Temporal integration of feature probability distributions

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Humans are surprisingly good at learning the statistical characteristics of their visual environment. Recent studies have revealed that not only can the visual system learn repeated features of visual search distractors, but also their actual probability distributions. Search times were determined by the frequency of distractor features over consecutive search trials. The search displays applied in these studies involved many exemplars of distractors on each trial and while there is clear evidence that feature distributions can be learned from large distractor sets, it is less clear if distributions are well learned for single targets presented on each trial. Here, we investigated potential learning of probability distributions of single targets during visual search. Over blocks of trials, observers searched for an oddly-colored target that was drawn from either a Gaussian or a uniform distribution. Search times for the different target colors were clearly influenced by the probability of that feature within trial blocks. The same search targets, coming from the extremes of the two distributions were found significantly slower during the blocks where the targets were drawn from a Gaussian distribution than from a uniform distribution indicating that observers were sensitive to the target probability determined by the distribution shape. In Experiment 2 we replicated the effect using binned distributions and revealed the limitations of encoding complex target distributions. Our results demonstrate detailed internal representations of target feature distributions and that the visual system integrates probability distributions of target colors over surprisingly long trial sequences.

Keywords: visual working memory, attentional templates, ensemble perception, probabilistic representations, visual search

1. Introduction

Imagine searching for your best friend in a busy mall. You know that she normally wears earth-colored shirts. You might not know the particular color she is wearing today but you also know her haircut is typically the same. How does the visual system represent such statistical regularity? Recent work shows how top-down knowledge about the variability of target features (the T-shirt and the hair cut) drive the formation of target templates and therefore visual search. For example, Witkowski and Geng (2019) showed that the visual system prioritizes more stable features over more variable ones and that the variability in the target feature influences the search templates. But how precisely are such target distributions encoded? Can the visual system learn the frequency of multiple target features over time and integrate their corresponding frequency into a target template that facilitates search?

Templates in visual working memory

The visual world is full of rich and complex information, so the visual system has to filter relevant from irrelevant information. Two main mechanisms facilitate search in the visual environment: relevant items are enhanced, and irrelevant items suppressed. Furthermore, searching for the same item multiple times results in faster searches, an effect called priming of attention shifts (Kristjánsson & Ásgeirsson, 2019).

A common assumption is that when we search the visual environment for particular targets we set up a template in visual working memory that contains the critical search features (Woodman et al., 2013). Templates are described as a mental representation of an item of interest and are thought to involve gain modulation of sensory neurons tuned to features of interest (Martinez-Trujillo & Treue, 2004; Maunsell & Treue, 2006; Reynolds & Heeger, 2009; Treue & Martínez-Trujillo, 1999). Templates are particularly important for distinguishing targets from distractors when target-distractor similarity is high (Becker, 2010; Duncan & Humphreys, 1989; Wang, Miller & Liu, 2015; Wolfe, 1994; Wolfe & Horowitz, 2004). Notably, target templates incorporate information about target variability (Witkowski & Geng, 2019) which results in a target template biased towards more reliable features enhancing target-to-distractor distinctiveness (Becker, 2010; Geng, DiQuattro & Helm, 2017; Geng & Witkowski, 2019; Navalpakkam and Itti, 2007). Mismatches between the target and its encoded templates harm visual search performance (Malcolm & Henderson, 2010; Schmidt & Zelinsky, 2009; Yang & Zelinsky, 2009) and search is more efficient for exact images of targets than verbally described or modified targets (e.g. following rotation; Hout & Goldinger, 2015).

Besides encoding target templates, the visual system also encodes templates for rejection (Arita, Carlisle & Woodman, 2012). Kristjánsson & Driver (2008) showed that repeated exposure to the same distractors over consecutive trials resulted in faster search times and Woodman and Luck (2007) found that when distractor features that are already encoded in working memory were present on a trial, search times were faster than in the absence of the memorized distractors. Facilitation was less strong than for the target but provided significant facilitation over neutral cues (Arita, Carlisle & Woodman, 2012; but see Becker, Hemsteger & Peltier, 2015). Salient distractors in the visual field are also successfully suppressed during repeated search trials (Chelazzi, Marini, Pascucci & Turatto, 2019; Gaspelin, Leonard, & Luck, 2015; Geng, Won & Carlisle, 2019; Töllner, Conci, & Müller, 2015; Vatterot and Vecera, 2012). Moreover, the strength

of attentional capture by salient distractors depends on the distractor statistics. For example, saccades are less likely to be captured by frequent onset distractors than for rare onset distractors within a block (Sayim, Grubert, Herzog, & Krummenacher, 2010) demonstrating that some information about the frequency of different distractors is encoded. Notably, distractor templates also appear to have wider tuning than target templates. They incorporate similar distractors that are currently not part of a visual stimulus set. A broad distractor template can generalize suppression to new distractors (Won & Geng, 2018). Efficient searches induced by distractor suppression require explicit or implicit knowledge about the distractors and recent evidence shows that even passive exposure to stimuli is sufficient to reduce distractor interference. Habituation reduces attentional capture during repeated exposure to distractors (Turatto, Bonetti, Pascucci & Chelazzi, 2018; Won & Geng, 2020).

Attentional priming influences templates

Past information strongly biases attentional priorities. Maljkovic and Nakayama (1994, 1996) showed how repeating a target resulted in faster searches than changing the target and distractor color, an effect described as *priming of pop-out*. These priming effects draw our attention to objects and features that we have recently attended to and are important to our current tasks and goals (see Kristjánsson & Ásgeirsson, 2019, for a review). Importantly, these effects are long lasting: Maljkovic and Nakayama (1994) showed that a target presented up to five trials in the past could influence current search times. Martini (2010) showed that priming contains two components: a fast-decay and a slow-decay component. Thompson & Milliken (2012) showed that for rare targets, interleaved with trials with frequent targets, priming could still occur for targets up to 16 trials later. Yashar and Lamy (2010) reported that priming of pop-out can also be observed in the temporal domain. Instead of presenting targets and distractors simultaneously, they used a rapid serial visual representation paradigm (RSVP). Targets had a unique color and appeared at random positions in the temporal stream and were selected faster when target features repeated from one RSVP stream to the next.

Repeating distractors during search also affects search times but switching a distractor feature into a target feature (a so-called role-reversal) reduces search efficiency more than the switch to a random new target, (Kristjánsson & Driver, 2008; Lamy, Antebi, Aviani, & Carmel, 2008; Maljkovic & Nakayama, 1994; Wang, Kristjánsson, & Nakayama, 2005). The visual system is also influenced by the frequency of different distractor features, suggesting that statistical information influences visual working memory templates (Chetverikov, Campana & Kristjánsson, 2020). In Michael, de Gardelle & Summerfield (2014) observers had to categorize a “target” array of visual stimuli by average color or shape. A 100-ms duration (“prime”) array that observers were supposed to ignore preceded the array to be judged. Judgments were faster when target variance (low or high) matched the variance of the prime display. The judgments were in other words primed by the preceding variance.

Priming is thought to activate a target template in visual working memory (Ásgeirsson, Kristjánsson & Bundesen, 2014; Bundesen, 1990; Bundesen, Habekost & Kyllingsbæk, 2005; Carlisle, Arita, Pardo & Woodman, 2011) that facilitates target detection (Wolfe, Horowitz, Kenner, Hyle, & Vasan 2004; Malcolm & Henderson, 2009; Vickery, King & Jiang, 2005) and determines the speed of target selection (Eckstein,

1998; Kim & Basso, 2008; Palmer, Verghese, & Pavel, 2000; Peltier & Becker, 2016; Eckstein, Thomas, Palmer, & Shimozaki, 2000; Verghese, 2001).

Do feature probability distributions influence templates?

Given the limits of visual working memory and attentional templates (Bundesen, 1990; Grubert & Eimer, 2013; Vickery, King & Jiang, 2005), how detailed are these templates? Optimal behavior would require a correct model of the environment or a “generative model” in terms of ideal observer approaches (Ma, 2019). Such models require detailed knowledge about the statistics of the environment. Whether this can occur for targets is yet unclear, but for distractors the answer is clear: Chetverikov et al. (2016, 2017a, 2017b, 2017c) investigated the probabilistic encoding of heterogeneous distractors in a visual search display. They showed that search times during role-reversals depended on the distractor probability. Using a method called Feature distribution learning (FDL) that utilizes priming and role reversals to assess internal representations of distractor distributions (see Chetverikov et al. 2019 for review, Tanrikulu et al. 2021) they found that search times were slower when the target feature was drawn from within a preceding distractor distribution than when it was drawn from outside the distribution range. Crucially, response times varied as a function of the distance between the previous distractor mean and the current target and the RT function resembled the shape of the probability distribution of the distractors. Observers were, in other words, sensitive to whether the distractor distribution was Gaussian or uniform, skewed or even bimodal (Chetverikov et al., 2017a), showing that distractor sets are encoded as probabilistic feature distributions and this information can serve as a visual search template (Chetverikov et al., 2020). This distribution learning extends into the periphery as well (Tanrikulu et al. 2020). Whether such information can also be integrated for targets that only involve a single exemplar on each trial is unknown. Can such limited information nevertheless be used by the visual system?

Current aims

Here we investigate whether observers can learn shapes of target distributions if multiple targets are shown over consecutive visual search trials where each trial contained a single target with a color drawn from distributions with different shapes. Encoding of target distributions over time presents a serious challenge for the visual system since single exemplars from a distribution must be temporally integrated over a series of trials. If targets are drawn for a large number of trials from a constant distribution and this distribution is encoded and forms a target template, then performance should reflect these encoded probabilities. Crucially, the most probable target should then yield faster, and more accurate search and rarer targets slower and less accurate search and the shape of the distribution would be reflected in these performance measures.

2. Experiment 1

2.1. Material and Methods

2.1.1. Procedure/Task

All participants took part in two experimental sessions lasting about 45 minutes. These sessions were preceded by a 70-trial training block. Each session consisted of 12 blocks containing 144 trials within a single block, resulting in a total of 1728 trials. Stimulus sets were presented for 300 ms and participants were encouraged to respond as quickly and accurately as possible. After the button press the next trial began. If observers made a mistake the word ERROR appeared on the screen for 1s. For motivational purposes participants' performance was scored and their score on the last trial was presented in the upper left corner of the screen. The score was computed as $\text{Score (on a single trial)} = 10 + (1 - \text{RT}) * 10$ for a correct response and $\text{Score (on a single trial)} = -|10 + (1 - \text{RT}) * 10| - 10$ for an error, where RT is the response time in seconds. Individual sessions were interrupted by three breaks, in which the total score was displayed on the screen.

2.1.2. Stimuli

Search displays consisted of 3 colored diamonds with one corner cut off. Participants searched for the **oddly colored diamond that differed the most in terms of its color** and indicated the location of the missing corner by pressing the arrow. All three diamonds appeared at random positions on a 6×6 invisible grid that subtended 17.5×17.5 degrees of visual angle on the screen. Individual diamonds had a diameter of 1.4° .

Over the course of a single block (144 trials) the color distributions that targets and distractors were drawn from was constant. Recent evidence indicates that the encoding of distractor distribution shape requires about 3-4 four trials with 36 diamonds (Chetverikov et al., 2016). We therefore use a similar number of exemplars from the distribution but presented them individually over adjacent search trials. Distractor colors were always drawn from a uniform distribution (see Figure 1B). In one session the target distribution was Gaussian and uniform in the other session. These two sessions were counterbalanced across subjects.

All parameters were based on previous research using uniform and Gaussian distractor distributions of orientation and color (Chetverikov et al., 2016, 2017a, 2017b; Hansmann-Roth, Chetverikov and Kristjánsson, 2019). We used a linearized color space with 48 isoluminant hues (luminance: 30 cd/m², background: $x = 0.31$, $y = 0.34$, $Y = 30.0$; all hues were defined in Commission Internationale de l'Éclairage, CIE, 1931, color space on the basis of the values obtained from an isoluminant circle in DKL color space) where adjacent hues are separated by approximately one average just-noticeable-difference, JND (based on data provided by Christoph Witzel, from Witzel & Gegenfurtner, 2013, 2015). Their data showed that JNDs for different hues are quite consistent across observers. Therefore, using average hues can partly correct for anisotropies of color space by dividing the color circle into equally perceptual discriminable steps. This approach, using the average hues to build a perceptually equal color space, was validated in studies of ensemble perception (Maule and Franklin, 2015, 2016).

Moreover, this color space has already successfully been used to examine feature distribution learning of distractor sets (Chetverikov et al. 2017b, Hansmann-Roth, Chetverikov & Kristjánsson, 2019). We pre-selected 6 equidistant colors to serve as target distribution means. The distractor distribution mean

was selected correspondingly, so that the distractor distribution was on the exact opposite side of the color wheel.

The uniform target distribution had a range of 24 colors and the Gaussian distribution was a truncated Gaussian with an SD of 6 JND to match the range of the uniform distribution. Color values outside $\pm 2SD$ were removed. The distractor distribution had a range of 8 colors. The uniform target distribution served as a control condition. Less probable colors from the Gaussian distribution are further away from the mean of the target distribution but they are also closer to the distractors potentially causing additional effects. Increased target to distractor similarity will affect reaction times as well. However, the strength of this effect can be controlled for by comparing reaction times for Gaussian and uniform distributions.

Figure 1: Example of a display used in the experiment and example of a target and distractor distribution. A. Screenshot of a single trial. The target is yellow in this case and the distractors are blue/purple. B. Example sketches of the target and distractor distributions. Target distributions were either a truncated Gaussian or a uniform distribution and the distractors were drawn from a uniform distribution.

2.1.3. Apparatus

All stimuli were displayed on a 24-inch calibrated LCD monitor (ASUS, VX248h). The resolution of the screen was set to 1920×1080 . All stimuli were displayed using Matlab R2016a and Psychtoolbox-3

(Brainard, 1997) that ran on a Desktop PC with Windows 10. The screen was color-calibrated using a Cambridge Research Systems ColorCal MK2 photometer.

2.1.4. Observers

30 observers (twenty-one female, age $M = 25.50$) took part in the experiment. All observers were naïve to the purpose of the study and had normal or corrected-to-normal vision. Participants with red-green color vision deficiencies were excluded through the use of Ishihara plates (Ishihara, 2004) and in a few cases by self-report. They all gave written, informed consent. All experiments were performed in accordance with the requirements of the local ethics committee and the Declaration of Helsinki. Participants took part in the experiment for course credit. Two participants had error rates over 30% and were replaced with new participants.

2.1.5. Data analysis

The main variable of interest is the reaction time as a function of the different target color probabilities. Since the different distributions were kept constant within a session, overall reaction times decrease over time, preventing us from comparing absolute reaction times for the different distributions. We were mainly interested in the variation in reaction time for the different probabilities depending on the distance between the target and its distribution mean. For the main analysis we therefore analyzed normalized reaction times by subtracting the average reaction time across each block (12 blocks per session) from the reaction times on each trial. Reaction times were log-transformed for the final statistical data analysis. However, all plots represent the geometric mean by converting the average $\log(RTs)$ back to their associated raw RTs which corresponds to the geometric mean not the arithmetic mean: $\text{mean}(\log RT) = \text{geometric_mean}(RT)$. Trials with incorrect responses and the trial immediately following an incorrect response were removed because of potential post-error slowing. Trials with search times exceeding the mean response time $\pm 3SD$ were also removed. To assess the influence of distribution shape we conducted repeated-measures ANOVAs, with Greenhouse–Geisser corrections, where applicable, after testing for sphericity using Mauchly tests. ANOVAs were conducted in the open source software R (R Development Core Team, 2012) using a random effects model from the *ez* package (Lawrence, 2016). Confidence intervals are presented on the non-log data, but all statistical tests are done on log-transformed search times.

2.2. Results

Before analysing the main aspect of the data to examine whether target distribution information is encoded, we first analysed average search times and accuracy for both target distributions. Overall search times did not differ between the two distribution types: $RT = 635.51$ ms ($CI = 10.35$) vs. $RT = 636.67$ ms ($CI = 10.37$), $t(29) = -0.13$, $p > .05$. The results for average accuracy were similar and also showed no difference between the two distribution types: 88.9 % ($CI = 1.01$) vs 87.9 % ($CI = 1.01$), $t(29) = 1.49$, $p > 0.05$.

2.2.1. The effects of target distributions on search performance

The main goal was to assess whether the shape of the target distribution was encoded over the course of the experiment. For the Gaussian target distribution, we expected slower searches for less probable feature values and faster searches for highly probable colors. The uniform target distribution where all colors are equiprobable served as a control so the difference in search time between the Gaussian and the uniform distribution provides evidence for the encoding of target color probabilities over time.

Firstly, we normalized the search times by subtracting the average response time during a session from the individual search times for each distance between the current target and the mean of the target distribution. Figure 2A plots the normalized search time as a function of this distance.

Figure 2: Average search time and accuracy as a function of the distance between the target and the target distribution mean. A) Normalized search time against the distance between current target to current target distribution mean for the uniform and normal distributions. B) Accuracy as a function of the current target to current target distribution distance. Error bars correspond to the 95% CI adjusted for within-subject variability (Morey, 2008).

A two-factor (distance $\times$ distribution type) repeated-measures ANOVA revealed a main effect of distance, $F(4.68, 135.72) = 36.59, p < .001, \eta^2_G = .33$, and of distribution type $F(1, 29) = 29.77, p < .001, \eta^2_G = .06$ and a significant interaction, $F(5.64, 163.56) = 5.88, p < .001, \eta^2_G = .07$, between the distance and the distribution type. Participants responded slower for the target colors furthest away from the distribution mean and most notably slower for colors drawn from the Gaussian than the uniform distribution. This shows how the search times were modulated by the frequency of targets as determined by the shape of the probability function. As previously described, the uniform distribution served as a control to separate the effects induced by the target frequency from the effects induced by the decreasing distance between target and distractors at the edge of the distribution. Probabilities for targets close to the mean were quite similar between the uniform and the Gaussian, due to the blocked design (different distributions were tested in different sessions). The crucial difference between the different distributions is visible when comparing the variations in search time for the different distances between target and the target distribution mean.

We also analyzed accuracy by distance of target from distractor mean and of distribution type (Figure 2B) to examine whether the encoding of the target frequency affects accuracy as well: A two-factor (distance $\times$ distribution type) repeated-measures ANOVA revealed a main effect of distance, $F(5.16, 149.64) = 8.42$, $p < .001$, $\eta^2_G = .04$ but not of distribution type $F(1, 29) = 0.57$, $p = .46$, $\eta^2_G = .00$ and no interaction, $F(4.44, 128.76) = 1.25$, $p = .25$, $\eta^2_G < .01$, between them. Accuracy was lower for colors further away from the distribution mean but equally low for the uniform and Gaussian distributions and therefore not driven by target probability. As targets became more similar to the distractors, accuracy was reduced.

2.2.2. The effect of distractors on search performance

In a second step we also analyzed the effect that the distractors have on the speed and accuracy of the target searches. Search times are known to be affected by distractor heterogeneity (Duncan & Humphreys, 1989; Rosenholtz, 2001; Wolfe et al. 1992). Figure 3A plots the average search times as a function of the distance between the two distractors separately for both target distributions. A two-factor (distribution type $\times$ distractor distance) repeated-measures ANOVA revealed a main effect of distance (between the two distractors), $F(3.28, 95.12) = 23.77$, $p < .001$, $\eta^2_G = .25$ but not of distribution type $F(1, 29) = 0.12$, $p = .89$, $\eta^2_G < .01$, nor a significant interaction, $F(6.1, 176.32) = 0.47$, $p = .96$, $\eta^2_G < .01$, between distance and distribution type. Search times for the target increased as the distractors became more dissimilar. This effect did not vary by distribution type, however.

Figure 3: Search time and accuracy as function of the distance between the two presented distractors. A) Search times as a function of the distance between the two distractors. Error bars correspond to 95% CI adjusted for within-subject variability (Morey, 2008). B) Accuracy as a function of the distance between the two distractors. Error bars correspond to the 95% CI adjusted for within-subject variability (Morey, 2008).

Figure 3B plots the accuracy by distance between the two distractors. A two-factor (distribution type $\times$ distractor distance) repeated-measures ANOVA revealed a main effect of distance (between the two distractors), $F(4.64, 134.56) = 37.74$, $p < .001$, $\eta^2_G = .07$, an effect of distribution type $F(2, 58) = 6.83$, $p < .01$, $\eta^2_G = 0.07$, and we found a significant interaction between distance and the distribution type, $F(7.36,$

213.44) = 1.40, $p = .04$, $\eta^2_G = .01$. Overall accuracy decreased as the distractors become more dissimilar and this was stronger for the uniform distribution especially when distractors were already quite dissimilar.

2.3. Discussion Experiment 1

We asked whether observers can learn the distribution of target colors over sequential presentations on visual search trials. Our results show that their performance reflects the shape of the target distribution indicating that observers temporally integrate distribution information over sequential trials even when only one exemplar of the distribution is presented on each trial. The critical observation is that search for the same target from the extremes of the two distributions was significantly slower when the distractors were drawn from a Gaussian distribution than when they were drawn from a uniform distribution. This indicates that observers were sensitive to the probability that these targets would appear within the block, a probability that is determined by the distribution shape. However, these effects are only clearly visible for the endpoints of the distributions. Search times were additionally affected by the target-distractor similarity and distractor heterogeneity. In Experiment 2 we attempted to enhance the effects of target probabilities on search times by using binned distributions (with the same color range as in Experiment 1) with fewer colors to enhance perceptual differences between the colors within the distribution.

3. Experiment 2

Participants performed the same visual search task, searching for the oddly colored diamond among two distractors. Target colors were drawn from three distributions with different color frequencies. If target probability is integrated over consecutive trials, we expected to see faster search for highly probable targets, slower for less probable targets.

3.1. Material and Methods

3.1.1. Procedure/Task

Each participant performed three sessions with differently binned target distributions. As in Experiment 1 distractors were constantly drawn from a uniform distribution (range 8 JND). The mean of the distractor distribution was again selected from the opposite side of the color wheel: target mean + 24 JND.

3.1.2. Stimuli

Figure 4 shows histograms for the different target distributions. The first target distribution resembled a binned distribution in which probabilities monotonically decreased with distance from the mean (Figure 4A), similar to the Gaussian distribution in Experiment 1. A second target distribution resembled a binned uniform distribution in which probabilities were identical and a third distribution resembled a binned distribution where the two probabilities of the distribution in a) outside the mean were switched (Figure 4C). This resulted in a more complex distribution shape with global and local maxima. Each binned distribution contained 5

different colors over the same range of 25 colors or 25 JNDs as in Experiment 1 (from the same color space). We will hereafter label these distributions monotonic, uniform and non-monotonic.

Figure 4: Histograms representing the three different distributions used in experiment 2. The x-axis denotes the color difference between the distribution mean and the target color on a current trial. a) resembles a binned distribution with the highest probability in the center and a monotonic decrease in probability to both sides, similar to the Gaussian distribution in Experiment 1. b) shows the binned uniform distribution and c) a binned distribution with the same probabilities as in a) but the two probabilities next to the mean are switched. This results in a non-monotonic distribution that has global and local maxima. For the purpose of clarity, we label these three distributions: monotonic, uniform and non-monotonic.

Neighboring colors were therefore 6 JND apart from each other. Each session lasted about 40 minutes and included an unrecorded training phase of 70 trials. Target distributions were blocked and counterbalanced across participants.

3.1.3. Apparatus

We used identical equipment as in Experiment 1.

3.1.4. Participants

Thirty observers (twenty-two female, age $M = 23.73$) took part. All were naïve to the purpose of the study and had normal or corrected-to-normal vision. Participants with red-green color vision deficiencies were excluded through Ishihara plates (Ishihara, 2004) and in a few cases by self-report. They all gave written, informed consent. The experiments were performed in accordance with the requirements of the local ethics committee and the Declaration of Helsinki. Participants took part in the experiment for course credit. Three participants with error rates higher than 30%, and two who did not finish all three sessions (due to COVID quarantine) were replaced with new participants.

3.1.5. Data analysis

We followed the same procedure as described for Experiment 1. The main variable of interest was reaction time as a function of different target color probabilities. Since the different distributions were constant within a session, overall reaction times decrease in later sessions as a function of learning. For the main analysis we

therefore analyzed normalized reaction times by subtracting the average reaction time across each session from the search times on each trial.

3.2. Results

We first analyzed average search times and overall accuracy for all three target distributions. As for experiment 1, we found no difference in overall search time between the three different distributions: RT (monotonic) = 620.61 (CI = 11.23) vs. RT (non-monotonic) = 637 ms (CI = 14.71) vs. RT (uniform) = 640.21 (CI = 12.72), $F(2,58) = 2.04$, $p > 0.05$. However, average accuracy differed between the distribution types. Accuracy for colors drawn from the monotonic distribution (89.8 %, CI = 1.3) was higher than for the non-monotonic (86 %, CI 1.5) and the uniform (86.2 %, CI = 1.44) distributions. A one-factor (distribution type) repeated-measures ANOVA showed a main effect of distribution type $F(2, 58) = 6.06$, $p = .004$, $\eta^2_G = .07$. But overall, the change in accuracy was rather small (about 3%).

3.2.1. The role of the target distribution on search performance

As in Experiment 1, our main interest was to evaluate whether the visual system is able to integrate the individual target colors into a probabilistic template. If the target color probabilities are encoded over blocks, search times should vary with target color probability. To assess this, search times were normalized by subtracting the average response time during a session from the individual search times for each distance. Figure 5A plots normalized search times as a function of distance between the current target and its underlying distribution for each target distribution shape. Overall, search times increased with distance from the distribution mean.

Figure 5: Search times of Experiment 2. A) Normalized average search time against absolute distance between current target to current target distribution mean for all three distributions. B) Normalized search times as a function of distance between the current target and the distribution mean. Data from the non-monotonic and the uniform distribution is plotted separately for trials in the first and the second half of a block. C) Differences between search times for the binned monotonic and the binned uniform distributions and between the binned non-monotonic and the binned uniform. D) Accuracy as a function of the current target to current target distribution distance. Error bars show 95% confidence intervals adjusted for within-subject variability (Morey, 2008).

A two-factor (distribution type $\times$ distance) repeated-measures ANOVA revealed main effects of distance (between the mean of the distribution and the current target color), $F(1.5, 43.5) = 163.99, p < .001, \eta^2_G = .57$ and of distribution type $F(2, 58) = 35.31, p < .001, \eta^2_G = .22$. Moreover, there was a significant interaction, $F(4, 116) = 7.84, p < .001, \eta^2_G = .06$, between distance and distribution type. Search times varied as a function of target color probability. As hypothesized, the steepest increase was found for the binned monotonic distribution. The global and local maxima of the non-monotonic distribution appeared not to be encoded by the visual system and this distribution was therefore encoded similarly to a uniform distribution.

Based on the results showing that a non-monotonic distribution and a uniform distribution led to the same results, we decided to further examine the search times for the non-monotonic distribution. For that we performed an exploratory analysis of the obtained data by splitting the blocks into smaller sequences and examining search times for the non-monotonic distribution on later trials only. The non-monotonic distribution contained global and local maxima and resembled a bimodal distribution. Bimodal distractor distributions require many learning trials until the visual system encodes the decrease in probability between the modes (Chetverikov et al. 2017). Here this resulted in the absence of a difference between the search times of the uniform and the non-monotonic target distribution. We therefore further examined whether search times differed during later parts of a trial block. As participants only see a single exemplar of the distribution on each trial, a certain number of trials with different probabilities must be encoded before observers can learn the distributions. In Figure 5B we compare search times as a function of target distance in the first and the second half of a block for the non-monotonic distribution and the uniform distributions only. For search times for colors drawn from a non-monotonic distribution we expected to see the slowest search times for the least probable color at Distance 6 and faster search times for the more probable color at Distance 12. Figure 5B shows that during later trials (Dashed line) within a block, the search times for the least probable color increased, while they simultaneously decreased for the colors at Distance 12 showing how observers gradually learn the non-monotonic distribution. A two-factor (block half $\times$ distance) repeated-measures ANOVA for the uniform distribution showed only a significant main effect of distance $F(2, 58) = 75.4, p < .001, \eta^2_G = .35$. However, a two-factor (block half $\times$ distance) repeated-measures ANOVA for the non-monotonic distribution showed, in addition to a main effect of distance $F(2, 58) = 62.27, p < .001, \eta^2_G = .45$ a significant interaction between distance and block half $F(2, 58) = 9.25, p < .001, \eta^2_G = .05$. This clearly demonstrates that search times change from the beginning of an encoding block towards later trials within a block. The two-factor (block half $\times$ distance) repeated-measures ANOVA for the monotonic distribution showed a significant main effect of distance $F(1.3, 37.7) = 130.71, p < .001, \eta^2_G = .65$, a small trend of block half, $F(1, 29) = 3.45, p = .07, \eta^2_G = .01$, but no significant interaction between distance and block half $F(2, 58) = 0.54, p > .05, \eta^2_G = .00$. Overall search times showed a small decrease during later trials, but there was not change in the shape of the response time function indicating that the non-monotonic distribution requires more trials to be encoded and search times change during later trials in the block.

Moreover, the monotonic increase for the binned uniform distribution (purple line in Figure 5A and 5B) shows that distance to the distractors also affected search times. To remove this effect from the results we subtracted the search times of the binned uniform distribution from the search times for the binned monotonic and non-monotonic distributions. Figure 5C plots the result of this calculation for all trials in the second half of the block. It appears that on later trials of the block, search times for the lowest probability color (at Distance 6) increase but decrease for the second lowest probability color (at Distance 12). Bonferroni-corrected repeated-measures t-tests ($p < 0.017$) showed a significant difference between search times at 12 JND: $t(29) = -5.04, p < .001$, but no differences between search times at 6 or 0 JND: $p > .05$. This shows that search times at the furthest distance are faster when colors are drawn from the non-monotonic

than the monotonic distribution. These results reflect the difference in color frequency at this distance. While the results for the non-monotonic distribution did not reveal the clearest pattern of distribution learning from the beginning of a block, later trials within a block clearly show search time patterns that are similar to the color distribution from which the target colors were drawn.

We also examined accuracy as a function of distance from the distribution mean. Figure 5D plots average accuracy for each of three distribution types. Overall accuracy decreased with distance from the distribution mean. A two-factor (distribution type $\times$ distance) repeated-measures ANOVA revealed a main effect of distance (between the mean of the distribution and the current target color), $F(1, 29) = 268.09$, $p < .001$, $\eta^2_G = .19$, but no main effect of distribution type $F(2, 58) = 2.36$, $p > .05$, $\eta^2_G = .07$. Moreover, there was no significant interaction between distance and distribution type for accuracy, $F(2, 58) = 0.27$, $p > .05$, $\eta^2_G = .00$.

Overall accuracy was affected only by the similarity between the target and the distractor distribution mean, but not by the probabilities of the different target colors. These results resemble the results from Experiment 1.

3.2.2. The effect of distractors on search performance

Finally, as in Experiment 1, we examined the effects of distractor heterogeneity on search times and accuracy. Figure 6A plots average search times as a function of the distance between the two distractors separately for all three target distributions. A two-factor (distribution type $\times$ distractor distance) repeated-measures ANOVA revealed a main effect of distance between the two distractors, $F(3.28, 95.12) = 23.77$, $p < .001$, $\eta^2_G = .25$ but no main effect of distribution type $F(2, 58) = 0.12$, $p = .89$, $\eta^2_G = .00$, nor a significant interaction, $F(6.1, 176.32) = 0.47$, $p = 0.96$, $\eta^2_G = .01$, between distance and distribution type. While search times increased as distractors became more dissimilar, this did not vary by distribution type.

Figure 6: Search times and accuracy as a function of the distractor distance. A) Average RT as a function of the distance between the two distractors. B) Proportion of correct trials as a function of the distance between the two distractors. Error bars correspond to 95% CI. Each colored line refers to one target distribution.

Figure 6B plots accuracy as a function of the distance between the two distractors. A two-factor (distribution type $\times$ distractor distance) repeated-measures ANOVA revealed a main effect of distance (between the two distractors), $F(4.64, 134.56) = 37.74, p < .001, \eta^2_G = .07$, a significant effect of distribution type $F(2, 58) = 6.83, p < .001, \eta^2_G = .07$, and a small but significant interaction, $F(7.36, 213.44) = 1.70, p = .04, \eta^2_G = .01$. Overall accuracy decreased as the distractors became more dissimilar. Accuracy, as previously shown, was higher for the binned monotonic distribution. Moreover, the reduction in accuracy was slightly stronger for the binned uniform and the non-monotonic distributions like what we observed in Experiment 1.

Overall, search times varied as a function of target probability showing that target distributions are encoded over time, albeit with less precision than the true distribution, even when the visual system is only presented with a single exemplar from the distribution. Accuracy was, however, less affected by distribution differences. Participants needed more time to find a target with a rare color, while accuracy was not affected. Moreover, Experiment 2 also revealed the limitations for more complex distributions that contain global and local maxima such as a bimodal distribution.

3.3. Discussion Experiment 2

Experiment 2 provides a conceptual replication of Experiment 1, showing that target probabilities over consecutive trials are integrated into a representation of the target distribution. Priming strength was affected by the frequencies of different target colors. Search times were slower for less probable target colors and fastest for the most frequent color. Interestingly, search time patterns for colors drawn from the non-monotonic distribution, that exhibited a more complex pattern of color frequencies, were similar to the search times for the uniform distribution.

4. General Discussion

Our study was inspired by recent work by Chetverikov et al. (2016, 2017a-c) who demonstrated that the shape of feature distributions is represented in detail and that these internal representations affect behavior. They presented a large number of individual feature exemplars from a distribution simultaneously on a single trial and following only a few trials reliable distribution encoding was visible in observers search performance.

Our current goal was to assess whether the visual system can learn probabilistic generative models of the environment by integrating *single* exemplars of a target distribution presented over consecutive visual search trials. We found that performance patterns reflected particular aspects of the shape of the distribution indicating that observers can temporally integrate distribution information over sequential trials. The key finding is that the same search targets, coming from the extremes of the two distributions were found significantly slower during blocks where the targets were drawn from a Gaussian distribution than when they were drawn from a uniform distribution indicating that observers were sensitive to the probability of these targets determined by the distribution shape. While Chetverikov et al. (2020) have shown that encoded probabilistic distractor distributions can serve as a visual search template our results confirm that this also

occurs for target distributions. Encoded information about the frequency of occurrences of targets and distractors can serve as a template to efficiently guide attention to the correct target. But while search times reflected the shape of the distribution, accuracy did not. Accuracy was overall high so this may reflect a ceiling effect.

Our results show that the visual system has a remarkable ability to temporally integrate information and build representations. This example is particularly interesting since it shows integration of single exemplars into a probabilistic template over time. This is surprising given how impoverished the information provided at any given instance is and suggests that target representations integrate information over trials in order to reflect expectations of all possible targets (Witkowski and Geng, 2019).

The differences in search times between the different distributions provide compelling evidence that target templates can be based on a prior probability distribution. The results also provide interesting complementary finding to Chetverikov et al. (2016, 2017a-c, 2019) on the learning of distractor distributions. But the results of Chetverikov et al. involved many exemplars on each trial. We attempted to involve as many exemplars as their results indicated were needed for the learning to emerge. Based on their results, we speculate that the impoverished encoding of the non-monotonic distribution in our Experiment 2 was due to the number of trials within a block. Distractor distributions with multiple modes require more exemplars to build a detailed template (Chetverikov et al, 2017a). However, we found some evidence that the bimodality of the target distribution was encoded following many trials. Future work should examine more complex probability distributions to assess the limits of encoding detailed probabilities into an attentional template.

Incidental learning over the course of an experiment from only a single exemplar of a feature distribution was recently also examined for a bimodal distribution of locations by Tran et al. (2017). Observers played a ‘Whack-a-mole’ game, with circles increasing in size at different locations on the screen and had to click on each circle within a given time limit before it disappeared, for a sequence of 180 trials. After the first part of the experiment, they were asked to again click on the screen mimicking the sequence of locations of the original sequence. The results revealed that only a bimodal distribution with zero density in between the modes was encoded, while continuous bimodal distributions were not. We similarly made our distributions discrete in the second experiment to reveal more details about encoding abilities. Tran et al. suggested that observers might have unimodal priors and that the number of exemplars were insufficient to overcome these priors. While in these experiments the observers were explicitly asked to mimic the locations of the previously seen circles, we did not inform observers about any distributions and only implicitly accessed the encoding of probabilities, potentially distinguishing between explicit and implicit mechanisms for assessing the learning of statistical information (Hansmann-Roth, Kristjánsson, Whitney & Chetverikov, 2020). However, our results from Experiment 2 with discrete distributions reveal a similar pattern in terms of the probabilistic knowledge acquired during a block, but encoding of the non-monotonic distribution with multiple local and global modes was limited. The non-monotonic distribution in our experiment did not only contain two modes but also a global maximum along with two local ones at the extremes with non-zero density in between.

Our results show how the frequency of targets or more generally speaking expectations modulate visual search behaviour through the implicit encoding and accumulation of information about the target distribution. These results are in accordance with more general view of how expectations shape visual perception. Visual perception is akin to Bayesian inference (Knill & Pouget, 2004); incoming sensory information is combined with prior knowledge about environmental statistics. Learning complex priors has been shown to affect a variety of visual tasks from motion perception (Chalk, Seitz & Seriès, 2010) to reproducing timing intervals (Acerbi, Wolpert & Vijayakumar, 2012). However, these studies typically provide observers with feedback on their performance enabling integration of information about the distribution and feedback. Learning complex priors required several hundreds of learning trials (Acerbi, Wolpert & Vijayakumar, 2012; Chalk et al. 2010; Koerding & Wolpert, 2004; Sanborn & Beierholm, 2016). We have added to this literature by showing how expectations through encoding of target distributions affect search behavior without providing any feedback that could have modulated the distribution learning.

Why are there no performance differences between the centres of the Gaussian and uniform distributions despite the differences in probability? While we do not have a definite answer, we note that the two conditions are performed in separate sessions and observers may have a “general” response speed with the fastest responses for the center of each distribution. The crucial differences between the different distributions are therefore visible when variations in search time for the different distances between target distribution means are compared.

Potential implications for findings on the priming of attention shifts

Previous results have shown how repeated targets during visual search are primed. Search is speeded (Maljkovic & Nakayama, Goolsby & Suzuki, 2001) and more accurate (Sigurdardottir et al., 2007; Ásgeirsson et al., 2014) when the same search is repeated on consecutive trials. This can be traced to dissociable target effects and distractor effects (Kristjánsson & Driver, 2005; 2008; Lamy et al., 2008; Wang et al., 2005). An intriguing possibility that is raised by the current findings is that priming of attention shifts through repetition of target identity reflects a special case of target distribution learning. This would entail that previous results where the target distribution is constant simply collapse to a distribution with a mean of that target value and with a variance of zero. We can also speculate that distractor priming effects (Kristjánsson & Driver, 2008; Lamy et al., 2008; Wang et al., 2005) may be limited cases reflecting the feature distribution learning of distractor sets seen in the studies of Chetverikov et al (2016; 2017a-c).

As examples of how such learning can dynamically influence visual perception, Geng and colleagues (Geng, DiQuattro, & Helm, 2017; Geng & Witkowski, 2019; Won & Geng, 2018; Yu & Geng, 2019) have shown how target templates assessed through search times for different targets are gradually biased away from distractors as search is repeated. Chen, Leber & Golomb (2019) have then shown how distractors can also alter feature perception.

Conclusions

We asked whether observers can distinguish between differently shaped distributions of target colors over sequential single presentations on visual search trials. Our results reveal that observer's performance reflected the distribution shape in that targets with colors at the extremes of the distributions were found faster when they were drawn from a uniform than a Gaussian distribution, which shows that performance was modulated by how frequent the targets at the extremes were. This ability of the visual system to integrate all this information is remarkable and it seems that the statistics of the incoming information are monitored far more closely than previous studies have suggested.

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Data availability

The datasets generated during and/or analysed during the current study are available in the Open Science Framework repository, available at: <https://osf.io/hjpb2/>.

A preprint of this manuscript has been recently published on PsyArXiv: Hansmann-Roth, S., Thorsteinsdóttir, S., Geng, J., & Kristjánsson, A. Temporal integration of feature probability distributions in working memory.

Compliance with Ethical Standards

Our study was conducted in compliance with ethical standards. All participants gave informed consent to participate in the experiment, and there was no conflict of interest to declare. No animals were used in the study and all procedures performed involving human participants were approved by the ethics committee of the National Bioethics committee in Iceland (Vísindasiðanefnd, <http://vsn.is>) and performed in accordance with their requirements and guidelines and the Declaration of Helsinki.

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