

Stage-specific priming of pop-out effects in the target-feature memory encoding and retrieval

Hongmei Xia^{a,*}, Fredrik Allenmark^a, Hermann J. Müller^a, Zhuanghua Shi^a

^a Neuro-Cognitive Psychology, Department of Psychology, LMU Munich, Munich, Germany

ARTICLE INFO

Keywords:

Priming of pop-out (PoP)
Visual search
Inter-trial effect
Visual working memory
Eye movements

ABSTRACT

Priming of Pop-out (PoP), when a target-defining feature repeats, accelerates visual search. While previous studies highlight the influence of display density—sparse versus dense arrays—on PoP, how display density interacts with memory encoding and retrieval stages remains unresolved. The present study disentangled the contributions of encoding (trial $n-1$) from retrieval (trial n) and tracked their influence on early orienting (pre-selective) versus late identification (post-selective) processes. Participants searched for a uniquely colored target under blocked and interleaved density regimes, with eye movements and manual responses recorded. By crossing sparse and dense displays across consecutive trials, four transition types were probed to determine where density exerts its effect. Color repetition reduced reaction times and first saccadic latency, and boosted first-saccade accuracy, but only when the current (i.e., the retrieval) display remained sparse. In contrast, dense displays showed fast responses, with the absence of PoP, due to saliency-driven guidance. Pre-selective eye-movement metrics showed robust PoP in sparse retrieval arrays, whereas dense retrieval arrays defaulted to saliency-driven guidance. Post-selective decision times were comparable across conditions, indicating that PoP drives only the early attentional guidance. These results indicate that while encoding reliably forms target templates, it is the retrieval context that switches feature-biasing mechanisms on or off, highlighting a dynamic interplay between memory and bottom-up salience in adaptive search.

1. Introduction

We navigate our world through visual search – recognizing a friend's face in a crowd or spotting a ripe tomato on a cluttered supermarket shelf. This reliance on selective attention, which adapts moment by moment to the features of recent target items, underlies our everyday efficiency. For instance, when searching for a red (target) among green objects (distractors), we become faster at detecting subsequent red targets even if their shape changes (Maljkovic & Nakayama, 1994). This phenomenon, known as priming of pop-out (PoP), reflects how our attentional system tunes itself to the history of what we've just searched.

PoP arises from the interplay of two critical stages: encoding and retrieval. During encoding, target-defining features (say, color) are incorporated in a visual working memory (VWM) representation on a given trial ($n-1$), creating a search template that biases attention toward what we attend to next (n) (Carlisle & Kristjánsson, 2018; Kristjánsson & Campana, 2010a). During retrieval on the subsequent trial (n), these encoded features are assessed against the current display to guide

attention efficiently toward the target item (Hillstrom, 2000; Huang & Pashler, 2005). Although researchers have made strides in isolating these mechanisms, search displays typically used in PoP are sparse, and we still lack a clear picture of how encoding and retrieval interact when task demands and item densities shift unpredictably. For example, pop-out targets frequently fail to pop out in sparse (low-density) displays, and the probability of initially selecting the target is considerably lower in sparse compared to dense displays (Rangelov et al., 2013, 2017). Additionally, the amount of attentional focusing required by the task modulates both dimension-based and space-based intertrial effects (Krummenacher et al., 2009). Thus, clarifying the interaction between two critical stages of PoP – encoding and retrieval – and display density is essential for understanding the mechanisms that shape PoP effects and guide adaptive search behavior.

The prevailing theory of PoP posits that the target features are encoded in VWM as a search template, thereby biasing attention toward matching features on subsequent trials (Carlisle & Kristjánsson, 2018; Gunseli et al., 2014). When a new search display appears, VWM matches

* Corresponding author at: Neuro-Cognitive Psychology, Department of Psychology, Ludwig-Maximilians-Universität (LMU) Munich, Leopoldstraße 13, 80802, Munich, Germany.

E-mail address: hon.xia@psy.lmu.de (H. Xia).

<https://doi.org/10.1016/j.actpsy.2026.106633>

Received 15 September 2025; Received in revised form 29 January 2026; Accepted 6 March 2026

Available online 10 March 2026

0001-6918/© 2026 The Authors. Published by Elsevier B.V. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

stored features to incoming stimuli, speeding up detection of repeated features. As a result, saccades toward targets that share features with previously attended items become both faster and more precise (Bundesen, 1990; Hollingworth et al., 2013; Maljkovic & Nakayama, 1994; McPeck et al., 1999). Moreover, neuroimaging work implicates the frontoparietal attention network, supporting the interplay of top-down control and bottom-up salience in orchestrating these priming effects (Awh et al., 2012; Kristjánsson et al., 2005).

Although PoP has demonstrated remarkable robustness across studies (Becker & Ansorge, 2013; Gokce et al., 2013), its strength wanes when we shift from sparse to dense search displays (Allenmark et al., 2021; Rangelov et al., 2013, 2017). Early PoP studies, which relied on displays with only a few distractors, consistently reported strong priming effects (Kristjánsson & Campana, 2010a; Maljkovic & Nakayama, 1994). However, when the search display consists of dozens of similar-colored items, PoP often shrinks or vanishes altogether (Rangelov et al., 2013). This decline has been attributed to isofeature suppression (Field et al., 1993; Zhaoping, 2005): Given the presence of a particular stimulus in a neuron's receptive field, the neuron's output is significantly weaker if similar stimuli are presented nearby. In dense arrays, where many distractors are closely spaced, they mutually inhibit each other through isofeature suppression. This causes individual distractors to produce weaker priority signals, boosting the relative salience of the target. By contrast, sparse arrays provide weaker lateral inhibition, making non-targets harder to filter out and heightening the need for inter-trial priming (Rangelov et al., 2013). Becker (2008) further showed that under such conditions, targets are not always the first item fixated but often the second, requiring additional feature-checking – an extra step that amplifies the role of priming for efficient detection.

Yet despite clear evidence that display density modulates PoP, we still lack consensus on whether this modulation arises during encoding (trial $n-1$) or retrieval (trial n). Proponents of the feature-priming hypothesis argue that successful integration of target features into VWM forms a search template, which automatically steers attention toward matching items on the next trial (Chun & Nakayama, 2000; Goolsby & Suzuki, 2001; Olivers & Humphreys, 2003). Sparse contexts, they suggest, reduce distractor competition and thus strengthen encoding of target features (Maljkovic & Nakayama, 1994; Rangelov et al., 2013). In contrast, advocates of the episodic-retrieval account posit that PoP hinges on reactivating priority tags from the previous display: matches speed up retrieval, whereas mismatches force observers to assemble new priority rules – a laborious process (Hillstrom, 2000; Huang & Pashler, 2005). From this perspective, high-density arrays shift control toward bottom-up salience, weakening the influence of past encoding (Li, 1999). To date, interleaving display densities within a single experiment – and thus simulating more realistic, unpredictable settings – remains rare, leaving the relative contribution of encoding and retrieval under dynamic conditions an open question.

More recent work suggests that PoP unfolds in at least two consecutive phases of attentional processing: a pre-selective phase that steers early orienting, and a post-selective phase of identification and decision-making (Becker et al., 2023). In the pre-selective stage, early attentional orienting reflects both bottom-up saliency and top-down feature priors. Here, top-down priming – our memory of previously attended features – often overrides raw salience, especially in dense arrays where learned feature priorities shape early guidance (Becker et al., 2023; Wolfe, 2020). At the same time, bottom-up saliency still matters: high-contrast items pop out and draw the gaze (Itti & Koch, 2001; Zelinsky, 2008), while feature distinctiveness – by how much a target differs from distractors – boosts early prioritization, guiding attention to pop-out items (Treisman & Gelade, 1980). The post-selective phase, by contrast, encompasses identification and decision processes: once an item enters focal attention, its unique attributes streamline discrimination from distractors, particularly when fine-grained identifications are required (Duncan & Humphreys, 1989).

Based on prior research, we derived three competing hypotheses

regarding how display density might modulate PoP. First, on an encoding-dominance account, PoP should be stronger when encoding takes place in sparse displays, yielding robust effects in sparse-sparse (SS) and sparse-dense (SD) inter-trial conditions, but weaker effects in dense-dense (DD) and dense-sparse (DS) conditions. Second, a retrieval-stage dominance account posits that PoP strength hinges on retrieval demands, so that sparse retrieval would enhance priming in the SS and DS conditions, whereas dense retrieval would attenuate priming in the DD and SD conditions. Third, if encoding and retrieval contribute interactively, an interaction-dominance pattern should emerge, with the strongest PoP in the SS condition, the weakest in the DD condition, and intermediate effects in the mixed-density conditions (DS and SD).

To adjudicate between these competing accounts, we manipulated display density independently at the encoding stage (trial $n-1$) and the retrieval stage (trial n), yielding four experimental conditions: dense encoding with dense retrieval (DD), sparse encoding with sparse retrieval (SS), dense encoding with sparse retrieval (DS), and sparse encoding with dense retrieval (SD). Participants searched for a color-defined target singleton and reported its orientation, while their eye movements were recorded. This factorial design was designed to provide a clean test of whether PoP is primarily constrained during encoding, during retrieval, or by the interaction between the two stages.

Building on this design, we further examined how density-dependent effects on PoP unfold across different stages of attentional processing. We reasoned that dense arrays increase target saliency, so that attentional guidance on trial n relies more strongly on bottom-up signals and less on the retrieval of feature-based priorities established on the previous trial $n-1$. In addition, we investigated whether these stage-specific effects primarily influence early attentional orienting (pre-selective processing) or later identification and decision-making (post-selective processing), expecting the balance between bottom-up salience and history-based feature biases to shift depending on where display density exerts its strongest influence.

2. Method

2.1. Participants

We recruited 18 volunteers (12 females, 6 males; $M = 25.6$ years, $SD = 3.8$ years) to ensure adequate power for detecting a medium-to-large PoP effect. Drawing on Rangelov et al. (2013), who observed a significantly stronger PoP effect (effect size $\eta_p^2 = 0.60$) in a similar paradigm, particularly in the variable condition, where red and green items served as both target and distractor features, we ran a power analysis with G*Power 3 (Faul et al., 2007) for a repeated-measures ANOVA ($f = 0.40$). Results indicated that a sample size of 17 would achieve a power of at least 0.85. Accordingly, we recruited 18 participants. They signed a written informed-consent form before the study and received 9 Euro per hour for their participation. The study was approved by the ethics committee of the LMU Munich Psychology Department.

2.2. Stimulus and apparatus

The experiment used a 19-in. screen with a resolution of 1536×864 pixels and a refresh rate of 85 Hz for displaying the visual stimuli, and employed PsychoPy (Peirce, 2007) for managing stimulus presentation and data collection. An Eyelink-1000 eye-tracker was used to record eye movements (at a sampling rate of 1 kHz). Participants sat in a dim, sound-attenuated experimental cabin, approximately 57 cm from the screen, with their head stabilized by a chinrest. Participants responded to the task by pressing the left or up arrow keys with their left or right index fingers, respectively.

Similar to the experimental design of Rangelov et al. (2013), the target could be either a blue grating (RGB: [0, 127, 255]) or a green grating (RGB: [0, 204, 51]), among distractors of the respective other color, presented against a black background (RGB: [0,0,0]). Each item

subtended $1.3^\circ \times 1.3^\circ$ of visual angle and appeared on one of three imaginary concentric circles (radii of 2.5° , 5° , 7.5° of visual angle, respectively). The inner, middle, and outer circles could hold up to 6, 12, and 16 items, respectively; however, the target appeared only on the middle circle, placed evenly across the 12 positions.

The experiment included two distinct display densities: a sparse array with three items (one target and two distractors), evenly spaced on the middle circle, and a dense array with 34 items (one target and 33 distractors), filling all possible positions. Fig. 1a depicts examples of the two display densities. Both targets and distractors featured either vertical or horizontal stripes. Stimulus orientation and color varied randomly across items.

Participants had to spot the target and discern its orientation,

pressing the up arrow key for the vertical and the left key for the horizontal. The program recorded their manual responses, noting the accuracy of identifying the target's orientation and the reaction time (RT). Simultaneously, it recorded participants' eye movements, capturing data on the time it took to fixate on the target, the number of eye movements (saccades) before homing in on the target, and the proportion of initial fixations made directly on the target.

2.3. Design and procedure

Participants completed two distinct experimental conditions – *blocked* and *interleaved* – each probing how display-density transitions shape PoP. In the *blocked* condition, trials were blocked by density: one block exclusively presented sparse displays, and another exclusively dense displays (order counterbalanced across participants). By contrast, the *interleaved* condition interleaved sparse and dense displays in a pseudorandom sequence. Across both conditions, the design incorporated four distinct patterns of inter-trial transitions:

- (1) Sparse→Sparse (SS): two consecutive sparse displays,
- (2) Dense→Dense (DD): two consecutive dense displays,
- (3) Sparse→Dense (SD): sparse followed by dense,
- (4) Dense→Sparse (DS): dense followed by sparse.

In the *blocked* conditions, only SS and DD transitions occurred; in the *interleaved* condition, all four types of transition appeared with equal probability. Target color (blue vs. green) was randomized per trial, allowing same-color repeats (e.g., blue → blue) or color switches (e.g., blue → green) to co-vary orthogonally with density transitions.

Each trial started with a white central fixation cross (RGB: 255, 255, 255), with participants had to fixate for 500 ms for the trial display to start; if they looked away, the cross turned red, prompting them to refocus. A sustained red cross signaled the experimenter to recalibrate eye-tracking (by pressing “o”). Once stable fixation resumed, the search array appeared, and participants located the uniquely colored target and reported its orientation: the up-arrow for vertical, the left-arrow for horizontal. They were instructed to respond both quickly and accurately. After responding, they received accuracy feedback for 1000 ms – a “correct” message for accurate answers and an “incorrect” message for mistakes. Immediately after feedback, the fixation cross for the next trial appeared.

The experiment consisted of 18 blocks, divided into six *blocked* conditions (three for sparse displays and three for dense displays) and 12 *interleaved* blocks. The doubling of the number of blocks ensured that the number of trials in each transition type was comparable across inter-trial transitions. Each block consisted of 64 trials, totaling 1152 trials per participant. Participants could take a brief break after each block, after which the experimenter recalibrated the eye tracker before starting the next block. The whole experiment took around 90 min to complete.

2.4. Data preprocessing

Trials with and RT below 200 ms or exceeding 2000 ms, as well as all those with incorrect responses, were low: 4.37% in the blocked condition and 2.24% in the interleaved condition. Error rates remained uniformly low across all conditions, showing minimal variance and no floor effects; therefore, their means and standard deviations are included in the Appendix but omitted from further analyses.

The remaining correct trials served as the basis for analyzing both the manual RT and the oculomotor measures. To ensure precise mapping of fixations onto the display, we first corrected for drift by computing each participant's average gaze position during fixation periods and shifting all recorded coordinates accordingly. We then extracted fixations during the search interval and labeled any fixation whose adjusted coordinates lay within a 2° radius of the target's center coordinates as a “target fixation”.

Four key oculomotor metrics were then extracted: (1) first fixation latency – the interval from search-array onset to the participant's first

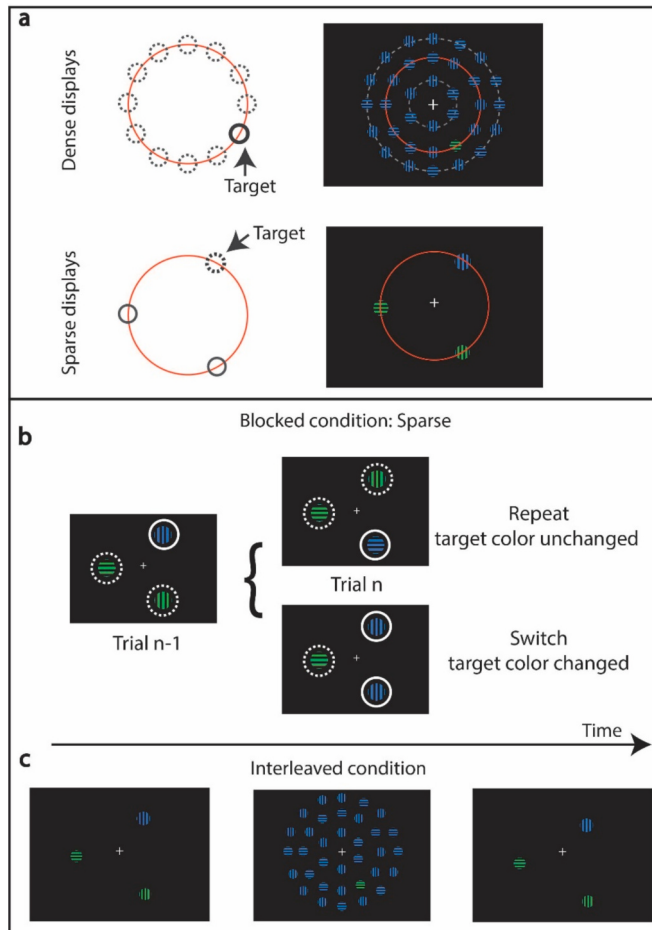


Fig. 1. Experimental Procedure and Design

Note. Fig. 1 illustrates the experimental setup and display configurations. (a) Examples of dense and sparse displays. In dense displays (top row), items were arranged on three concentric circles with radii of 2.5° , 5° , and 7.5° , respectively. The target appeared randomly at one of the 12 positions on the middle circle. In sparse displays (bottom row), only three items (one target and two distractors) were presented at three equidistant positions on the middle circle. Dashed outlines indicate the target on trial $n-1$, solid outlines the target on trial n . (b) Example of the blocked condition in which only sparse displays appear. Trial sequences illustrate repeat and switch trials: on repeat trials, the target color remains unchanged from trial $n-1$ to trial n (e.g., both targets are blue), whereas in switch trials, the target color on trial n corresponds to the distractor color on trial $n-1$ (e.g., the target is green on trial $n-1$ and blue on trial n). (c) Example of the interleaved condition in which dense and sparse displays alternated unpredictably, yielding four possible inter-trial density transitions: DD (Dense → Dense), DS (Dense → Sparse), SD (Sparse → Dense), and SS (Sparse → Sparse). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

fixation on the target (importantly, this measure does not necessarily correspond to the latency of the very first saccade; it may encompass multiple intervening saccades and fixations prior to the initial fixation on the target); (2) number of saccades before target fixation – the number of eye movements launched before landing on the target; (3) proportion of first saccades to target – the fraction of trials in which the very first saccade after display onset landed directly on the target; (4) post-selective latency – the latency between the final response and the saccade that landed on the target. We calculated the PoP effect by the difference between the color-repetition and color-switch trials in the RTs and the oculomotor metrics.

In addition to standard gaze metrics, we also visualized the spatial distribution of first-fixation landing locations using kernel density estimation (KDE) heatmaps. These heatmaps provide an intuitive view of where participants' eyes landed first, indicating the precision of early attentional guidance across conditions. To enable meaningful spatial averaging across trials, fixation coordinates were rotated such that the target always appeared at a fixed reference location on the display (e.g., right side of the array). This allowed for consistent comparison of attentional focus across density and color conditions.

3. Results

3.1. Blocked-condition performance

Mean RTs. Fig. 2a shows that dense displays expedited overall RTs, and repeating the target color speeded responses further, revealing robust PoP when displays stayed sparse (SS) but only numerical priming in dense arrays (DD). A repeated-measures (rm) ANOVA confirmed main effects of color repetition ($F(1,17) = 22.52, p < .001, \eta_p^2 = 0.570$) and density ($F(1,17) = 52.06, p < .001, \eta_p^2 = 0.754$), and a significant interaction ($F(1,17) = 11.82, p = .0031, \eta_p^2 = 0.410$). Post-hoc Bonferroni-adjusted tests showed that the PoP effect (color switch vs. repeat, 74 ms) was significant in sparse displays ($t(17) = 4.83, p < .001$, Cohen's $d = 0.33$), whereas it was only numerically positive (18 ms) in dense displays ($t(17) = 1.95, p = .068$, Cohen's $d = 0.33$).

First-saccade Proportion. Participants launched their initial saccade straight to the target far more often in dense displays, but the benefits of color repeats were more evident in sparse displays (Fig. 2b). An rm-ANOVA yielded significant main effects of color repetition ($F(1,17) = 21.39, p < .001, \eta_p^2 = 0.557$) and density ($F(1,17) = 152.66, p < .001, \eta_p^2 = 0.900$), plus a significant interaction ($F(1,17) = 18.69, p < .001, \eta_p^2 = 0.524$). Further pairwise contrasts revealed a 19.5% gain in PoP in sparse displays ($t(17) = 4.59, p < .001$, Cohen's $d = 1.32$), but not reliable PoP in dense displays ($t(17) = -1.06, p = .61$, Cohen's $d = -0.12$).

First Fixation Latency. Dense displays shortened initial fixation latencies, and repeated colors saved more time; yet, only sparse displays showed significant PoP. We obtained main effects of color repetition ($F(1,17) = 52.27, p < .001, \eta_p^2 = 0.756$) and display density ($F(1,17) = 52.80, p < .001, \eta_p^2 = 0.756$), plus a significant interaction ($F(1,17) = 30.98, p < .001, \eta_p^2 = 0.646$). In sparse trials, color switches caused costs of 73 ms compared to repeats ($t(17) = 6.90, p < .001$, Cohen's $d = 0.77$), whereas there were no costs for dense color switches vs. repeats ($t(17) = 1.01, p = .65$, Cohen's $d = -0.099$).

Number of Saccades. A similar pattern emerged in the number of saccades (Fig. 3d). Again, both main effects were significant: density ($F(1,17) = 50.51, p < .001, \eta_p^2 = 0.682$) and color repetition ($F(1,17) = 7.75, p = .013, \eta_p^2 = 0.858$). The significant interaction ($F(1,17) = 30.25, p < .001, \eta_p^2 = 0.566$) and post-hoc contrasts revealed sparse switch displays to require 0.31 more saccades than repeat displays ($t(17) = 5.65, p < .001$, Cohen's $d = 1.16$), whereas was no such difference for dense displays ($t(17) = 1.01, p = .65$, Cohen's $d = 0.12$).

Post-selective Decision Time. Once the eyes landed on the target, neither density ($F(1,17) = 4.14, p = .058, \eta_p^2 = 0.195$) nor color repetition ($F(1,17) = 2.28, p = .149, \eta_p^2 = 0.118$) influenced the residual

decision time. The interaction between density and repetition was also not significant ($F(1,17) = 0.28, p = .606, \eta_p^2 = 0.016$), indicating that display density does not modulate PoP at the late stage in the blocked condition.

As shown by the above post-hoc contrasts, PoP was evident across pre-selective metrics – first-saccade proportion, first-fixation latency, and the number of saccades before landing on the target – in sparse displays, but not in dense displays. And PoP was absent in the post-selective decision for both displays.

3.2. Interleaved-condition performance

Fig. 3 presents the performance differences in the interleaved condition, which included all four possible inter-trial transitions (SS, DD, SD, and DS).

RTs. Fig. 3a plots mean RTs alongside the PoP effects. Repeating the target color shortened RTs significantly ($F(1,17) = 58.79, p < .001, \eta_p^2 = 0.776$) and shifting between sparse and dense displays drove significant RT changes ($F(3,51) = 75.00, p < .001, \eta_p^2 = 0.437$). Crucially, a significant interaction emerged ($F(3,51) = 21.32, p < .001, \eta_p^2 = 0.749$), revealing priming to be dependent on the density sequence. Post-hoc pair-wise contrasts indicated a clear hierarchy: keeping density high (DD) yielded the fastest responses ($ps < 0.001$), sparse-to-dense transitions (SD) afforded faster RTs than dense-to-sparse transitions (DS, $p < .001$, Cohen's $d = 0.87$), and keeping density sparse (SS) produced the slowest overall responses. The color repetition effect, an index of PoP, failed to show priming of RTs when the current (trial n) display was dense (DD and SD, $ps > 0.9$), yet it drove powerful PoP boosts after transitions to sparse displays (DS and SS, $ps < 0.001$).

A follow-up rmANOVA of the PoP effect itself (color-switch RT minus color-repeat RT) confirmed that current (trial n) sparse displays gave rise to significantly stronger PoP compared to dense displays ($F(1,17) = 38.29, p < .001, \eta_p^2 = 0.692$), whereas preceding display density failed to impact the current PoP effect ($F(1,17) = 0.11, p = .74, \eta_p^2 = 0.006$). No crossover interaction emerged ($F(1,17) = 0.10, p = .757, \eta_p^2 = 0.006$), and Bonferroni-adjusted comparisons showed that, regardless of whether the previous (encoded) display was dense or sparse, PoPs always dropped when the current (retrieved) display was dense. Together, these results point to a critical conclusion: retrieval-stage density governs RT performance and PoP effects, with dense arrays improving performance regardless of the encoding density, whereas sparse retrieval arrays yield strong repetition benefits but slower responses overall.¹

First-Saccade Proportion. Fig. 3b shows that repeating the target color significantly boosted the likelihood that the very first eye movement landed on the target ($F(1,17) = 100.88, p < .001, \eta_p^2 = 0.856$), and density transition significantly modulated the first-saccade proportion ($F(3,51) = 68.60, p < .001, \eta_p^2 = 0.801$). The interaction ($F(3,51) = 32.83, p < .001, \eta_p^2 = 0.659$) confirms that priming manifested only under specific density sequence conditions. Post-hoc contrasts revealed a clear pattern: when the current display was dense (DD and SD), participants directed their first saccade to the target far more often than when it was sparse (DS and SS, all $ps < 0.001$). Most interestingly, the color repetition effect, an indicator of PoP, was significantly positive when the current display was sparse (DS and SS, $ps < 0.001$) as well as for the dense-to-dense transition (DD, $p = .025$, Cohen's $d = 0.23$), but not for

¹ We additionally conducted a within-participant comparison of priming-of-pop-out (PoP) strength between the blocked and interleaved conditions. For each participant, display density (SS and DD), and dependent measure (RT and eye-movement metrics), we computed the difference in PoP between the blocked and interleaved conditions. These difference scores did not show a consistent modulation by display density (all $ps > 0.09$), indicating that increased block-wise predictability did not systematically enhance PoP beyond the effects attributable to retrieval-stage display density.

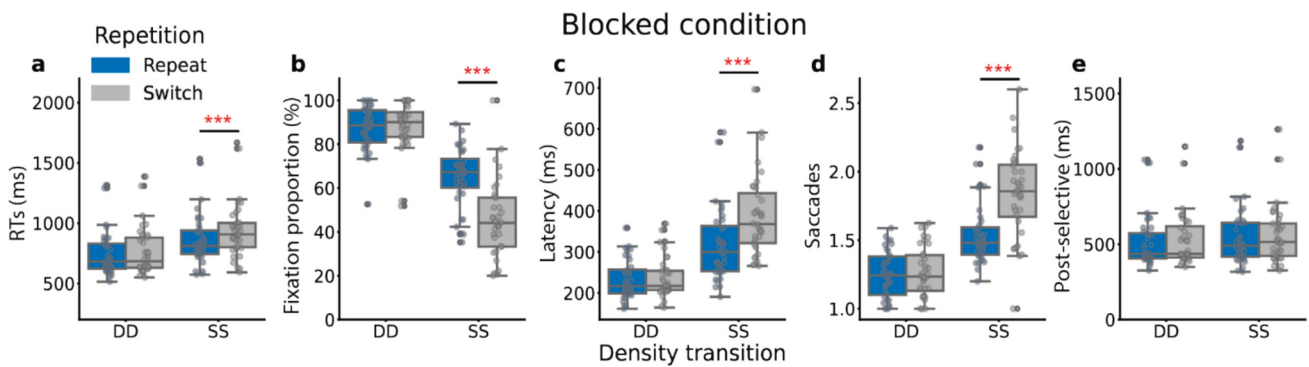


Fig. 2. Performance measures and PoP effects in the block condition across display density transitions

Note. (a) Reaction times (RTs) in ms, (b) proportion of first saccade landing on the target, (c) first fixation latency, (d) number of saccades before landing on the target, and (e) post-selective stage time (RT – first fixation latency). * $p < .05$, $p < .01$, * $p < .001$.

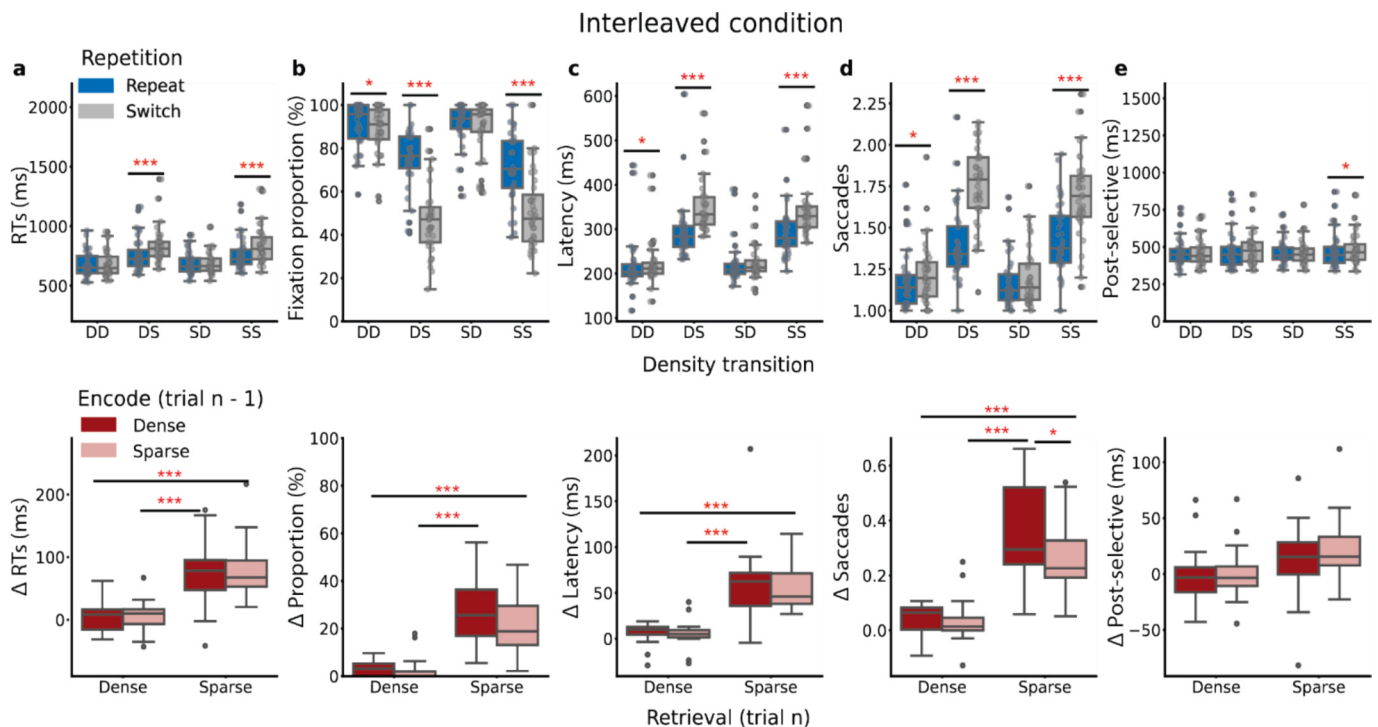


Fig. 3. Performance measures and PoP effects in the interleaved condition across display density transitions (DD, DS, SD, SS) and color repetition (Repeat vs. Switch)

Note. The upper panel depicts mean values for different measures, whereas the lower panel displays the PoP effect, calculated as the performance difference between switch and repeat trials, separated by encoding density (trial $n-1$) and retrieval density (trial n). Column-wise: (a) reaction times (RTs), (b) proportion of first saccade landing on the target, (c) first fixation latency, (d) number of saccades before landing on the target, and (e) post-selective stage (RT – first fixation latency). * $p < .05$, $p < .01$, * $p < .001$.

the sparse-to-dense transition (SD, $p > .99$).

A follow-up rmANOVA zeroed in on the locus of this effect: retrieval-stage density governed first-saccade accuracy (current density: $F(1,17) = 68.17$, $p < .001$, $\eta_p^2 = 0.800$), whereas encoding density left no imprint (previous density: $F(1,17) = 2.54$, $p = .129$, $\eta_p^2 = 0.130$). No interaction emerged ($F(1,17) = 1.30$, $p = .269$, $\eta_p^2 = 0.071$). Bonferroni-adjusted comparisons confirmed that, regardless of the previous density, the first saccade landed significantly more often on the target when the current display was dense ($ps < 0.001$).

First fixation latency. Fixation latency echoed the patterns seen in RTs and first-saccade proportions: repeating the target color reduced the first fixation latency ($F(1,17) = 68.98$, $p < .001$, $\eta_p^2 = 0.795$), and density switches drove robust shifts in latency ($F(3,51) = 121.32$, $p < .001$, $\eta_p^2 = 0.877$). Their interaction ($F(3,51) = 26.70$, $p < .001$, $\eta_p^2 = 0.611$) confirmed that PoP hinged on the density sequence (Fig. 3c). Post-hoc

tests revealed a similar story: when the current display was sparse (DS or SS), color switches triggered markedly slower fixations (DS: $t(17) = 5.90$, $p < .001$, Cohen's $d = 0.90$; SS: $t(17) = 8.81$, $p < .001$, Cohen's $d = 0.89$). Yet, priming stalled completely when a sparse display flipped to dense (SD: $t(17) = 1.53$, $p = .57$, Cohen's $d = 0.12$) and when density remained dense (DD: $t(17) = 2.11$, $p = .20$, Cohen's $d = 0.10$).

A further rmANOVA of PoP-driven latency gains isolated the driving force: retrieval-stage density speeded fixations ($F(1,17) = 45.63$, $p < .001$, $\eta_p^2 = 0.729$), while encoding density left no mark ($F(1,17) = 0.23$, $p = .637$, $\eta_p^2 = 0.013$). No interaction emerged ($F(1,17) = 0.23$, $p = .636$, $\eta_p^2 = 0.013$). Bonferroni-adjusted contrasts showed that, regardless of encoding density, dense retrieval arrays shortened first-fixation times compared to sparse ones (both $ps < 0.001$).

Number of saccades. The number of saccades required to reach the target reflected a similar pattern to the RTs and first-saccade proportions

(Fig. 3d). Color repetition significantly reduced the required saccades, $F(1,17) = 101.51, p < .001, \eta_p^2 = 0.857$, and display density transition drove changes in eye-movement efficiency, $F(3,51) = 78.32, p < .001, \eta_p^2 = 0.821$. Critically, the interaction was significant, $F(3,51) = 37.37, p < .001, \eta_p^2 = 0.687$, confirming that the benefit of repeating the target color depended on the density transition. Post-hoc contrasts revealed the repetition benefit (PoP) – i.e., fewer saccades on repeated trials – to be robust in current (trial n) sparse displays (DS: $t(17) = 8.30, p < .001$, Cohen's $d = 1.61$; SS: $t(17) = 9.05, p < .001$, Cohen's $d = 1.13$). In current dense displays, PoP was largely attenuated: no reliable effect emerged following sparse-to-dense transitions (SD: $t(17) = 1.62, p = .49$, Cohen's $d = 0.19$), whereas a modest but statistically significant repetition benefit was observed when density remained dense (DD: $t(17) = 3.11, p = .025$, Cohen's $d = 0.23$). A follow-up rmANOVA of saccades confirmed that retrieval density yields significant influence ($F(1,17) = 67.25, p < .001, \eta_p^2 = 0.570$), with encoding density playing only a small role ($F(1,17) = 6.14, p = .024, \eta_p^2 = 0.265$) and no interaction ($F(1,17) = 2.79, p = .11, \eta_p^2 = 0.141$). Regardless of prior density, dense retrieval arrays consistently reduced saccade count: participants needed far fewer eye movements to find the target when the current display was dense (p s < 0.001). These results indicate that retrieval-stage density has a stronger influence on saccadic efficiency, with sparse retrieval conditions leading to the highest saccade counts of PoP effects.

Post-selective Decision Time. At the decision stage, color repetition engendered only a slight speed-up ($F(1,17) = 5.17, p = .036, \eta_p^2 = 0.233$), while density transition left RTs largely unaffected ($F(3,51) = 3.21, p = .075, \eta_p^2 = 0.159$) and failed to interact with priming ($F(3,51) = 2.02, p = .134, \eta_p^2 = 0.106$). These results indicate that post-selective decision processes are rather insensitive to display density and contribute minimally to PoP.

Spatial Patterns of First Fixations. In the interleaved condition (Fig. 4b), fixation patterns revealed a notable interaction between display density and color repetition. In sparse displays, initial fixations (i.e., the first fixation made after display onset, regardless of target location) were more tightly clustered around the target on repeat trials than on switch trials, suggesting a stronger PoP effect when guidance was otherwise weak. In contrast, in dense displays, initial fixations were consistently target-centered across both repeat and switch trials, indicating uniformly strong attentional guidance regardless of color repetition.

4. Discussion

The present study investigated whether the influence of display density on PoP operates during the encoding stage (trial $n-1$), the retrieval stage (trial n), or both. Additionally, we examined how these effects unfold across early attentional orienting versus late decision stages. By holding density constant in ‘blocked’ trial blocks and shuffling it in ‘interleaved’ blocks, the design teased apart the encoding–/retrieval-stage contributions to PoP.

Consistent with prior work, sparse displays yielded significant priming: participants' eyes landed on repeated-color targets faster and with fewer saccades (Becker et al., 2023; Becker & Ansorge, 2013), and manual responses accelerated (Rangelov et al., 2013). Dense arrays, by contrast, as seen in Rangelov et al. (2013) and Becker (2008), reduced PoP effects, especially during the pre-selective stage. Dense displays would have engendered strong isofeature suppression (Field et al., 1993; Li, 1999), allowing salient targets to pop out automatically and attenuate the benefit of search history. Consistent with this, the heatmaps depicted in Fig. 4 reveal a clear pattern: In sparse displays, participants' attention was attracted more toward non-targets, especially on color-switch trials; in contrast, this ‘distraction’ was eliminated in dense displays, which enabled the target to stand out more prominently. This pattern indicates that these dynamics are reshaped by context. Weak bottom-up saliency under sparse conditions forces the system to lean on active encoding of target features, thus bringing feature-priming

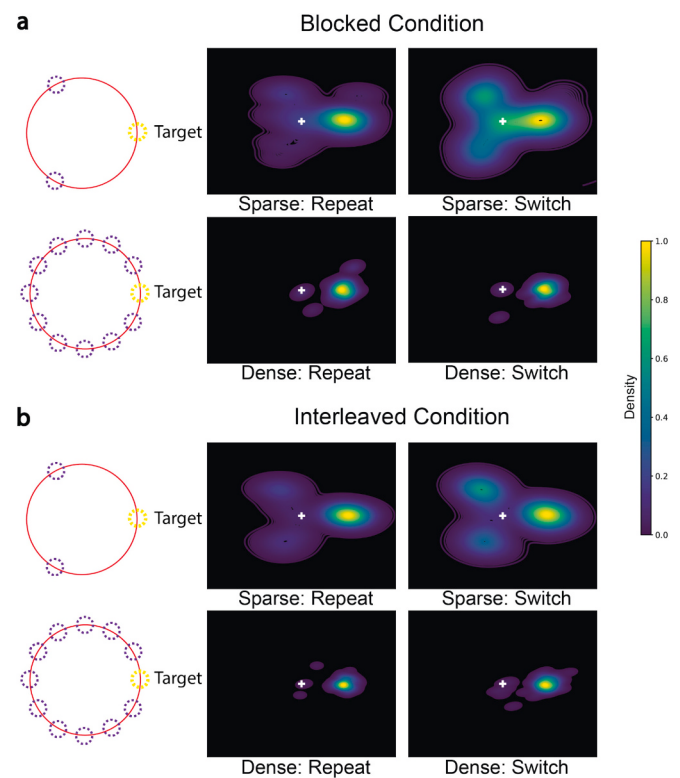


Fig. 4. Heatmaps of Initial Fixation Landing Locations

Note. To standardize target positions across trials, fixation coordinates were rotated to a fixed reference point (left panel). The left-panel sketches show item positions for sparse and dense displays, with yellow-highlighted targets aligning with the high-density warmest regions in the heatmaps on the right. The heatmaps illustrate the kernel density estimates of initial-fixation landing locations for two main conditions: blocked (a) and interleaved (b), with warmer colors representing higher densities. Each heatmap further categorizes data into four conditions, combining two factors: sparse vs. dense displays and repeated vs. switched target color. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

mechanisms to the fore (Kristjánsson et al., 2005; Kristjánsson & Campana, 2010b; Maljkovic & Nakayama, 1994).

Specifically, in blocked trial blocks with dense displays, PoP all but vanished: saliency-driven selection overpowered the effect of any encoded template at retrieval. Of note, however, the absence of statistically significant PoP effects under dense conditions does not necessarily imply the absence of priming, as strong salience-driven guidance may lead to near-ceiling performance, curtailing the room for additional repetition-related benefits to become manifest in reaction-time and oculomotor measures. If so, the small numerically positive (though non-significant) PoP effects evident in RTs under dense conditions may simply reflect insufficient statistical power to detect small effects. In interleaved blocks, however, signatures of encoding emerged even when trial $n-1$ was dense, with significant PoP in both DD and DS sequences across eye-movement metrics (see left panel of Fig. 3b-d). Analyses confirmed that retrieval-stage density dictates the magnitude of PoP, while encoding density exerts no reliable effect. These findings suggest that PoP involves a flexible mechanism which adopts the least effortful strategy given the demands posed by the visual context. When salience is weak in sparse displays, attention becomes more reliant on stored feature templates for guidance; when inter-item separation decreases in dense displays, attention defaults to an automatic, bottom-up salience-driven mode of operation (Wolfe, 2020). In interleaved settings, observers appear to monitor current density and deploy the least effortful strategy suited to the visual context (Irons & Leber, 2018; Zhang & Leber, 2024), relying on search history when bottom-up saliency is

weak, as in sparse displays, and shifting to saliency-driven selection when dense displays afford strong bottom-up guidance.

Eimer et al. (2010) similarly demonstrated that repeating target features facilitates attentional allocation during the early processing stage. This was indexed by the N2pc component – a lateralized negative deflection in the event-related potential (ERP) occurring about 200 ms after stimulus onset over posterior electrodes contralateral to the attended item. The N2pc is widely regarded as a neural marker of attentional selection, reflecting the focusing of visual-spatial attention onto a candidate target and the suppression of competing distractors. Eimer et al. showed that when the target color repeated across trials, N2pc onset occurred earlier, signifying expedited perceptual-attentional selection. Our findings dovetail with this electrophysiological evidence: feature-biasing mechanisms operate primarily during the pre-selective stage to accelerate target detection, as shown by shortened initial-saccade latencies. In the interleaved block, participants appear to have adopted a unified attentional strategy – one that encoded feature history equally in sparse and dense trials, as shortened latencies were independent of the prior (trial $n-1$) density. Becker et al. (2023) similarly found that early selection was shaped by trial history, reporting that when the target color repeated, display density no longer influenced how quickly the target was localized. Unlike Becker et al., though, we did not pre-cue the target color, making attentional allocation more sensitive to local feature contrast, which is impacted by display density.

Becker et al. (2023) laid out two distinct ways in which local features might influence PoP, beyond simple, early orienting. Their non-target biasing hypothesis assumes that display density does not directly enhance target pop-out; instead, it improves performance only when attention is misdirected to nontargets, which then need to be rejected. In this account, higher density facilitates nontarget grouping, making such rejection more efficient. Consistent with this view, Becker et al. (2023) reported no set-size effect (search performance changes as the number of items in the display varies) on the proportion of first fixations landing on the target when its color was either repeated or pre-cued. Instead, the inverse set-size effect (i.e., increases in local feature contrast reducing search time) appeared in overall RTs, driven by shorter dwell times once the target had already been fixated. In contrast, their bottom-up view posits that high local feature contrast enhances target-distractor discriminability, leading to inter-trial priming that can only occur in sparse displays.

Our findings diverge from their non-target biasing account. We observed evidence of a set-size effect on the proportion of first fixations directed to the target even in color-repeat trials (see Appendix), suggesting that density influenced early attentional guidance rather than only later identification. Notably, we did not observe a comparable effect on target dwell times. Our findings align with Eimer et al. (2010), who found that N2pc modulations tied to PoP did not extend into decision-related ERPs. ERPs are electroencephalographic signals that are time-locked to specific sensory or cognitive events. Thus, by providing a ‘running commentary’ on how the brain processes information over time, they permit early perceptual-attentional stages to be separated from later decision-related stages.

Furthermore, the absence of post-selective priming in the present study also runs counter to the non-target biasing account. Note, though, that without a pre-cueing (target knowledge) condition in our study (in contrast to Becker et al., 2023), the extent to which explicit foreknowledge might sustain feature-contrast effects into post-selective phases remains untested. Nonetheless, the pronounced PoP observed in early oculomotor and reaction-time measures underscores that feature history shapes search primarily by steering initial attentional allocation, with minimal carryover into subsequent decision and response stages.

The observation that PoP accelerates pre-selective orienting while leaving post-selective decision processes largely unaffected aligns with neurophysiological evidence for a specific cortical circuit underlying priming. Beyond ERP markers of early selection (Eimer et al., 2010),

invasive recordings show that this history-dependent bias emerges from synchronized activity between the Frontal Eye Field (FEF) and mid-level visual cortex (area V4). The FEF serves as a priority map where target-distractor discrimination unfolds earlier and more robustly on repeat trials (Bichot & Schall, 2002), directly predicting the shortened saccadic latencies we observed. Crucially, this modulation is confined to areas governing salience representation and orienting: the Supplementary Eye Field (SEF), which monitors performance and post-decision outcomes, shows no such repetition enhancement, mirroring our finding that post-selective decision times remain invariant.

Lesion studies further support this ‘pre-selective’ neural locus, showing that intact V4 is necessary for PoP (Walsh et al., 2000), while recent laminar analyses identify V4’s extragranular layers as the generator of the N2pc component (Herrera et al., 2022; Westerberg et al., 2021, 2022). This connects the cortical microcircuitry of feature enhancement directly to scalp-recorded ERP markers of attentional capture. Furthermore, the robust PoP we observed in sparse retrieval contexts likely stems from ‘attentional templates’ active before the search array appears. Westerberg and Schall (2021) revealed that PoP-related neural differences emerge in the pre-stimulus epoch, suggesting the brain proactively tunes feature-selective neuron populations in anticipation of the target. In our study, this preparatory tuning effectively guided attention when competition was low (sparse displays) but was largely overridden by the potent, automatic bottom-up salience signals generated by isofeature suppression in dense arrays. Thus, neurophysiology frames PoP as a proactive, top-down gain control mechanism that fine-tunes the early visual salience map (FEF/V4) prior to selection, rather than facilitating the post-perceptual decision stage.

Meanwhile, the gaze patterns in sparse displays tell an interesting story: as revealed by the heatmaps in Fig. 4, the eye movements scattered across distractors before eventually homing in on the target in sparse displays. Only about 70% of fixations landed on the target, often after multiple saccades, regardless of whether the target color was repeated or switched (Fig. 2b and d). In dense array, by contrast, attention was allocated to the target almost instantly, with over 95% of first fixations landing on the searched-for item; witness the tight clusters of early fixations around the target in dense, but not sparse, displays in Fig. 4. These patterns echo Rangelov et al. (2017), who reported perfect first-fixation selection in dense displays versus lower rates in sparse ones. Crucially, color repetition in our sparse trials lifted initial-fixation rates by roughly 20% – a clear testament to intertrial priming bolstering guidance when bottom-up salience is lacking.

The novelty of our study lies in the *interleaved*-density design, offering a unique window into how the encoding (trial $n-1$) and retrieval (trial n) stages separately shape PoP. Encoding succeeded equally in both dense and sparse displays – that is, observers reliably stored the target’s color regardless of display density. Retrieval, however, revealed a different story. When the current (trial n) array remained sparse, stored features sprang into action: repeated colors drove robust PoP across pre-selection markers, compensating for weak bottom-up salience (Kristjánsson & Campana, 2010b). In dense retrieval arrays, strong isofeature suppression (Field et al., 1993; Li, 1999) dominated, leaving limited room for additional behavioral benefits from encoded templates to be expressed behaviorally. Stage-specific analyses drove this point home. In the pre-attentive phase, sparse retrieval preserved encoded guidance, whereas dense retrieval shifted control to saliency-driven control, minimizing attentional competition. Once the eyes landed on the target, in the post-selective phase, encoded features lost their sway: both sparse and dense retrieval conditions produced nearly identical decision-time profiles, in line with Eimer et al.’s (2010) observation that PoP effects rarely extend into the confirmation and response stages. Together, these results pinpoint retrieval context to play a critical role in shaping whether PoP effects are behaviorally expressed.

Against this background, the present findings help clarify how display density modulates PoP. In particular, they allow us to distinguish between the competing accounts proposed in the Introduction. PoP

effects did not reliably depend on the density of the preceding encoding display, nor did they follow the interaction pattern predicted by the interaction-dominance account. Instead, across reaction time and oculomotor measures, PoP effects were consistently determined by the density of the current retrieval display. This pattern provides converging evidence in favor of the retrieval-stage dominance account, according to which retrieval context governs whether encoded feature information is behaviorally expressed. It is worth noting that the present design was not optimized to track gradual changes in search efficiency across blocks. Future studies that explicitly examine how PoP evolves as observers become more or less efficient at target selection may provide further insight into whether block-wise learning modulates PoP effects, particularly in dense displays.

Participants in the interleaved blocks defaulted to a sparse-oriented encoding strategy – storing the target's color on every trial ($n-1$), regardless of display density. This strategy may reflect an adaptation to the variability in display types, ensuring robust performance across trials (Theeuwes, 2018) – specifically, in situations with unpredictable density shifts. Retrieval context, however, proved to be the true arbiter of priming: when observers encountered a sparse array, their encoded template sprang into action, driving robust PoP (Maljkovic & Nakayama, 1996). In dense retrieval displays, by contrast, rapid saliency-driven guidance (Field et al., 1993; Li, 1999) overrode any benefit from prior encoding. In essence, successful encoding doesn't guarantee priming; only a retrieval environment that lacks overpowering saliency endows stored features with the power to guide search.

Future research could map how encoding heuristics shift as the balance of sparse versus dense trials changes. Manipulating the distribution of sparse and dense trials could provide critical insights into this adaptive process. For example, an 80% sparse/20% dense protocol may amplify top-down feature encoding, while a 20% sparse/80% dense regime may tip the scales toward automatic, saliency-based search. Systematically varying these proportions could help clarify how encoding strategies shift to optimize performance under different task environments.

Also, one potential limitation of the present design is that, on switch trials, the target and distractor colors were fully exchanged across consecutive trials, with the previous distractor color always becoming the target color and vice versa. As a result, the observed pre-selective PoP effects may reflect a combination of enhanced processing of repeated target features and residual suppression of previously ignored distractor features (i.e., negative priming). The current design therefore does not allow us to fully disentangle whether early attentional biases

primarily arise from target facilitation, distractor inhibition, or their joint contribution (see Lamy et al., 2008; Lamy & Kristjánsson, 2013). Future work could address this issue by introducing neutral colors or partial feature changes, thereby isolating target- and distractor-specific influences on pre-selective attentional guidance.

5. Conclusion

The present study, which combined eye-movement metrics with manual reaction times, confirmed that PoP thrives in sparsely populated displays yet falters amid dense clutter. Crucially, encoding consistently transfers critical target features into visual working memory regardless of display density. Retrieval context, however, emerges as the true gatekeeper: sparse retrieval arrays unleash the stored templates to facilitate search, whereas dense retrieval arrays let bottom-up saliency control search, thereby reducing the observable impact of encoded biases on performance. By disentangling the contributions of encoding and retrieval, these findings sharpen our understanding of PoP, revealing retrieval-stage density as the pivotal factor that determines whether search history enhances or yields to saliency-driven guidance. This stage-specific process illustrates how attentional strategies dynamically recalibrate to match the demands of ever-changing display properties.

CRedit authorship contribution statement

Hongmei Xia: Writing – original draft, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Fredrik Allenmark:** Writing – review & editing, Validation, Software, Methodology, Formal analysis, Conceptualization. **Hermann J. Müller:** Writing – review & editing, Validation, Supervision, Project administration, Funding acquisition, Conceptualization. **Zhuanghua Shi:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization.

Funding

This study was supported by the German Science Foundation (DFG) research grant MU773/16-2, awarded to HJM and ZS.

Declaration of competing interest

The authors declare no conflicts of interest.

Appendix A. Set-size effects

In Becker et al. (2023), set-size analysis and the inverse set-size effect were crucial tools for evaluating and distinguishing between competing theoretical accounts of visual search, namely the bottom-up view, top-down view, and the non-target biasing hypothesis. The set-size effect refers to how visual search performance (i.e., reaction time) changes as the number of items in the display (the 'set size') varies. According to isofeature suppression (Field et al., 1993; Zhaoqing, 2005), increasing local feature contrast (e.g., achieved by increasing set size) benefit search, leading to faster search in dense displays compared to sparse displays. This effect is termed as inverse set-size effect. On this ground, we provide further set-size analysis here. It should be noted, in our study, we only had two levels of set size (sparse vs. dense).

A.1. Data preprocessing

We examined set-size effects separately for color-repeat and color-switch trials. To do so, we ran one-way ANOVAs with Density Transition Type (DD, DS, SD, SS) as the factor, analyzing reaction times (RTs) and eye-movement measures within each color condition. Importantly, given that we only had two levels, set size was not treated as a direct independent variable; instead, its influence was assessed indirectly by testing how different density transitions—such as switching from sparse to dense displays—affected performance. This approach also allowed us to evaluate whether the set-size effect depended on the encoding density of the previous trial (trial $n-1$).

A.2. Blocked condition

Reaction times (RTs). A one-way ANOVA with density transition (SS vs. DD) as the factor was conducted separately for color-repeat and color-switch trials. For color-repeat trials, results revealed marginally faster responses in dense displays, $F(1,34) = 3.21$, $p = .082$, with an average 120 ms advantage for dense over sparse displays. For color-switch trials, the effect was significant, $F(1,34) = 6.01$, $p = .020$, with responses 176 ms faster in dense displays. This pattern represents an *inverse set-size effect*—that is, performance improved when more items were present in the display (dense) compared to fewer items (sparse), opposite to the classic set-size effect, where larger set sizes usually slow responses.

First-fixation proportion. A robust inverse set-size effect was observed in color-repeat trials, $F(1,34) = 37.27$, $p < .001$, with 22% more first fixations directed to the target in dense displays compared to sparse displays. The effect was even stronger in color-switch trials, $F(1,34) = 81.89$, $p < .001$, with a 43% advantage for dense displays. These results clearly show that even in color-repeat trials, display density reliably modulated early attentional guidance, increasing the likelihood that the very first fixation landed on the target.

First-fixation latency. A significant inverse set-size effect was found for color-repeat trials, $F(1,34) = 12.87$, $p = .001$, with targets fixated 85 ms faster in dense compared to sparse displays. In color-switch trials, the effect was stronger, $F(1,34) = 36.80$, $p < .001$, with a 152 ms advantage for dense displays. Thus, even when the target color repeated, dense displays facilitated faster initial allocation of attention.

Number of saccades. A significant inverse set-size effect was observed in color-repeat trials, $F(1,34) = 21.63$, $p < .001$, with 0.31 fewer saccades required before target fixation in dense compared to sparse displays. A similar effect emerged in color-switch trials, $F(1,70) = 86.45$, $p < .001$, with 0.63 fewer saccades in dense displays. This indicates that dense displays supported more efficient attentional guidance regardless of color condition.

Post-selective decision time. No significant set-size effects were observed in either color-repeat or color-switch trials ($p \geq .55$), indicating that density did not influence post-fixation decision processes.

A.3. Interleaved condition

Reaction times (RTs). A one-way ANOVA with Density Transition (SS, SD, DS, DD) as the factor was again conducted separately for color-repeat and color-switch trials. For color-repeat trials, the effect was marginally significant, $F(3,68) = 2.60$, $p = .059$, with DD responses 85–86 ms faster than DS and SS ($ps = 0.018$). For color-switch trials, the effect was highly significant, $F(3,68) = 7.96$, $p < .001$: responses were 154–158 ms faster in DD than DS and SS, and 142–156 ms faster in SD than DS and SS ($ps < 0.001$). Thus, dense retrieval displays consistently yielded faster detection, particularly under color switches.

First-fixation proportion. Significant inverse set-size effects were found for color-repeat trials, $F(3,68) = 12.32$, $p < .001$, and color-switch trials, $F(3,68) = 45.68$, $p < .001$. In repeat trials, DD transitions produced 16–19% higher proportions of first fixations to the target than DS and SS ($ps < 0.001$), while SD also exceeded DS and SS by 16–19%. In switch trials, DD outperformed DS and SS by 38–41%, and SD by 39–42% ($ps < 0.001$). Thus, even in color-repeat trials, dense displays enhanced early attentional guidance, with DD transitions producing the strongest bias toward the target.

First-fixation latency. Inverse set-size effects were observed for color-repeat trials, $F(3,68) = 10.21$, $p < .001$, and color-switch trials, $F(3,68) = 27.04$, $p < .001$. In repeat trials, latencies in DD were 76–77 ms faster than in DS and SS, while in switch trials DD was 127–132 ms faster. SD transitions also improved latencies relative to DS and SS in both conditions ($ps < 0.001$). These results mirror the fixation-proportion findings: dense displays accelerated the very first fixation on the target, including under color-repeat conditions.

Number of saccades. A significant inverse set-size effect was observed in color-repeat trials, $F(3,68) = 9.21$, $p < .001$, and in color-switch trials, $F(3,68) = 35.61$, $p < .001$. In repeat trials, participants made 0.23–0.25 fewer saccades in DD and 0.24–0.26 fewer in SD compared to DS and SS. In switch trials, the effect was stronger: 0.47–0.50 fewer saccades in DD, and 0.49–0.56 fewer in SD ($ps < 0.001$). Dense displays thus promoted more efficient search paths across both trial types.

Post-selective decision time. No significant set-size effects were found in either color-repeat or color-switch trials ($p \geq .82$), suggesting that density did not influence post-fixation decision proc.

Across both blocked and interleaved conditions, dense displays consistently facilitated visual search, as reflected in faster reaction times, higher proportions of first fixations to the target, shorter latencies for initial fixation, and fewer saccades before target acquisition. These advantages were evident in both color-repeat and color-switch trials, though they were typically stronger under switches. By contrast, post-selective decision times remained unaffected, suggesting that display density primarily influenced early guidance and search efficiency rather than later decision-making.

Appendix B. Exploratory analyses of block-wise changes in search efficiency and priming of pop-out

To examine whether participants' search behavior and priming of pop-out (PoP) changed across blocks, we conducted a set of exploratory analyses focusing on the blocked condition and the first three blocks of the experiment, where learning-related changes in search efficiency are most likely to occur. These analyses were restricted to participants who completed dense displays first, and to dense-display trials only (as suggested by an anonymous reviewer).

B.1. Block-wise changes in search efficiency

Search efficiency was assessed using multiple dependent measures, including reaction time (RT), first-fixation latency, number of saccades, and the probability that the first fixation landed on the target. For each measure, we fitted linear mixed-effects models with block number (Blocks 1–3, treated as a continuous predictor) as a fixed effect and random intercepts for participants. These analyses revealed a consistent improvement in search efficiency across blocks. Reaction times decreased significantly with increasing block number ($\beta = -15$ ms per block, $p = .040$). A similar pattern was observed in eye-movement measures: first-fixation latency decreased across blocks ($p = .021$), the number of saccades was reduced ($p = .008$), and the probability that the first fixation landed on the target increased ($p = .001$). Together, these results indicate that participants were less efficient at locating the target early on in the task and became progressively more efficient with experience in dense displays.

B.2. Block-wise changes in priming of pop-out

Next, we examined whether PoP varied as a function of block. PoP was computed separately for each participant and block as the difference between switch and repeat trials (or the reverse difference for proportion measures), yielding one PoP estimate per participant and block. Because this resulted in a single PoP value per participant per block, block-wise changes in PoP were assessed using repeated-measures analyses of variance (rmANOVAs) with block as a within-subject factor.

Across all dependent measures (RT, first-fixation latency, number of saccades, first-fixation proportion, and post-selection measures), PoP did not show a statistically reliable modulation by block (all $ps \geq 0.16$). Inspection of the descriptive data suggested some numerical variability in PoP across blocks, but no consistent or monotonic block-wise pattern.

To address the possibility that block-wise changes in absolute PoP may be constrained by overall improvements in task performance, we additionally computed relativized PoP measures. For each participant and block, PoP was expressed as a proportion of the corresponding absolute performance level in that block (e.g., PoP divided by mean RT, first-fixation latency, saccade count, or first-fixation proportion). These relativized PoP values were then entered into repeated-measures analyses of variance with block as a within-subject factor. Across all dependent measures, relativized PoP did not show a statistically reliable modulation by block (all $ps \geq 0.18$). Notably, relativization further reduced any impression of an early-block advantage, indicating that numerical block-wise differences are unlikely to reflect systematic changes in priming strength.

In sum, these exploratory analyses demonstrate that search efficiency in dense displays improves reliably across early blocks of the experiment, while PoP does not show a significant or consistent block-wise modulation. Because the experiment was not designed to specifically track learning-related changes across blocks, these findings should be interpreted cautiously. Future studies explicitly designed to examine learning trajectories will be necessary to more directly assess how changes in search efficiency modulate priming of pop-out, particularly under conditions of high display density.

Appendix C. Tables performance and pop effects across density transitions

To complement the inferential analyses reported in the **Results**, we provide full descriptive statistics for performance in both the blocked and interleaved conditions. [Table 1](#) presents the raw performance measures, separately for repeated and switched target-defining features. Measures include error rate, reaction times (RTs), first-fixation proportion, first-fixation latency, number of saccades before target fixation, and post-selective stage duration. Results are broken down by density transitions (*Sparse-to-Sparse [SS]*, *Sparse-to-Dense [SD]*, *Dense-to-Sparse [DS]*, *Dense-to-Dense [DD]*). In the blocked condition, only SS and DD transitions are possible, whereas the interleaved condition includes all four transitions.

Building on these values, [Table 2](#) reports the corresponding priming of pop-out (PoP) effects, calculated as the difference between repeat and switch trials. Positive values indicate stronger benefits of repetition (i.e., performance advantages in repeated trials), whereas negative values suggest reduced or reversed effects. This provides a more direct view of how trial history modulated performance across density transitions.

Table 1

Descriptive performance measures across density transitions in blocked and interleaved conditions.

Performance is reported separately for trials with repeated and switched target-defining features. Measures include error rate (%), reaction times (ms), proportion of first fixations on the target (%), first-fixation latency (ms), number of saccades before target fixation, and post-selective stage duration (ms). Values are mean $\pm$ SD.

Measure Metrics	Density Transition	Blocked Condition		Interleaved Condition	
		Repeat	Switch	Repeat	Switch
Error rate (%)	SS	1.57 $\pm$ 2.18	2.49 $\pm$ 3.15	0.98 $\pm$ 0.99	1.89 $\pm$ 1.65
	SD	/	/	0.45 $\pm$ 0.63	0.92 $\pm$ 1.12
	DS	/	/	1.32 $\pm$ 1.5	2.11 $\pm$ 2.18
	DD	0.58 $\pm$ 0.74	0.87 $\pm$ 1.24	0.41 $\pm$ 0.52	1.29 $\pm$ 1.0
RTs (ms)	SS	865.61 $\pm$ 36.25	939.34 $\pm$ 38.45	762.48 $\pm$ 22.37	840.92 $\pm$ 26.27
	SD	/	/	689.26 $\pm$ 16.57	695.25 $\pm$ 17.37
	DS	/	/	762.96 $\pm$ 23.68	836.76 $\pm$ 25.08
	DD	745.6 $\pm$ 30.61	763.56 $\pm$ 33.1	677.29 $\pm$ 17.72	682.69 $\pm$ 17.53
Proportion (%)	SS	65.22 $\pm$ 2.25	45.71 $\pm$ 2.94	72.04 $\pm$ 2.68	50.37 $\pm$ 2.89
	SD	/	/	91.17 $\pm$ 1.72	89.38 $\pm$ 2.17
	DS	/	/	75.16 $\pm$ 2.38	47.93 $\pm$ 2.92
	DD	87.19 $\pm$ 1.68	88.37 $\pm$ 1.83	91.21 $\pm$ 1.73	88.6 $\pm$ 1.88
Latency (ms)	SS	317.77 $\pm$ 14.84	390.54 $\pm$ 16.28	306.11 $\pm$ 14.64	360.48 $\pm$ 15.75
	SD	/	/	230.63 $\pm$ 11.6	226.87 $\pm$ 7.54
	DS	/	/	296.07 $\pm$ 11.66	371.94 $\pm$ 20.46
	DD	260.51 $\pm$ 28.17	238.06 $\pm$ 8.24	222.18 $\pm$ 13.36	235.64 $\pm$ 17.69
Saccades	SS	1.53 $\pm$ 0.04	1.85 $\pm$ 0.05	1.45 $\pm$ 0.04	1.7 $\pm$ 0.04
	SD	/	/	1.17 $\pm$ 0.03	1.21 $\pm$ 0.03
	DS	/	/	1.4 $\pm$ 0.04	1.77 $\pm$ 0.05
	DD	1.31 $\pm$ 0.07	1.27 $\pm$ 0.03	1.18 $\pm$ 0.03	1.24 $\pm$ 0.04
Post-selective (ms)	SS	549.82 $\pm$ 33.22	560.56 $\pm$ 32.04	470.53 $\pm$ 19.37	469.03 $\pm$ 16.52
	SD	/	/	468.38 $\pm$ 14.71	469.03 $\pm$ 16.51
	DS	/	/	471.62 $\pm$ 20.88	482.79 $\pm$ 18.05
	DD	513.17 $\pm$ 27.75	529.82 $\pm$ 29.78	462.94 $\pm$ 16.18	461.13 $\pm$ 15.4

Table 2
Priming of Pop-Out (PoP) Effects Across Density Transitions.

Table 2 reports the PoP effects, calculated as the performance difference between repeated and switched target-defining features. Positive values indicate stronger benefits of repetition, while negative values indicate reduced or reversed effects. Measures match those in Table 1 for consistency: error rate (%), reaction times (RTs, ms), proportion of first saccade on the target (%), first-fixation latency (ms), number of saccades before target fixation, and post-selective stage duration (ms).

Measure Metrics	Blocked Condition		Interleaved Condition			
	SS	DD	SS	SD	DS	DD
Error rate (%)	0.92 ± 1.82	0.28 ± 1.28	0.91 ± 1.65	0.47 ± 1.02	0.79 ± 2.21	0.88 ± 0.91
RTs (ms)	73.73 ± 15.27	17.96 ± 9.22	78.44 ± 11.38	5.99 ± 6.12	73.8 ± 12.07	5.4 ± 5.86
Proportion (%)	19.51 ± 4.25	-1.18 ± 1.11	21.67 ± 2.78	1.79 ± 1.46	27.22 ± 3.41	2.61 ± 1.05
Latency (ms)	72.77 ± 9.95	-22.45 ± 27.23	54.36 ± 6.46	-3.76 ± 11.71	75.88 ± 14.7	13.46 ± 4.79
Saccades	0.31 ± 0.05	-0.05 ± 0.07	0.25 ± 0.03	0.03 ± 0.02	0.36 ± 0.04	0.05 ± 0.02
Post-selective (ms)	10.74 ± 12.71	16.65 ± 8.11	20.53 ± 7.23	0.65 ± 5.85	11.17 ± 8.35	-1.82 ± 6.75

Data availability

Data will be made available on request.

References

Allenmark, F., Gokce, A., Geyer, T., Zinchenko, A., Müller, H. J., & Shi, Z. (2021). Inter-trial effects in priming of pop-out: Comparison of computational updating models. *PLoS Computational Biology*, 17(9), Article e1009332. <https://doi.org/10.1371/journal.pcbi.1009332>

Awh, E., Belopolsky, A. V., & Theeuwes, J. (2012). Top-down versus bottom-up attentional control: A failed theoretical dichotomy. *Trends in Cognitive Sciences*, 16(8), 437–443. <https://doi.org/10.1016/j.tics.2012.06.010>

Becker, S. I. (2008). The mechanism of priming: Episodic retrieval or priming of pop-out? *Acta Psychologica*, 127(2), 324–339. <https://doi.org/10.1016/j.actpsy.2007.07.005>

Becker, S. I., & Ansong, U. (2013). Higher set sizes in pop-out search displays do not eliminate priming or enhance target selection. *Vision Research*, 81, 18–28. <https://doi.org/10.1016/j.visres.2013.01.009>

Becker, S. I., Grubert, A., Horstmann, G., & Ansong, U. (2023). Which processes dominate visual search: Bottom-up feature contrast, top-down tuning or trial history? *Cognition*, 236, Article 105420. <https://doi.org/10.1016/j.cognition.2023.105420>

Bichot, N. P., & Schall, J. D. (2002). Priming in macaque frontal cortex during popout visual search: feature-based facilitation and location-based inhibition of return. *Journal of Neuroscience*, 22(11), 4675–4685.

Bundesen, C. (1990). A theory of visual attention. *Psychological Review*, 97(4), 523–547. <https://doi.org/10.1037/0033-295X.97.4.523>

Carlisle, N. B., & Kristjánsson, Á. (2018). How visual working memory contents influence priming of visual attention. *Psychological Research*, 82(5), 833–839. <https://doi.org/10.1007/s00426-017-0866-6>

Chun, M. M., & Nakayama, K. (2000). On the functional role of implicit visual memory for the adaptive deployment of attention across scenes. *Visual Cognition*, 7(1–3), 65–81. <https://doi.org/10.1080/135062800394685>

Duncan, J., & Humphreys, G. W. (1989). Visual search and stimulus similarity. *Psychological Review*, 96(3), 433–458. <https://doi.org/10.1037/0033-295X.96.3.433>

Eimer, M., Kiss, M., & Cheung, T. (2010). Priming of pop-out modulates attentional target selection in visual search: Behavioural and electrophysiological evidence. *Vision Research, Visual Search and Selective Attention*, 50(14), 1353–1361. <https://doi.org/10.1016/j.visres.2009.11.001>

Faul, F., Erdfelder, E., Lang, A.-G., & Buchner, A. (2007). G*power 3: A flexible statistical power analysis program for the social, behavioral, and biomedical sciences. *Behavior Research Methods*, 39(2), 175–191. <https://doi.org/10.3758/bf03193146>

Field, D. J., Hayes, A., & Hess, R. F. (1993). Contour integration by the human visual system: Evidence for a local “association field.”. *Vision Research*, 33(2), 173–193. [https://doi.org/10.1016/0042-6989\(93\)90156-Q](https://doi.org/10.1016/0042-6989(93)90156-Q)

Gokce, A., Müller, H. J., & Geyer, T. (2013). Positional priming of pop-out is nested in visuospatial context. *Journal of Vision*, 13(3), 32. <https://doi.org/10.1167/13.3.32>

Goolsby, B. A., & Suzuki, S. (2001). Understanding priming of color-singleton search: Roles of attention at encoding and “retrieval.”. *Perception & Psychophysics*, 63(6), 929–944. <https://doi.org/10.3758/BF03194513>

Gunseli, E., Meeter, M., & Olivers, C. N. L. (2014). Is a search template an ordinary working memory? Comparing electrophysiological markers of working memory maintenance for visual search and recognition. *Neuropsychologia*, 60, 29–38. <https://doi.org/10.1016/j.neuropsychologia.2014.05.012>

Herrera, B., Westerberg, J. A., Schall, M., Maier, A., Woodman, G. F., Schall, J. D., & Riera, J. J. (2022). Resolving the mesoscopic missing link: Biophysical modeling of EEG from cortical columns in primates. *NeuroImage*, 263, 119593.

Hillstrom, A. P. (2000). Repetition effects in visual search. *Perception & Psychophysics*, 62(4), 800–817. <https://doi.org/10.3758/BF03206924>

Hollingworth, A., Matsukura, M., & Luck, S. J. (2013). Visual working memory modulates rapid eye movements to simple onset targets. *Psychological Science*, 24(5), 790–796.

Huang, L., & Pashler, H. (2005). Attention capacity and task difficulty in visual search. *Cognition*, 94(3), B101–B111. <https://doi.org/10.1016/j.cognition.2004.06.006>

Irons, J. L., & Leber, A. B. (2018). Characterizing individual variation in the strategic use of attentional control. *Journal of Experimental Psychology. Human Perception and Performance*, 44(10), 1637–1654. <https://doi.org/10.1037/xhp0000560>

Itti, L., & Koch, C. (2001). Computational modelling of visual attention. *Nature Reviews Neuroscience*, 2(3), 194–203. <https://doi.org/10.1038/35058500>

Kristjánsson, Á., & Campana, G. (2010a). Where perception meets memory: A review of repetition priming in visual search tasks. *Attention, Perception, & Psychophysics*, 72(1), 5–18. <https://doi.org/10.3758/APP.72.1.5>

Kristjánsson, Á., & Campana, G. (2010b). Where perception meets memory: A review of repetition priming in visual search tasks. *Attention, Perception, & Psychophysics*, 72(1), 5–18. <https://doi.org/10.3758/APP.72.1.5>

Kristjánsson, Á., Vuilleumier, P., Malhotra, P., Husain, M., & Driver, J. (2005). Priming of color and position during visual search in unilateral spatial neglect. *Journal of Cognitive Neuroscience*, 17(6), 859–873. <https://doi.org/10.1162/0898929054021148>

Krummenacher, J., Müller, H. J., Zehetleitner, M., & Geyer, T. (2009). Dimension- and space-based intertrial effects in visual pop-out search: Modulation by task demands for focal-attentional processing. *Psychological Research*, 73(2), 186–197. <https://doi.org/10.1007/s00426-008-0206-y>

Lamy, D., Antebi, C., Aviani, N., & Carmel, T. (2008). Priming of pop-out provides reliable measures of target activation and distractor inhibition in selective attention. *Vision Research*, 48(1), 30–41. <https://doi.org/10.1016/j.visres.2007.10.009>

Lamy, D. F., & Kristjánsson, Á. (2013). Is goal-directed attentional guidance just intertrial priming? A review. *Journal of Vision*, 13(3), Article 14. <https://doi.org/10.1167/13.3.14>

Li, Z. (1999). Contextual influences in V1 as a basis for pop out and asymmetry in visual search. *Proceedings of the National Academy of Sciences*, 96(18), 10530–10535. <https://doi.org/10.1073/pnas.96.18.10530>

Maljkovic, V., & Nakayama, K. (1994). Priming of pop-out: I. Role of features. *Memory & Cognition*, 22(6), 657–672. <https://doi.org/10.3758/BF03209251>

Maljkovic, V., & Nakayama, K. (1996). Priming of pop-out: II. The role of position. *Perception & Psychophysics*, 58(7), 977–991. <https://doi.org/10.3758/BF03206826>

McPeck, R. M., Maljkovic, V., & Nakayama, K. (1999). Saccades require focal attention and are facilitated by a short-term memory system. *Vision Research*, 39(8), 1555–1566. [https://doi.org/10.1016/S0042-6989\(98\)00228-4](https://doi.org/10.1016/S0042-6989(98)00228-4)

Olivers, C. N. L., & Humphreys, G. W. (2003). Attentional guidance by salient feature singletons depends on intertrial contingencies. *Journal of Experimental Psychology. Human Perception and Performance*, 29(3), 650–657. <https://doi.org/10.1037/0096-1523.29.3.650>

Peirce, J. W. (2007). PsychoPy—Psychophysics software in Python. *Journal of Neuroscience Methods*, 162(1), 8–13. <https://doi.org/10.1016/j.jneumeth.2006.11.017>

Rangelov, D., Müller, H. J., & Zehetleitner, M. (2013). Visual search for feature singletons: Multiple mechanisms produce sequence effects in visual search. *Journal of Vision*, 13(3), 22. <https://doi.org/10.1167/13.3.22>

Rangelov, D., Müller, H. J., & Zehetleitner, M. (2017). Failure to pop out: Feature singletons do not capture attention under low signal-to-noise ratio conditions. *Journal of Experimental Psychology: General*, 146(5), 651–671. <https://doi.org/10.1037/xge0000284>

Theeuwes, J. (2018). Visual selection: Usually fast and automatic; seldom slow and volitional. *Journal of Cognition*, 1(1), 29. <https://doi.org/10.5334/joc.13>

Treisman, A. M., & Gelade, G. (1980). A feature-integration theory of attention. *Cognitive Psychology*, 12(1), 97–136. [https://doi.org/10.1016/0010-0285\(80\)90005-5](https://doi.org/10.1016/0010-0285(80)90005-5)

Walsh, V., Le Mare, C., Blaimire, A., & Cowey, A. (2000). Normal discrimination performance accompanied by priming deficits in monkeys with V4 or TEO lesions. *Neuroreport*, 11(7), 1459–1462.

Westerberg, J. A., & Schall, J. D. (2021). Neural mechanism of priming in visual search. *Attention, Perception, & Psychophysics*, 83(2), 587–602.

Westerberg, J. A., Schall, M. S., Maier, A., Woodman, G. F., & Schall, J. D. (2022). Laminar microcircuitry of visual cortex producing attention-associated electric fields. *Elife*, 11, Article e72139.

- Westerberg, J. A., Sigworth, E. A., Schall, J. D., & Maier, A. (2021). Pop-out search instigates beta-gated feature selectivity enhancement across V4 layers. *Proceedings of the National Academy of Sciences*, 118(50), Article e2103702118.
- Wolfe, J. M. (2020). Visual search: How do we find what we are looking for? *Annual Review of Vision Science*, 6, 539–562. <https://doi.org/10.1146/annurev-vision-091718-015048>
- Zelinsky, G. J. (2008). A theory of eye movements during target acquisition. *Psychological Review*, 115(4), 787–835. <https://doi.org/10.1037/a0013118>
- Zhang, T., & Leber, A. B. (2024). Investigating an effort avoidance account of attentional strategy choice. *Attention, Perception, & Psychophysics*, 86(6), 1989–2002. <https://doi.org/10.3758/s13414-024-02927-1>
- Zhaoping, L. (2005). CHAPTER 93—The primary visual cortex creates a bottom-up saliency map. In L. Itti, G. Rees, & J. K. Tsotsos (Eds.), *Neurobiology of attention* (pp. 570–575). Academic Press. <https://doi.org/10.1016/B978-012375731-9/50097-5>.