimulus blanking on the detection of intrasaccadic displacements of translating objects. *Vision Research*, *42*, 2021–2030.
- Higgins, E., & Rayner, K. (2015). Transsaccadic processing: stability, integration, and the potential role of remapping. *Attention, Perception, & Psychophysics*, *77*, 3–27.
- Joiner, W. M., Cavanaugh, J., FitzGibbon, E. J., & Wurtz, R. H. (2013). Corollary discharge contributes to perceived eye location in monkeys. *Journal of Neurophysiology*, *110*, 2402–2413.
- Joiner, W. M., FitzGibbon, E. J., & Wurtz, R. H. (2010). Amplitudes and directions of individual saccades can be adjusted by corollary discharge. *Journal of Vision*, *10*(2):22, 1–12, doi:10.1167/10.2.22. [PubMed] [Article]
- Li, W., Piëch, V., & Gilbert, C. D. (2004). Perceptual learning and top-down influences in primary visual cortex. *Nature Neuroscience*, *7*, 651–657.
- Macmillan, N. A., & Creelman, C. D. (2004). *Detection theory: A user's guide*. Hove, UK: Psychology Press.
- Matsuda, K., Nagami, T., Kawano, K., & Yamane, S. (2000). A new system for measuring eye position on a personal computer. Program No. 744.02 [online]. *2000 Neuroscience Meeting Planner*. New Orleans: Society for Neuroscience.
- Matsuda, K., Takemura, A., Miura, K., Ogawa, T., &

- Kawano, K. (2014). An advanced real-time monocular/binocular eye tracking system using a high frame-rate digital camera. Program No. 626.09 [online]. *2014 Neuroscience Meeting Planner*. Washington, DC: Society for Neuroscience.
- Melcher, D., & Colby, C. L. (2008). Trans-saccadic perception. *Trends in Cognitive Sciences*, *12*, 466–473.
- Miller, E. K., & Cohen, J. D. (2001). An integrative theory of prefrontal cortex function. *Annual Review of Neuroscience*, *24*, 167–202.
- Müsseler, J., Van Der Heijden, A. H., Mahmud, S. H., Deubel, H., & Ertsey, S. (1999). Relative mislocalization of briefly presented stimuli in the retinal periphery. *Perception & Psychophysics*, *61*, 1646–1661.
- Neupane, S., Guitton, D., & Pack, C. C. (2014). Gamma coherence accompanies receptive field remapping in monkey area v4. Program No. 288.04 [online]. *2014 Neuroscience Meeting Planner*. Washington, DC: Society for Neuroscience.
- Neupane, S., Pack, C. C., & Guitton, D. (2013). Spatiotemporal structure of peri-saccadic LFP receptive fields in monkey area V4. Program No. 365.06 [online]. *2013 Neuroscience Meeting Planner*. San Diego, CA: Society for Neuroscience.
- Niemeier, M., Crawford, J. D., & Tweed, D. B. (2003). Optimal transsaccadic integration explains distorted spatial perception. *Nature*, *422*, 76–80.
- Ogmen, H., Agaoglu, M., & Herzog, M. (2015). Reference-frame selection in motion perception. *Journal of Vision*, *15*(12): 284, doi:10.1167/15.12.284. [Abstract]
- Ostendorf, F., Kiliyas, J., & Ploner, C. J. (2012). Theta-burst stimulation over human frontal cortex distorts perceptual stability across eye movements. *Cerebral Cortex*, *22*, 800–810.
- Ostendorf, F., Liebermann, D., & Ploner, C. J. (2010). Human thalamus contributes to perceptual stability across eye movements. *Proceedings of the National Academy of Sciences USA*, *107*, 1229–1234.
- Pouget, A., Beck, J. M., Ma, W. J., & Latham, P. E. (2013). Probabilistic brains: Knowns and unknowns. *Nature Neuroscience*, *16*, 1170–1178.
- Read, J. C. (2002). A Bayesian model of stereopsis depth and motion direction discrimination. *Biological Cybernetics*, *86*, 117–136.
- Robinson, D. L., & Wurtz, R. H. (1976). Use of an extraretinal signal by monkey superior colliculus neurons to distinguish real from self-induced stimulus movement. *Journal of Neurophysiology*, *39*, 852–870.
- Sayim, B., Grubert, A., Herzog, M. H., & Krummehner, J. (2010). Display probability modulates attentional capture by onset distractors. *Journal of Vision*, *10*(3):10, 1–8, doi:10.1167/10.3.10. [PubMed] [Article]
- Sommer, M. A., & Wurtz, R. H. (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature*, *444*, 374–377.
- Sommer, M. A., & Wurtz, R. H. (2008). Brain circuits for the internal monitoring of movements. *Annual Review of Neuroscience*, *31*, 317–338.
- Sperry, R. W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *Journal of Comparative and Physiological Psychology*, *43*, 482.
- Stocker, A. A., & Simoncelli, E. P. (2006). Noise characteristics and prior expectations in human visual speed perception. *Nature Neuroscience*, *9*, 578–585.
- Supèr, H., Spekreijse, H., & Lamme, V. A. (2001). Two distinct modes of sensory processing observed in monkey primary visual cortex (V1). *Nature Neuroscience*, *4*, 304–310.
- Tolias, A. S., Moore, T., Smirnakis, S. M., Tehovnik, E. J., Siapas, A. G., & Schiller, P. H. (2001). Eye movements modulate visual receptive fields of V4 neurons. *Neuron*, *29*, 757–767.
- Troncoso, X. G., McCamy, M. B., Jazi, A. N., Cui, J., Otero-Millan, J., Macknik, S. L., . . . Martinez-Conde, S. (2015). V1 neurons respond differently to object motion versus motion from eye movements. *Nature Communications*, *6*, 8114.
- Umeno, M. M., & Goldberg, M. E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *Journal of Neurophysiology*, *78*, 1373–1383.
- Vaziri, S., Diedrichsen, J., & Shadmehr, R. (2006). Why does the brain predict sensory consequences of oculomotor commands? Optimal integration of the predicted and the actual sensory feedback. *Journal of Neuroscience*, *26*, 4188–4197.
- Von Helmholtz, H. (1925). *Helmholtz's treatise on physiological optics*. New York: Optical Society of America.
- Von Holst, E., & Mittelstaedt, H. (1950). Das Refferenzprinzip. Wechselwirkungen zwischen Zentralnervensystem und Peripherie. *Naturwissenschaften*, *37*, 464–476.
- Walker, M. F., Fitzgibbon, E. J., & Goldberg, M. E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye

- movements. *Journal of Neurophysiology*, 73, 1988–2003.
- Wei, X. X., & Stocker, A. A. (2015). A Bayesian observer model constrained by efficient coding can explain anti-Bayesian percepts. *Nature Neuroscience*, 18, 1509–1517.
- Weiss, Y., Simoncelli, E. P., & Adelson, E. H. (2002). Motion illusions as optimal percepts. *Nature Neuroscience*, 5, 598–604.
- Wurtz, R. H., Joiner, W. M., & Berman, R. A. (2011). Neuronal mechanisms for visual stability: Progress and problems. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 492–503.
- Zimmermann, E., Morrone, M. C., & Burr, D. C. (2013). Spatial position information accumulates steadily over time. *Journal of Neuroscience*, 33, 18396–18401.
- Zirnsak, M., Steinmetz, N. A., Noudoost, B., Xu, K. Z., & Moore, T. (2014). Visual space is compressed in prefrontal cortex before eye movements. *Nature*, 507, 504–507.