Distractor suppression operates exclusively in retinotopic coordinates

Yayla A. Ilksoy[1, 2], Dirk van Moorselaar[1, 2], Benchi Wang[4, 5, 6, 7], Sander A. Los[1, 2] & Jan Theeuwes[1, 2, 3]

[1] Vrije Universiteit Amsterdam, Amsterdam, The Netherlands

[2] Institute Brain and Behavior Amsterdam (iBBA), Amsterdam, the Netherlands

[3] William James Center for Research, ISPA-Instituto Universitario, Lisbon, Portugal

[4] Key Laboratory of Brain, Cognition and Education Sciences (South China Normal University), Ministry of Education, Guangzhou, China

[5] Institute for Brain Research and Rehabilitation, South China Normal University, Guangzhou, China

[6] Center for Studies of Psychological Application, South China Normal University, Guangzhou, China

[7] Guangdong Key Laboratory of Mental Health and Cognitive Science, South China Normal University, Guangzhou, China

Numbe of pages: 34
Number of figures: 8
Number of words for abstract: 202
Number of words for introduction: 648
Number of words for discussion: 841

Corresponding author: Correspondence should be addressed to Yayla Ilksoy, Department of Experimental and Applied Psychology, Vrije Universiteit Amsterdam, Van der Boechorststraat 7, 1081 BT Amsterdam, The Netherlands. Email: y.a.ilksoy@vu.nl

Acknowledgments: This research was supported by a NWO Open competition grant 406.21.GO.034 and by a European Research Council (ERC) advanced grant 833029 – [LEARNATTEND].[1]

---

[1] The authors declare no competing financial interests.

Abstract

Our attention is influenced by past experiences, and recent studies have shown that individuals learn to extract statistical regularities in the environment, resulting in attentional suppression of locations that are likely to contain a distractor (high-probability location). However, little is known as to whether this learned suppression operates in retinotopic (relative to the eyes) or spatiotopic (relative to the world) coordinates. In the current study, two circular search arrays were presented side by side. Participants learned the high-probability location from a learning array presented on one side of the display (e.g., left). After several trials, participants shifted their gaze to the center of the other search array (e.g., located on the right side) and continued searching without any location probability (labelled as "test array"). Due to the saccadic eye movement, the test array contained both a spatiotopic matching and a retinotopic matching location relative to the original high-probability location. The current findings show that, following saccadic eye movements, the learned suppression remained in retinotopic coordinates only, with no measurable transfer to spatiotopic coordinates. Even in a rich environment, attentional suppression still operated exclusively in retinotopic coordinates. We speculate that learned suppression may be resolved by changing synaptic weights in early visual areas.

Keywords: Attentional suppression; retinotopic; spatiotopic; statistical learning

Significance statement

In our daily lives, attention is shaped by past experiences, guiding us to suppress locations that are likely to contain distractions. While this phenomenon has been studied extensively with static search displays, the real world is dynamic - we are constantly moving our eyes. This study addressed this issue by investigating what happens when we learn to suppress a likely distractor location while making eye movements. Do we suppress the same location in space (spatiotopic), or does the learned suppression persist relative to our eyes (retinotopic)? The current findings provide clear evidence of suppression in retinotopic coordinates only.

Introduction

Where and what we attend is not only influenced by the dynamics of sensory input (bottom–up) and our current goal states (top–down or behavioral relevance) but also heavily influenced by what we have encountered in the past. One example of selection biases implemented by selection history comes from recent studies demonstrating that human observers can learn to extract statistical regularities in the environment resulting in attentional suppression of locations that are likely to contain a distractor, effectively reducing the amount of distraction (Wang & Theeuwes, 2018a, 2018b, 2018c). The general idea is that just like top-down, and bottom-up attention, selection history also feeds into an integrated priority (salience) map, ultimately resulting in a winner-take-all competition that determines the allocation of covert and overt attention (Theeuwes, 2019; Theeuwes et al., 2022). The notion of learning-induced plasticity within the spatial priority map is important, as it can explain how lingering biases from former attentional deployments come about. While it is generally agreed that spatial priority maps are topographically organized maps of the external visual world (e.g., Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Thompson & Bichot, 2005), it remains largely unclear how the "external world" is represented within these maps. As such it remains unclear whether suppression effect due to statistical learning, which is thought to operate via changes of weights within the spatial priority map, operates in retinotopic (relative to the eyes) or spatiotopic (relative to the world) coordinates.

Researchers have identified potential spatial priority map candidates among various brain regions, such as the superior colliculus (Bisley, 2011; Krauzlis et al., 2013; Noudoost et al., 2010; Wurtz et al., 2011), caudate nucleus (Kim & Hikosaka, 2013; Yamamoto et al., 2012), and regions in the posterior parietal (Bisley & Goldberg, 2010; e.g., LIP) and frontal cortices (Thompson et al., 2005; Thompson & Bichot, 2005; e.g., FEF). Regardless of whether these regions are cortical or subcortical, it is generally accepted that retinotopy is preserved throughout the brain, suggesting that priority maps are retinotopically organized. Nevertheless, a topographical representation would be more appropriate as it reflects the external visual world upon which we act (e.g., Bisley & Goldberg, 2010; Fecteau & Munoz, 2006; Thompson & Bichot, 2005). If a location is relevant for selection or requires suppression, it makes sense to connect it to external world coordinates rather than retinal location. In line with both views, previous studies have shown that both endogenous attention (Golomb et al., 2008, 2010) and exogenous attention (Mathôt & Theeuwes, 2010a, 2010b) rely on retinotopic maps, which are progressively transformed into spatiotopic maps following saccades. Moreover, a recent study by van Moorselaar & Theeuwes (2023) showed that people can learn to prioritize a likely target location within objects, irrespective of the object's orientation in space. This implies that statistical learning is not necessarily limited to retinotopic maps. However, no study to date has explored whether history-driven suppression effects persist in retinotopic coordinates or transfer to spatiotopic coordinates after eye movements.

In the present study, we adopted the additional singleton task used by Wang and Theeuwes (2018a) in which the distractor singleton was presented more often in one location than in all other locations. Critically, this regularity was only present when participants were performing the task at one side of the display (labelled as "learning array"). After performing several trials within this learning array (e.g., on the left side), participants shifted their gaze to another display (e.g., the one on the right) and continued the search task, but now without any statistical regularities included (labelled as “test array”). Due to the saccadic eye movement towards the test location, it contained both a spatiotopic matching and a retinotopic matching location relative to the suppressed location in the learning array. The question then was whether the learned suppression within the learning array would stay in retinotopic coordinates, transfer to spatiotopic coordinates, or relies on both coordinate systems.

Experiment 1

Methods

The Ethical Review Committee of the Faculty of Behavioral and Movement Sciences of the Vrije Universiteit Amsterdam approved the present study. Twenty-four adults (20 females, mean age: 23.8 years old) were recruited for money compensation or course credits. They all signed informed consent before the study and reported normal or corrected-to-normal visual acuity. Sample size was predetermined based on a previous study that initially reported learned suppression due to statistical learning (Wang & Theeuwes, 2018a). In their study, the effect size of the main effect (partial eta-squared) of distractor condition (high-probability location, low-probability location, and no-distractor) was 0.85. With 24 subjects and alpha = .001, power for this critical effect would be larger than 0.99.

Apparatus and stimuli Participants were tested in a dimly lit laboratory, with their chin held on a chinrest located 70 cm away from a 24-in. liquid crystal display (LCD) color monitor. The experiment was created in *OpenSesame* (Mathôt et al., 2012) and run on a Dell Precision 3640 computer. An eye-tracker (EyeLink 1,000) was used to monitor participants' eye movements and the sampling rate was set to 1,000 Hz.

A modified additional singleton paradigm was adopted. The visual search display consisted of six discrete stimuli with different shapes (one circle vs. five diamonds, or vice versa), each containing a vertical or horizontal gray line (0.2° × 1°) inside (see Figure 1). The stimuli were presented on an imaginary circle with a radius of 3.5°, centered at the fixation (a white cross measuring 0.5° × 0.5°) against a black background (RGB: 0/0/0). The radius of the circle stimuli was 1°, the diamond stimuli were subtended by 1.55° × 1.55°, and each had a red or green outline.

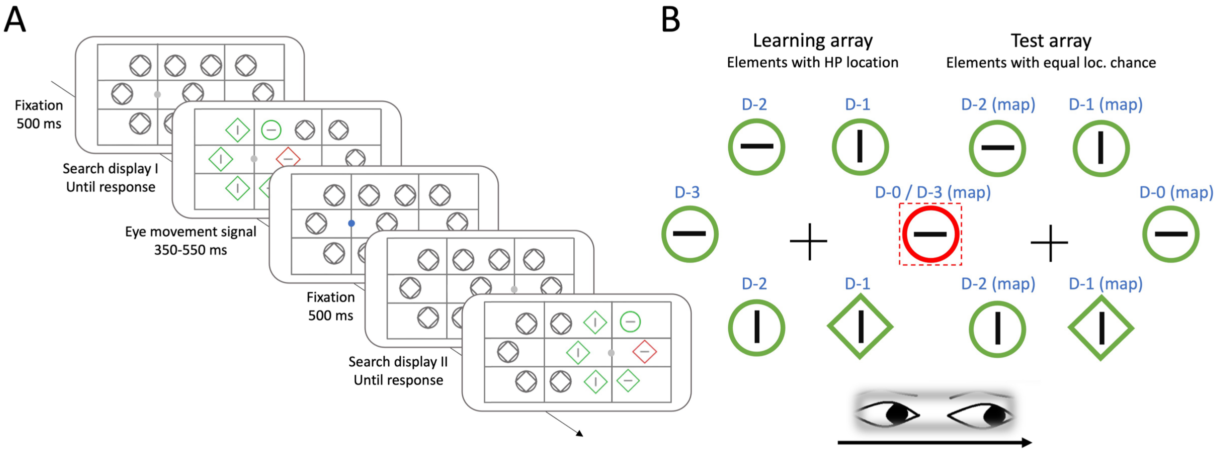

Figure 1. Stimuli and design. **(A)** An example of a trial sequence. In this example, the fixation switches from left (Search display I) to right (Search display II). The gridlines and placeholders were introduced in Experiment 2 and not present in Experiment 1. **(B)** Possible stimulus locations. The high-probability distractor location was always in the center of the screen (D-0). In the test array, location D-3 (map) represents the spatiotopic location and location D-0 (map) the retinotopic location. The location of the learning array (left or right), and consequently the position of the HP location within the learning array, was counterbalanced across participants.

Experimental design Every trial started with a fixation cross that remained visible throughout the trial. The fixation cross was presented horizontally at either 3.5° to the left or 3.5° to the right of the center of the screen. After 500 ms, a search array was presented and centered at the fixation cross for 2000 ms or until response. Participants searched for one circle (target) among five diamonds (distractors) or vice versa and responded to the orientation of the line segment as fast as possible, by pressing the ‘up’ arrow key for vertical and the ‘left’ arrow key for horizontal with their right hand. The inter-trial interval (ITI) was randomly chosen from 350 to 550 ms.

A target was presented in each trial with an equal probability of being a circle or diamond. A uniquely colored distractor singleton was present in 66.7% of the trials, with the same shape as the other distractors but with a different color (red or green with an equal probability). All conditions were randomized within each block. For each search array, the target could appear at each of the six locations. Importantly, two types of search arrays were presented: a learning and test array. For the learning array in the distractor singleton present condition, the distractor singleton had a high proportion of 63% to be presented at the center of the display (e.g., the furthest right location of the left search array or the furthest left location of the right search array). This location is called the high-probability (HP) location. Each of the other locations independently had a low proportion of 7.4% to contain a distractor singleton (low-probability location). For the test array, all the locations contained a distractor singleton equally often (16.7% in distractor-present trials). The target location was determined randomly on each trial.

The experiment consisted of six blocks of 250 trials each. The first two blocks only presented the learning array on one side of the display. The position of the learning array (left or right), and consequently the position of the HP location within the learning array, was counterbalanced across participants. After the first two blocks, the learning array alternated with the test array, which was presented on the opposite side of the display. Every few trials, specifically after a randomly selected sequence of 8, 9, or 10 consecutive trials for the learning array and 4 or 5 consecutive trials for the test array, a white dot appeared at the previous fixation location during the ITI period. Following this, participants had to immediately move their eyes to the other fixation on the opposite side of the display to perform the search task for the other search array. Crucially, the location at the center of the screen was shared by the learning and test array: This was the HP location of the learning array and the spatiotopic location of the test array. The retinotopic location was at the opposite side of the test array (see Figure 1B for an illustration). In blocks three to six, the learning and test arrays were presented in 165 and 85 trials, respectively.

There were two practice sessions before the experiment started: one practice session of 15 trials with only the learning array that remained in the same location (as in the first two blocks of the experiment) and one practice session of 40 trials that alternated between the learning and test array (as in block three to six of the experiment). If participants did not achieve more than 70% accuracy or were not faster than 1100 ms on average in the practice sessions, they had to repeat the session. If participants did not respond or made an erroneous response, a warning message was presented. At the end of the experiment participants were asked whether they noticed the statistical regularities (subjective measure) and on which location within the array they thought the high-probability distractor location was (objective measure). Notably, these questions were interspersed with unrelated questions that were included to avoid influencing responses to the study-related questions.

Participants were instructed to fixate on the fixation cross in every trial. A warning sound was played if eyes deviated from fixation (see Data analysis for further details). Before every block, the eye tracker was calibrated, and an automatic drift check was performed at the beginning of every 10 trials.

Statistical analysis Participants with an average accuracy below 2.5 standard deviation from the overall RT were excluded as outliers and replaced. Trials on which the response times (RTs) were slower than 200 ms and trials on which RTs were faster or slower than 2.5 standard deviations from the average response time per array per block per participant were excluded from analyses. Subsequently, participants with an average RT faster than 2.5 standard deviations of the group mean were excluded as outliers and replaced. Trials in which eyes deviated from fixation were also excluded. Eye deviations were determined by identifying instances where fixations extended beyond 2.5° from the fixation cross for more than 75 ms (Golomb et al., 2008; Mathôt & Theeuwes, 2010a; Talsma et al., 2013). For RT analyses, only trials with a correct response were included.

The main analysis was separated into two analytical approaches. First, to ascertain that observers learned to suppress the HP location, learning array RTs and error rates were analyzed using repeated-measures analysis of variance (ANOVAs) followed by planned comparisons with paired-sample t-tests. Where sphericity was violated, Greenhouse-Geiser corrected p-values are reported. To then determine whether the learned attentional bias, once established, transferred to retinotopic or spatiotopic coordinates, the analysis of the test array included only data from those participants who exhibited visual statistical learning effect in the learning array. This effect was characterized by either faster RTs or lower error rates in the HP location than in the low-probability (LP) distractor location. In contrast to the conventional ANOVA approach here we relied on linear mixed models (LMMs) and generalized mixed models (GLMMs) approaches for RT and error rate respectively, where the data is not averaged but instead grouped per participant. For the present purposes, this approach has two main advantages. First, a range of continuous and categorical variables can be added to a single model such that rather than excluding large subsets of data in a series of control analyses, which inevitably reduces power (Brysbaert & Stevens, 2018), various control factors that could potentially modulate the effect of interest can be simultaneously included allowing for a more refined control. Specifically, in all adopted models Distractor condition (retinotopic location, LP location and spatiotopic location) was incorporated into the fixed-effects structure as an ordered factor. In addition to the main effect of interest, the following factors were entered into the fixed-effects structure: intertrial location distractor and target priming (i.e., whether the position of a distractor or target repeated from one trial to the next; yes, no), array switch (i.e., whether the array position was the same as on the previous trial or had switched; yes, no), target and distractor position (0-5), learning array position (left, right), awareness of the HP distractor location (response to objective measure, see Procedure and design for further details; correct, incorrect), target color (red, green), target shape (circle, diamond) and target line orientation (horizontal, vertical). Second, and most importantly, this approach allowed us to evaluate whether suppression was best characterized by a model resulting from a gradient centered at either the retinotopic or the spatiotopic location, indicative of retinotopic or spatiotopic suppression respectively (see Figure 2A and B), or alternatively by a model in which both retinotopic and spatiotopic suppression exerted their effects simultaneously (see Figure

2C). For this purpose, the model included a linear, as well as a quadratic coefficient of Distractor condition (retinotopic, LP, spatiotopic). The degrees of freedom of all coefficients were estimated using Satterwaite's method for approximating degrees of freedom and the F statistics, Z-scores and the corresponding p-values were obtained from the *lmerTest* package (Kuznetsova et al., 2017) in R (R Core Team, 2018). Alll fixed effects were dummy coded. following guidelines by Barr et al. (2013), by-participants random intercepts and by-participant random slopes for Distractor condition were included in the random-effects structure.

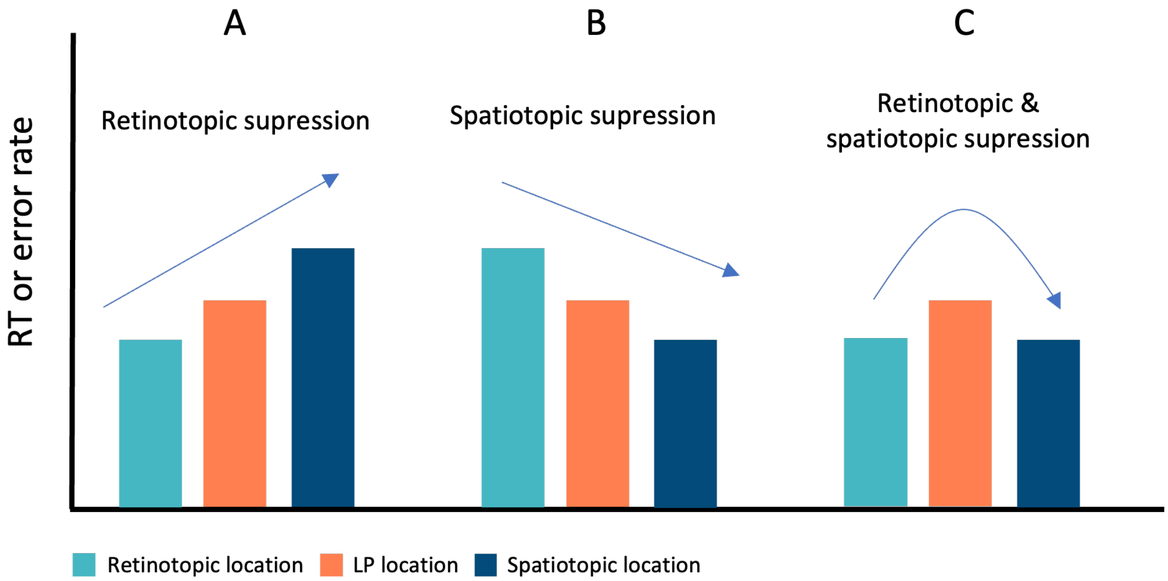

Figure 2. The three hypothesized outcomes in the test array. Each bar represents the mean RT or error rate when the distractor is presented at a certain distractor location (retinotopic, LP and spatiotopic location). **(A)** An increasing slope across retinotopic, LP and spatiotopic locations suggests retinotopic suppression. **(B)** A decreasing slope across retinotopic, LP and spatiotopic locations suggests spatiotopic suppression. **(C)** A negative parabola across retinotopic, LP and spatiotopic locations suggests both retinotopic and spatiotopic suppression.

Results

In total, four participants were excluded and replaced based on their RTs (three participants) and because too many trials were removed due to eye movements (one participant). Exclusion of incorrect responses (7.7%), data trimming (3.3%) and trials with eye movements (10.7%) resulted in an overall loss of 21.7% of the trials for the RT analyses and 14% of the trials for the error rate analyses.

Learning array Before investigating how distractor suppression remaps following a saccade, we first examined to what extent distractor learning took place in the learning array. Repeated-measures ANOVAs with Distractor condition (no distractor, HP location and LP location) as a within-subject factor revealed a reliable main effect on both mean RTs (F (2, 46) = 104.709, $p < .001$, $n_p^2 = .82$; see Figure 3A and 3B) and mean error rates (F (2, 46) = 32.057, $p < .001$, $n_p^2 = .58$; see Figure 3C and 3D). Subsequent planned comparisons showed that relative to no distractor trials, RTs were slower and error rates were higher when the distractor appeared at the HP and LP location (all *t*'s > 3.9 and *p*'s < .001). Critically, RTs were faster (*t* (23) = 5.27, $p < .001$) and error rates were lower (*t* (23) = 3.9, $p < .001$) when the distractor appeared at the HP location compared to the LP location, indicative of learned attentional suppression at the high probability distractor location.

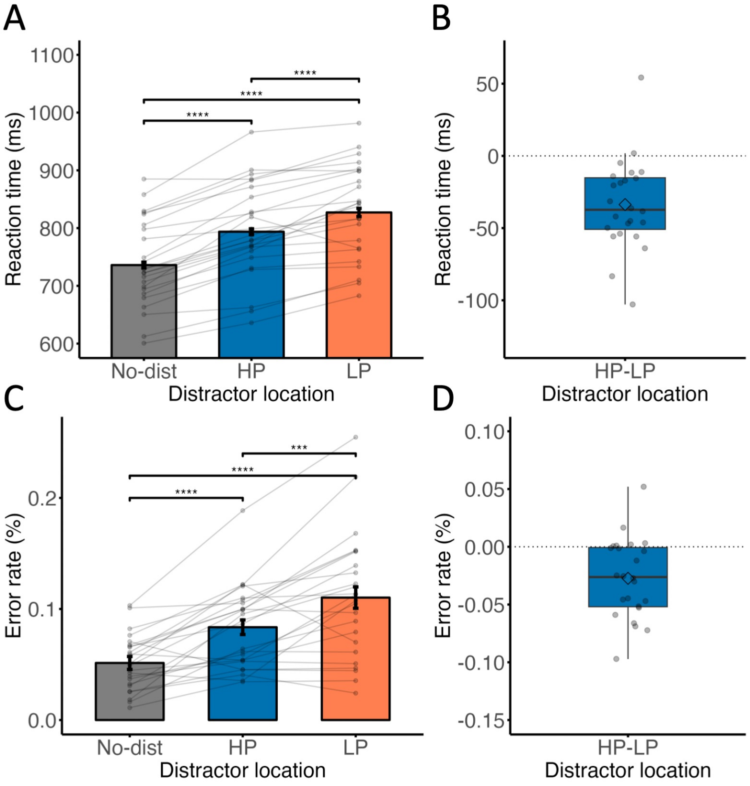

Figure 3. RTs (A and B) and error rates (C and D) in Experiment 1 as a function of distractor location for learning arrays. The bars represent the condition means, and each gray dot represents the mean of an individual participant. Error bars represent 95% within-subjects confidence intervals (Morey, 2008). The significance bars represent the planned comparisons with paired-sample t-tests. The diamonds in the boxplots represent the mean difference scores and the horizontal lines represent the median difference scores. **(A)** RTs in the learning array. The bars show a clear attentional capture effect with slower RTs when the distractor is present. **(B)** The boxplot displays the RT differences between the HP and LP condition in the learning array. Most subjects had faster RTs when the distractor is presented at the HP location compared to the LP location. **(C)** Error rates in the learning array. The bars show a clear attentional capture effect with higher error rates when the distractor is present. **(D)** The boxplot displays the error rate differences between the HP and LP condition in the learning array. Most subjects have lower error rates when the distractor is presented at the HP location compared to the LP location.

Test array After having established reliable suppression within the learning array, we next set out to establish the dynamics of this learned suppression following a saccade by limiting the analysis to only those participants that showcased learning within the training array (*N* = 22 for RT; *N* = 18 for error rate). We considered three possible scenarios: suppression is retinotopically organized, spatiotopically organized or a combination of both (see Figure 2). Previous work by Wang and Theeuwes (Wang & Theeuwes, 2018a, 2018b) showed that not only the HP location but also its nearby locations were suppressed by learning statistical regularities. In other words, the location that was furthest away from the HP location showed the smallest spatial gradient suppression effect. In the current paradigm, the retinotopic and spatiotopic locations are furthest away from each other. Therefore, in the case of a retinotopic suppression effect, we expect a gradient from the retinotopic location towards the spatiotopic location. Conversely, if the suppression effect is spatiotopic, we expect the gradient to occur in the opposite direction. As visualized in Figure 4A, progression from the retinotopic towards the spatiotopic location was characterized by a systematic increase in RTs (linear $\beta = 24.00$, SE = 8.16, $t\,(21.7) = 2.94$, $p = .008$), in line with the scenario in Figure 2A. The error rates yielded a similar pattern although the fitted slope across the retinotopic, LP and spatiotopic locations was not significant (linear $\beta = 0.31$, SE = 0.18, $z = 1.7$, $p = .08$; quadratic $\beta = -0.25$, SE = 0.18, $z = -1.38$, $p = .17$; see Figure 4C). Together these findings demonstrate that the observed statistical learning effect did not transfer to spatiotopic coordinates, but instead remained in retinotopic coordinates following a saccade.

Discussion

The current findings show that following a saccadic eye movement, suppression due to statistical learning remained in retinotopic coordinates only, with no measurable transfer to spatiotopic coordinates. While this is an important finding, it should be noted that in the current set-up there were no visual environmental landmarks as the search display was presented on the background of a blank empty screen. Also, with each saccade, the entire display shifted from side to side, making the entire visual field move along with the eye movements. It is therefore possible that the absence of a spatiotopic effect has to do with the absence of any visual landmarks. To that end, a second experiment was conducted with a grid and placeholders in the display to create more structure by introducing visual landmarks (see Figure 1).

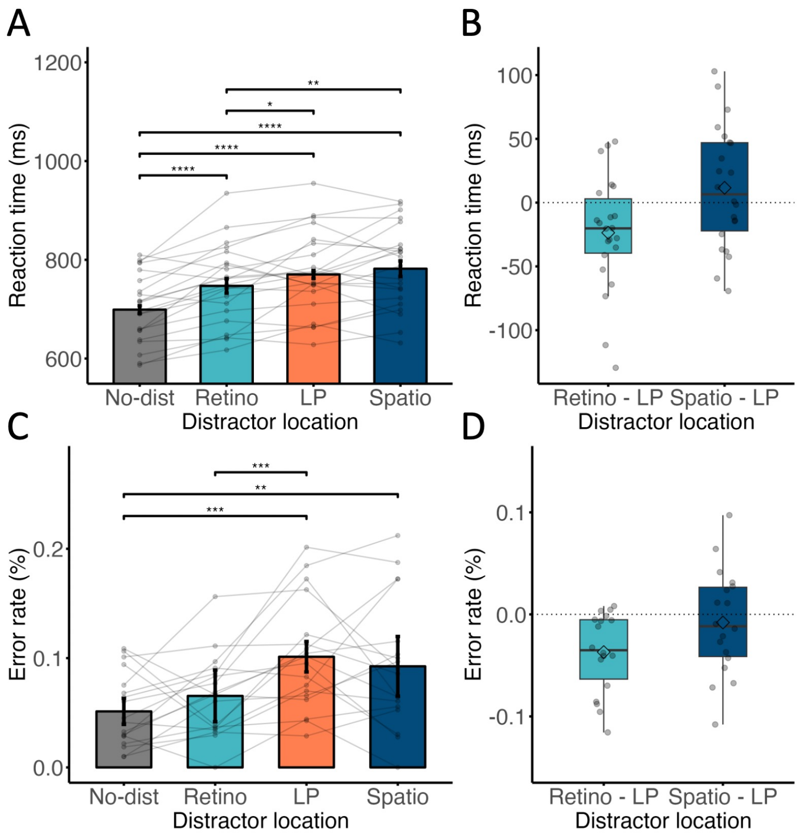

Figure 4. RTs (A and B) and error rates (C and D) in Experiment 1 as a function of distractor location for test arrays. **(A)** RTs in the test array. The bars show a systematic increase in RTs across the retinotopic, LP and spatiotopic locations (linear $\beta = 24.00$, SE = 8.16, t (21.7) = 2.94, p < .008). (B) The boxplot displays the RT differences between the retinotopic and LP location and the spatiotopic and LP location. (C) Error rates in the test array. While conventional t-tests show that error rates at the retinotopic location are lower relative to the LP location (t (17) = 4.01, *p* < .001), the GLMM showed no significant slope across the distractor locations (linear $\beta = 0.31$, SE = 0.18, z = 1.7, *p* = .08; quadratic $\beta = -0.25$, SE = 0.18, z = -1.38, *p* = .17) (D) The boxplot displays the error rate differences between the retinotopic and LP location and the spatiotopic and LP location.

Experiment 2a

Methods

Experiment 2a was identical to Experiment 1 except for the following changes. The experiment was conducted in an online environment on a JATOS server (Lange et al., 2015). In the first experiment, the detected effect size of the variable of interest in the test array was smaller than what is typically observed in studies exploring visual statistical learning (Wang & Theeuwes, 2018a). This, coupled with the increased noise in online studies, led us to decide on expanding the participant sample size in Experiment 2a. Fifty adults (23 females, mean age: 27.9 years old) were recruited for monetary compensation via the online platform Prolific (www.prolific.co; £10.33). Because the experiment was conducted online, our control over the experimental settings was restricted, and as a result we report the stimuli in terms of pixels instead of visual degrees. The search arrays (search radius was 150 pixels; diamond stimuli were subtended by 56 × 56 pixels, circle stimuli had radius of 45 pixels) were presented inside a gray-colored grid with 4 × 4 horizontal and vertical lines (see Figure 1A). To ensure that the grid remained noticeable, we modified the line thickness three times within each block. At the onset of each block, gridlines were consistently presented with a thickness of 3 pixels. Every 50 trials, the gridline thickness randomly alternated, transitioning between 1, 5, and 7 pixels. Dark gray placeholders in the form of a circle imposed upon a diamond were presented at all possible stimulus locations. To ensure that the participants maintained fixation effectively before initiating saccades, the stimulus display was presented for only 150 ms, which is a duration that is too short to make any directed eye movements within the search array (Fischer & Ramsperger, 1984; Fischer & Weber, 1993; Heeman et al., 2019). The experiment consisted of five blocks of 200 trials each, with the first block only consisting of arrays presented on one side of the display (either left or right, counterbalanced across participants).

Results

Five participants were identified as outliers and replaced based on their mean accuracy and mean RT. Furthermore, seven participants with an average accuracy below 60%, indicative of chance-level performance, were identified and replaced. Three additional participants were substituted due to stimuli being displayed for over 180 ms (instead of the intended 150 ms) in more than 50% of the trials, attributable to the refresh rate of their personal computers. Exclusion of incorrect responses (18.3%) and data trimming (2.1%) resulted in an overall loss of 20.5% of the trials for the RT analyses and 2.1% of the trials for the error rate analyses.

Learning array For the learning array, repeated-measures ANOVAs with Distractor condition (no distractor , HP location and LP location) as within-subjects factor showed a main effect for both mean RTs (F (2, 98) = 50.093, p < .001, n_p^2 = .51) and mean error rates (F (2, 98) = 97.32, p < .001, n_p^2 = .67). As before, subsequent planned comparisons revealed slower RTs and higher error rates when the distractor was presented at the HP location and LP location compared to the no distractor condition (all t’s > 3.3, all p’s < .02; see Figure 5A and 5C). Crucially, in comparison to the LP location, RTs were faster (t (49) = 3.26, p = .002; see Figure 5B), and error rates were lower (t (49) = 4.92, p < .001; see Figure 5D) at the HP location, indicating attentional suppression at the high probability distractor location.

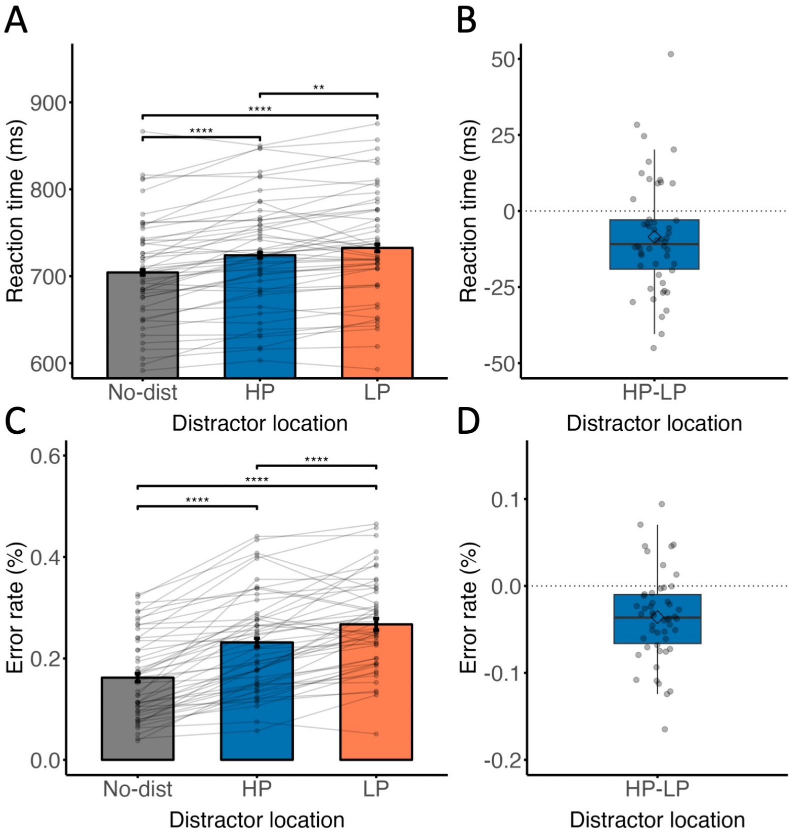

Figure 5. RTs (A and B) and error rates (C and D) in Experiment 2 as a function of distractor location for learning arrays. **(A)** RTs in the learning array. The bars show a clear attentional capture effect with slower RTs when the distractor is present. **(B)** The boxplot displays the RT differences between the HP and LP condition in the learning array. Most subjects had faster RTs when the distractor is presented at the HP location compared to the LP location. **(C)** Error rates in the learning array. The bars show a clear attentional capture effect with higher error rates when the distractor is present. **(D)** The boxplot displays the error rate differences between the HP and LP condition in the learning array. Most subjects have lower error rates when the distractor is presented at the HP location compared to the LP location.

Test array Having established a learned attentional bias in the learning array, we next set out to examine whether that bias continued to persist in retinotopic coordinates after a saccade is made in the presence of environmental landmarks by again including only those participants that demonstrated the hypothesized effect in the learning array (*N* = 38 for RT; *N* = 42 for error rate). As visualized in Figure 6A, and counter to Experiment 1, the data was no longer characterized by a linear increase from the retinotopic, to the LP to the spatiotopic location (β =

6.71, SE = 6.13, *t* (38.5) = 1.093, *p* = .28). Instead, RTs were fastest at the LP location relative to the retinotopic and the spatiotopic location (quadratic β = 21.95, SE = 6.52, *t* (131.15) = 3.37, *p* < .001), a pattern that is inconsistent with any of the models outlined in Figure 2. By contrast, error rates did showcase a systematic rise from the retinotopic location towards the spatiotopic location (linear β = 0.21, SE = 0.1, *z* = 2.2, *p* = .028; see Figure 6C). Together, these findings again demonstrate that there was no evidence that learned spatial suppression would be remapped in spatiotopic coordinates following a saccade, not even when visual landmarks provided more visual structure.

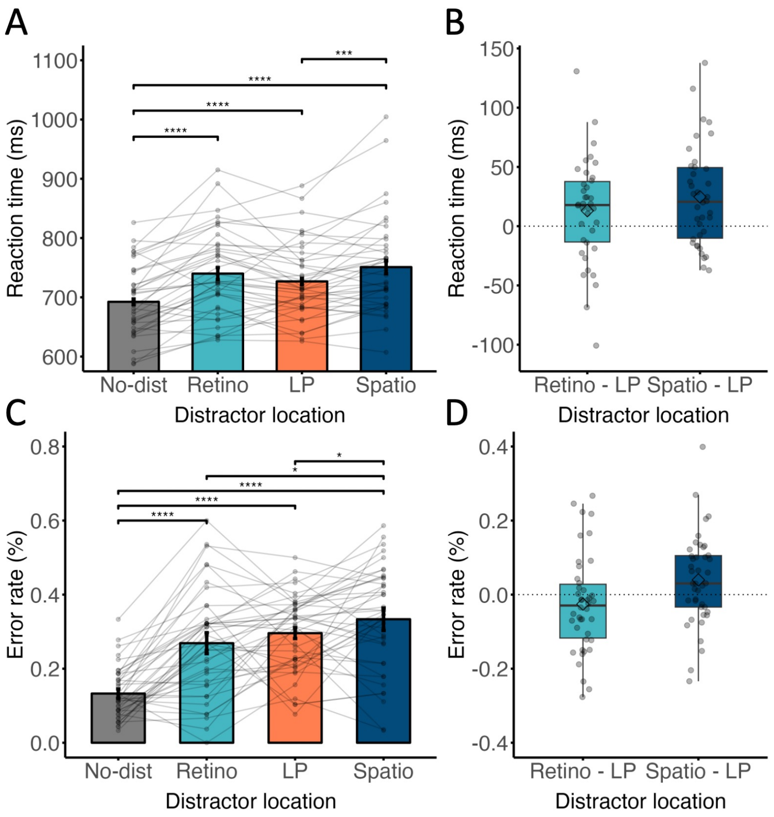

Figure 6. RTs (A and B) and error rates (C and D) in Experiment 2 as a function of distractor location for test arrays. **(A)** RTs in the test array. The bars show that the RTs are lowest when the distractor is presented at the LP location, which is inconsistent with any of the expected scerarios. **(B)** The boxplot displays the RT differences between the retinotopic and LP location and the spatiotopic and LP location. **(C)** The bars show a systematic increase in error rates across the retinotopic, LP and spatiotopic locations (linear β = 0.21, SE = 0.1, z = 2.2, p = .028) **(D)** The boxplot displays the error rate differences between the retinotopic and LP location and the spatiotopic and LP location.

Discussion

In Experiment 2a, we added a grid and placeholders to the search display to impose a spatial reference frame and promote spatiotopic processing. However, as in Experiment 1, there was no transfer of the learned spatial suppression to the spatiotopic location after eye movements. If anything, the data suggests that the learned suppression still persisted in retinotopic coordinates, characterized by a positive error rate slope across the retinotopic towards the spatiotopic location (in line with the scenario in Figure 2A). But in contrast to Experiment 1, the slope seemed to be mainly driven by an increase from the LP to the spatiotopic location and not by the increase from the retinotopic to the LP location. Additionally, this pattern occurred only for the error rates and not for the RTs. A possible explanation for this discrepancy is that the stimuli were only presented for 150 ms and not until response, making the task very challenging. As a result, participants may have been more inclined to make fast guesses, resulting in less informative reaction times. Experiment 2b addressed this issue by extending the stimulus display duration to 2000 ms or until a response was made.

Experiment 2b

Methods

Experiment 2b was identical to Experiment 2a, except that the stimuli were presented for 2000 ms or until response (as in Experiment 1). In Experiment 2b, we anticipated the effect size to fall between that of Experiment 1 and Experiment 2a. This expectation was based on the controlled environment of Experiment 1 leading to a higher effect size, and the challenging nature of the task in Experiment 2a resulting in a lower effect size. Thirty-two adults (16 females, mean age: 27.25 years old) were recruited for monetary compensation via the online platform Prolific (www.prolific.co; £9.25).

Results

One participant was identified as an outlier and replaced based on their average RT. Exclusion of incorrect trials (9.1%) and data trimming (2.3%) resulted in an overall loss of 11.3% of the trials for the RT analyses and 2.3% of trials for the error rate analyses.

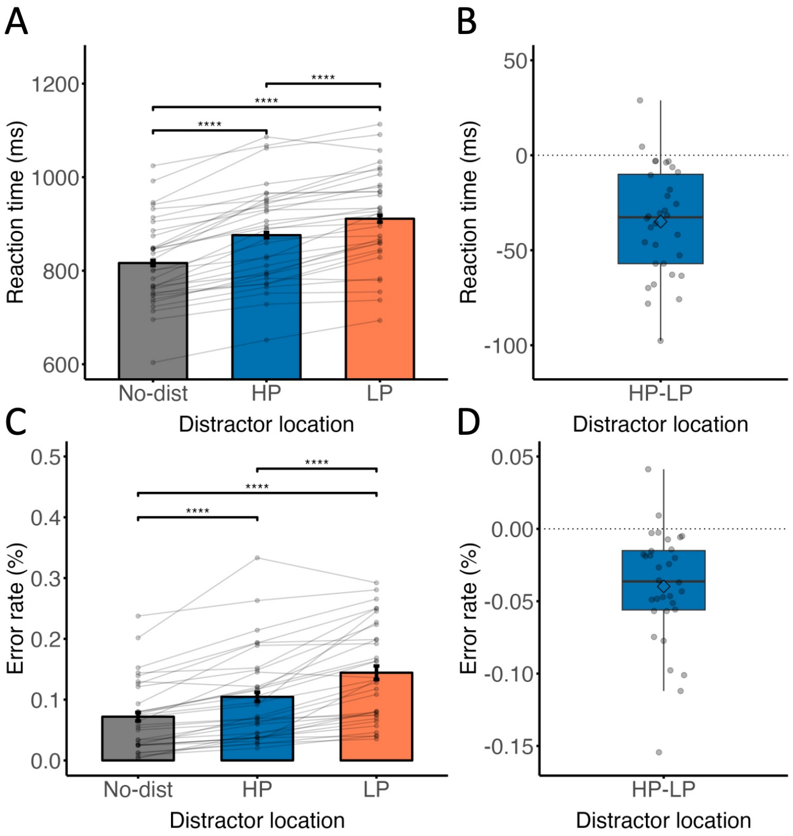

Figure 7. RTs (A and B) and error rates (C and D) in Experiment 3 as a function of distractor location for learning arrays. **(A)** RT in the learning array. The bars show a clear attentional capture effect with slower RTs when the distractor is present. **(B)** The boxplot displays the RT differences between the HP and LP condition in the learning array. Most subjects have faster RTs when the distractor is presented at the HP location compared to the LP location. **(C)** Error rates in the test array. The bars show a systematic increase in error rates across the retinotopic, LP and spatiotopic locations (linear β = 15.710.52, SE = 3.310.12, z = 4.4974 p < .001) **(D)** The boxplot displays the error rate differences between the retinotopic and LP location and the spatiotopic and LP location.

Learning array For the learning array, repeated-measures ANOVAs with within-subjects factor Distractor condition (no distractor, HP location and LP location) yielded a main effect for RTs (*F* (2, 62) = 135.29, $p < .001$, n_p^2 = .81) as well as for error rates (*F* (2, 62) = 66.38, $p < .001$, n_p^2 = .68). Subsequent planned comparisons confirmed that relative to the no distractor condition RTs were slower and error rates were higher at the HP and LP locations (all t's > 5.7, all p's < .001; see Figure 7A and 7C). Crucially, participants were faster (*t* (31) = 6.91, $p < .001$; see Figure 7B) and had lower error rates (*t* (31) = 5.73, $p < .001$; see Figure 7D) when the distractor appeared at the HP location compared to the LP location.

Test array Counter to Experiment 2, as visualized in Figure 8A and 8C respectively, both RT (linear β = 21.87, SE = 10.21, *t* (31.72) = 2.14, *p* = .04) and error rate (linear β = 0.52, SE = 0.12, *z* = 4.49 $p < .001$) were characterized by a systematic increase across the retinotopic, LP and spatiotopic locations. Together with the previous experiments these findings show that at least under the present conditions there is no evidence whatsoever that learned spatial suppression is remapped into spatiotopic coordinates following a saccade.

Discussion

Experiment 2b replicated the results of Experiment 1 and demonstrated that, following eye movements, suppression effects due to statistical learning remain in retinotopic coordinates, while there was no transfer of the suppression to spatiotopic coordinates, even when visual landmarks are present to impose a spatial reference frame.

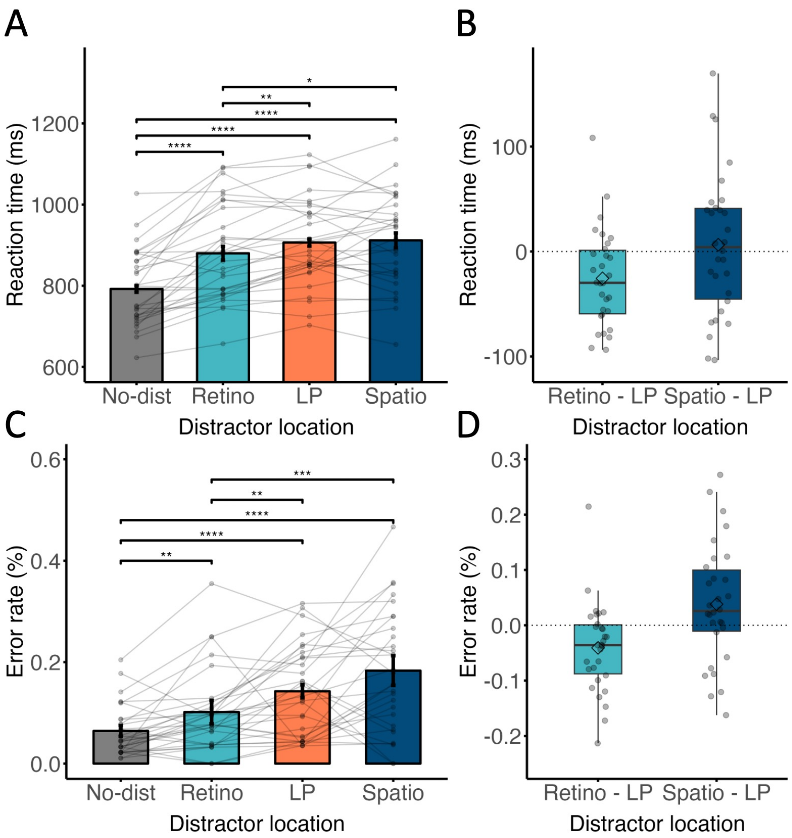

Figure 8. RTs (A and B) and error rates (C and D) in Experiment 3 as a function of distractor location for test arrays. **(A)** RTs in the test array. Similar to experiment 1, the bars show a positive slope across the retinotopic, LP and spatiotopic locations (linear β = 15.4121.87, SE = 7.1210.21, t (31.720.9) = 2.174, p = .0384) **(B)** The boxplot displays the RT differences between the retinotopic and LP location and the spatiotopic and LP location. **(C)** Error rates in the test array. The bars show a systematic increase in error rates across the retinotopic, LP and spatiotopic locations (linear β = 15.710.52, SE = 3.310.12, z = 4.4974 p < .001) **(D)** The boxplot displays the error rate differences between the retinotopic and LP location and the spatiotopic and LP location.

General Discussion

The present study shows that participants learn the statistical regularities presented in the display and adapt their selection priorities accordingly. More importantly, the current study provides compelling new evidence that the attentional suppression effect due to statistical learning operates in retinotopic coordinates rather than spatiotopic coordinates. Following a saccade to a new location, we see that the location relative to the eyes is suppressed.

These findings provide some important insight about the underlying mechanism. Given that suppression is only found in retinotopic coordinates, it is possible that learned suppression is resolved by changing synaptic weights in early visual areas, as the initial input to visual cortex is retinotopic. Importantly, it has been suggested that the brain exclusively encodes spatial information within retinotopic maps and does not contain explicit spatiotopic representations (Golomb et al., 2008; Golomb & Kanwisher, 2012; Mathôt & Theeuwes, 2011). Indeed, it has been shown that retinotopy is preserved throughout higher visual areas (Golomb & Kanwisher, 2012). A plausible mechanism for representing topographic maps involves the remapping of retinotopic maps, potentially triggered by eye movement signals, such as a corollary discharge. Notably, behavioral studies on endogenous attention (Golomb et al., 2008, 2010) and exogenous attention (Mathôt & Theeuwes, 2010b) reveal a gradual remapping of attention from retinotopic to spatiotopic coordinates following eye movements. It has been suggested that the frontal eye field (FEF) is a central source of remapping, with early visual cortices playing a comparatively minor role (Mathôt & Theeuwes, 2011). Given the findings of the current study, the question remains as to why this remapping phenomenon does not seem to apply to the observed suppression effects. This leads to the hypothesis that the suppression effect observed in the current study may be resolved primarily in early visual cortices, without extending to the FEF, in contrast to top-down or bottom-up attentional processes.

Alternatively, some studies suggest that only attended items are remapped, which raises the possibility that suppression effects may not be remapped to spatiotopic coordinates (Golomb & Mazer, 2021; Gottlieb et al., 1998; Joiner et al., 2011). In other words, it is feasible that selection history-driven attentional enhancement undergoes similar remapping as exogenous and endogenous attention, while selection history-driven attentional suppression remains in retinotopic coordinates. Indeed, van Moorselaar and Theeuwes (2023) demonstrated that attentional enhancement resulting from statistical learning does not always rely on a retinotopic reference frame but can also occur within objects, irrespective of the object's location in space. To test whether history-driven attentional enhancement can be remapped to spatiotopic coordinates, the current study should be repeated with a likely target location instead of a likely distractor location.

It is noteworthy that participants exhibited retinotopic suppression not only in Experiment 1, where eye fixations were regulated, but also in Experiment 2. In the latter case, the inability to control eye movements during the search meant that the search location labelled as retinotopic did probably not consistently align with the same location on the participant's retina. In other words, subjects suppressed the same location with respect to the fixation cross even when they could freely move their eyes during search. This suggests that the suppression effect is not only tied to retinotopic coordinates but also extends to a head-centered egocentric (i.e. self-referenced) representation. Consistent with this observation, Jiang & Swallow (2013, 2014) conducted a series of experiments demonstrating that attentional enhancement due to probability cuing is dependent on the participants' viewpoint. Participants were tasked with locating a T among L's displayed on a tablet mounted on a stand. Unbeknownst to the participants, the target appeared more frequently in one quadrant compared to the others. As expected, the study revealed an attentional bias towards the quadrant that was likely to contain the target. However, intriguingly, when participants moved around the tablet, the attentional facilitation appeared to move along with the participant's viewpoint rather than remaining in the spatiotopic location. It is important to note that in these experiments, each trial began with a fixation dot randomly placed within a central region and participants were allowed to freely move their eyes during search. This implies that the likely target location was not learned in a retinotopic manner (i.e., relative to the eyes) but within an egocentric reference frame (i.e., relative to the head-body). Consequently, it appears that there is not only a lack of remapping of statistical learning effects from retinotopic to spatiotopic coordinates following eye movements but also an absence of updating the egocentric reference frame to an environmentally stable reference frame after body and head movements (but also see Jiang et al., 2014; Smith et al., 2010; Zheng et al., 2021). Given our continuous eye and body movements, the practical use of learned attentional biases becomes uncertain when they are not remapped from retinotopic or egocentric coordinates to spatiotopic coordinates.

In summary, the findings of the current study indicate that, following saccadic eye movements, suppression effects persist in retinotopic coordinates, with no observed transfer of suppression to spatiotopic coordinates. It remains unclear whether there are situations in which implicit attentional biases are remapped to spatiotopic coordinates.

References

Barr, D. J., Levy, R., Scheepers, C., & Tily, H. J. (2013). Random effects structure for confirmatory hypothesis testing: Keep it maximal. *Journal of Memory and Language*, *68*(3), 255–278. https://doi.org/10.1016/J.JML.2012.11.001

Bisley, J. W. (2011). The neural basis of visual attention. *The Journal of Physiology*, *589*(1), 49–57. https://doi.org/10.1113/JPHYSIOL.2010.192666

Bisley, J. W., & Goldberg, M. E. (2010). Attention, intention, and priority in the parietal lobe. *Annual Review of Neuroscience*, *33*, 1–21. https://doi.org/10.1146/ANNUREV-NEURO-060909-152823

Brysbaert, M., & Stevens, M. (2018). Power Analysis and Effect Size in Mixed Effects Models: A Tutorial. *Journal of Cognition*, *1*(1). https://doi.org/10.5334/JOC.10

Fecteau, J. H., & Munoz, D. P. (2006). Salience, relevance, and firing: a priority map for target selection. *Trends in Cognitive Sciences*, *10*(8), 382–390. https://doi.org/10.1016/J.TICS.2006.06.011

Fischer, B., & Ramsperger, E. (1984). Human express saccades: extremely short reaction times of goal directed eye movements. *Experimental Brain Research*, *57*(1), 191–195. https://doi.org/10.1007/BF00231145/METRICS

Fischer, B., & Weber, H. (1993). Express saccades and visual attention. *Behavioral and Brain Sciences*, *16*(3), 553–567. https://doi.org/10.1017/S0140525X00031575

Golomb, J. D., Chun, M. M., & Mazer, J. A. (2008). The Native Coordinate System of Spatial Attention Is Retinotopic. *Journal of Neuroscience*, *28*(42), 10654–10662. https://doi.org/10.1523/JNEUROSCI.2525-08.2008

Golomb, J. D., & Kanwisher, N. (2012). Higher Level Visual Cortex Represents Retinotopic, Not Spatiotopic, Object Location. *Cerebral Cortex*, *22*(12), 2794–2810. https://doi.org/10.1093/CERCOR/BHR357

Golomb, J. D., & Mazer, J. A. (2021). *Annual Review of Vision Science Visual Remapping*. https://doi.org/10.1146/annurev-vision-032321

Golomb, J. D., Pulido, V. Z., Albrecht, A. R., Chun, M. M., & Mazer, J. A. (2010). Robustness of the retinotopic attentional trace after eye movements. *Journal of Vision*, *10*(3). https://doi.org/10.1167/10.3.19

Gottlieb, J. P., Kusunoki, M., & Goldberg, M. E. (1998). The representation of visual salience in monkey parietal cortex. *Nature 1998 391:6666*, *391*(6666), 481–484. https://doi.org/10.1038/35135

Heeman, J., Van der Stigchel, S., Munoz, D. P., & Theeuwes, J. (2019). Discriminating between anticipatory and visually triggered saccades: Measuring minimal visual saccadic response time using luminance. *Journal of Neurophysiology*, *121*(6), 2101–2111. https://doi.org/10.1152/JN.00378.2018/ASSET/IMAGES/LARGE/Z9K0041950090006.JPEG

Jiang, Y. V., & Swallow, K. M. (2013). Spatial reference frame of incidentally learned attention. *Cognition*, *126*(3), 378–390. https://doi.org/10.1016/J.COGNITION.2012.10.011

Jiang, Y. V., & Swallow, K. M. (2014). Changing viewer perspectives reveals constraints to implicit visual statistical learning. *Journal of Vision*, *14*(12). https://doi.org/10.1167/14.12.3

Jiang, Y. V., Won, B. Y., Swallow, K. M., & Mussack, D. M. (2014). Spatial reference frame of attention in a large outdoor environment. *Journal of Experimental Psychology. Human Perception and Performance*, *40*(4), 1346–1357. https://doi.org/10.1037/A0036779

Joiner, W. M., Cavanaugh, J., & Wurtz, R. H. (2011). Modulation of shifting receptive field activity in frontal eye field by visual salience. *Journal of Neurophysiology*, *106*(3), 1179–1190. https://doi.org/10.1152/JN.01054.2010/ASSET/IMAGES/LARGE/Z9K0091109170009.JPEG

Kim, H. F., & Hikosaka, O. (2013). Distinct Basal Ganglia Circuits Controlling Behaviors Guided by Flexible and Stable Values. *Neuron*, *79*(5), 1001–1010. https://doi.org/10.1016/J.NEURON.2013.06.044

Krauzlis, R. J., Lovejoy, L. P., & Zénon, A. (2013). Superior colliculus and visual spatial attention. *Annual Review of Neuroscience*, *36*, 165–182. https://doi.org/10.1146/ANNUREV-NEURO-062012-170249

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/JSS.V082.I13

Lange, K., Kühn, S., & Filevich, E. (2015). "Just Another Tool for Online Studies” (JATOS): An Easy Solution for Setup and Management of Web Servers Supporting Online Studies. *PLOS ONE*, *10*(6), e0130834. https://doi.org/10.1371/JOURNAL.PONE.0130834

Mathôt, S., Schreij, D., & Theeuwes, J. (2012). OpenSesame: An open-source, graphical experiment builder for the social sciences. *Behavior Research Methods*, *44*(2), 314–324. https://doi.org/10.3758/S13428-011-0168-7/FIGURES/4

Mathôt, S., & Theeuwes, J. (2010a). Evidence for the predictive remapping of visual attention. *Experimental Brain Research*, *200*(1), 117–122. https://doi.org/10.1007/S00221-009-2055-3/FIGURES/2

Mathôt, S., & Theeuwes, J. (2010b). Gradual remapping results in early retinotopic and late spatiotopic inhibition of return. *Psychological Science*, *21*(12), 1793–1798. https://doi.org/10.1177/0956797610388813/ASSET/IMAGES/LARGE/10.1177_0956797610388813-FIG2.JPEG

Mathôt, S., & Theeuwes, J. (2011). Visual attention and stability. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *366*(1564), 516–527. https://doi.org/10.1098/RSTB.2010.0187

Morey, R. D. (2008). Confidence Intervals from Normalized Data: A correction to Cousineau (2005). *Tutorials in Quantitative Methods for Psychology*, *4*(2), 61–64. https://doi.org/10.20982/TQMP.04.2.P061

Noudoost, B., Chang, M. H., Steinmetz, N. A., & Moore, T. (2010). Top-down control of visual attention. *Current Opinion in Neurobiology*, *20*(2), 183–190. https://doi.org/10.1016/J.CONB.2010.02.003

Smith, A. D., Hood, B. M., & Gilchrist, I. D. (2010). Probabilistic Cuing in Large-Scale Environmental Search. *Journal of Experimental Psychology: Learning Memory and Cognition*, *36*(3). https://doi.org/10.1037/a0018280

Talsma, D., White, B. J., Mathôt, S., Munoz, D. P., & Theeuwes, J. (2013). A Retinotopic Attentional Trace after Saccadic Eye Movements: Evidence from Event-related Potentials. *Journal of Cognitive Neuroscience*, *25*(9). https://doi.org/10.1162/jocn_a_00390

Team, R. C. (2018). *A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.* Available Online: Www. R-Project. Org/(Accessed on 11 September 2020). https://scholar.google.com/scholar?hl=nl&as_sdt=0%2C5&q=R+Core+Team.+%282020%29.+A+language+and+environment+of+statistical+computing.+R+Foundation+for+Statistical+Computing.&btnG=

Theeuwes, J. (2019). Goal-driven, stimulus-driven, and history-driven selection. *Current Opinion in Psychology*, *29*, 97–101. https://doi.org/10.1016/J.COPSYC.2018.12.024

Theeuwes, J., Bogaerts, L., & van Moorselaar, D. (2022). What to expect where and when: how statistical learning drives visual selection. *Trends in Cognitive Sciences*, *26*(10), 860–872. https://doi.org/10.1016/J.TICS.2022.06.001

Thompson, K. G., & Bichot, N. P. (2005). A visual salience map in the primate frontal eye field. *Progress in Brain Research*, *147*(SPEC. ISS.), 249–262. https://doi.org/10.1016/S0079-6123(04)47019-8

Thompson, K. G., Bichot, N. P., & Sato, T. R. (2005). Frontal eye field activity before visual search errors reveals the integration of bottom-up and top-down salience. *Journal of Neurophysiology*, *93*(1), 337–351. https://doi.org/10.1152/JN.00330.2004/ASSET/IMAGES/LARGE/Z9K0010542991014.JPEG

van Moorselaar, D., & Theeuwes, J. (2023). Statistical Learning Within Objects. *Psychological Science*, *34*(4), 501–511. https://doi.org/10.1177/09567976231154804/FORMAT/EPUB

Wang, B., & Theeuwes, J. (2018a). Statistical Regularities Modulate Attentional Capture. *Journal of Experimental Psychology: Human Perception and Performance*, *44*(1), 13–17. https://doi.org/10.1037/XHP0000472

Wang, B., & Theeuwes, J. (2018b). How to inhibit a distractor location? Statistical learning versus active, top-down suppression. *Attention, Perception, and Psychophysics*, *80*(4), 860–870. https://doi.org/10.3758/S13414-018-1493-Z/FIGURES/5

Wang, B., & Theeuwes, J. (2018c). Statistical regularities modulate attentional capture independent of search strategy. *Attention, Perception, and Psychophysics*, *80*(7), 1763–1774. https://doi.org/10.3758/S13414-018-1562-3/FIGURES/6

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*(1564), 492–503. https://doi.org/10.1098/RSTB.2010.0186

Yamamoto, S., Monosov, I. E., Yasuda, M., & Hikosaka, O. (2012). What and Where Information in the Caudate Tail Guides Saccades to Visual Objects. *Journal of Neuroscience*, *32*(32), 11005–11016. https://doi.org/10.1523/JNEUROSCI.0828-12.2012

Zheng, L., Dobroschke, J. G., & Pollmann, S. (2021). Egocentric and Allocentric Reference Frames Can Flexibly Support Contextual Cueing. *Frontiers in Psychology*, *12*. https://doi.org/10.3389/fpsyg.2021.711890