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## Attentional priority is determined by predicted feature distributions

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### Abstract

Visual attention is often characterized as being guided by precise memories for target objects. However, real-world search targets have dynamic features that vary over time, meaning that observers must predict how the target *could look* based on how features are expected to change. Despite its importance, little is known about how target feature predictions influence feature-based attention, or how these predictions are represented in the target template. In Experiment 1 (N=60 university students), we show observers readily track the statistics of target features over time and adapt attentional priority to predictions about the distribution of target features. In Experiments 2a (N=480 university students), we show that these predictions are encoded into the target template as a distribution of likelihoods over possible target features, which are independent of memory precision for the cued item. These results provide a novel demonstration of how observers represent predicted feature distributions when target features are uncertain and show that these predictions are used to set attentional priority during visual search.

### Keywords

Attention; Predictions; Variability; Bayesian Learning; Feature Distribution

### Introduction

Observers have access to an immense amount of sensory information in natural environments but only a subset is relevant for behavior. Optimizing behavior in such environments requires knowledge of which information to prioritize and which to ignore (Gottlieb, 2018; Niv et al., 2015; Nobre & Stokes, 2019; Wolfe, 2021; Wolfe & Horowitz, 2017). However, which information to prioritize is often not immediately obvious. For example, when searching for a friend in the park you are unlikely to know exactly how she will look that day, or the features that will distinguish her from others in the crowd because her clothes vary from day to day. One way to address this uncertainty is to make predictions about the distribution of features your friend *could have* rather than trying to match your friend to any single instance of her that you have previously seen (i.e., a single memory). If

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she normally wears warm colored shirts, prioritizing only a specific shirt you have seen her wear before (e.g., a red t-shirt) is likely to be incorrect since her shirt color might be any color between yellow and pink. However, maintaining a predictive distribution across a set of colors she is likely to wear can help determine attentional priority in situations where a single precise memory is unlikely to be correct. Such scenarios are commonplace in daily life. Yet, previous studies have only measured attentional priority as a function of memory precision for known target features (e.g., a single red t-shirt), rather than predictions about the distribution of ways the target *could look* (e.g., all warm colored shirts). The current experiments test if the inherent uncertainty of target objects informs attentional priority, and whether this uncertainty is encoded in predictions about possible upcoming target features.

Theories of attention use the concept of the target template to describe how the weighting of task-relevant information is implemented in service of attentional priority (Chelazzi et al., 1993; Duncan & Humphreys, 1989; Mehrpour et al., 2020; Olivers et al., 2006; Woodman et al., 2013; Zhang & Luck, 2009). Target templates have historically been characterized as storing a single target's remembered identity (Olivers et al., 2011; Vickery et al., 2005). Many studies have found that more precise memories produce faster and more accurate search (Hout & Goldinger, 2015; Malcolm & Henderson, 2009; Schmidt & Zelinsky, 2009; Yang & Zelinsky, 2009). For example, Hout and Goldinger (2015) gave participants a single target that was either identical to the cue, a rotated version of the cue, or a new exemplar of the same category. The authors found that search was most efficient when the cue was an exact match for the target. However, most real-world targets have variable features that change over time, creating uncertainty about their exact features. Such targets may be missed by highly precise templates because the actual features of the target will often be a poor match to the target template.

One way attentional systems might overcome this limitation and mitigate the effects of uncertainty is by representing a predicted distribution of target features within the target template (Knill & Pouget, 2004; Ma & Jazayeri, 2014); that is, representing a distribution of expected features rather than any single feature. Theories of perception consider such probabilistic representations of sensory data critical to cognition (Clark, 2013; Friston, 2010; Trapp et al., 2021), and show that perception is often linked to a prior belief about what we are likely to see in the world (Kok et al., 2012; Press et al., 2019, 2020). Indeed, probabilistic expectations are thought to interact with attentional mechanisms to guide spatial attention to likely target locations (Chun & Jiang, 1998; Foley et al., 2017; Geng & Behrmann, 2005; Vossel et al., 2006). Similarly, others have shown that probabilistic expectations about distractor features are used to bias attention away from possible distractors in an upcoming task (Chetverikov et al., 2017, 2020; Huang et al., 2021; Lee & Geng, 2020; Won et al., 2021). These studies show that expectations about the upcoming search environment increase the efficiency of attentional processing. Despite this, few studies have asked whether the target template encodes predicted target feature distributions to guide attention when the features of the target are uncertain.

One benefit of maintaining predictive representations of target feature distributions is that this information can be used to reduce uncertainty by setting attentional priority for features with lower variability. For example, if the friend you are searching for wears only

warm colored shirts, but pants of any color, prioritizing the low-variability distribution of shirt colors over the high-variability distribution of pant colors will maximize predictive information in the target template (i.e., minimize target uncertainty). Target features encoded into working memory are known to be remarkably sensitive to the task-relevance of information (Becker et al., 2010; Boettcher et al., 2020; Geng & Witkowski, 2019; Nobre & Stokes, 2019; Rajsic et al., 2020), and it has been shown that object features are flexibly removed or compressed so that only the most informative features are used to guide attention (Bravo & Farid, 2012, 2016; Kerzel & Huynh Cong, 2021; Reeder et al., 2017; Woodman & Vogel, 2008; Zivony & Lamy, 2016). Previous work has also shown that when sensory information differs in reliability, perception is optimally weighted toward the most reliable cue (Fetsch et al., 2012; Hillis et al., 2004), resulting in a “push-pull” dynamic for attentional priority (Foley et al., 2017; Kozyrev et al., 2019; Mehrpour et al., 2020; Pinsk et al., 2004). However, it is still unknown whether feature-based attentional biases depend on probabilistic representations of the expected target, or merely on the precision of memories for target features. Linking predictions about target feature distributions to attentional priority would show that attentional biases are inherently connected to predictive processes that minimize our uncertainty about the upcoming task, rather than being only a consequence of the quality of memories from previously seen targets.

In the current studies we investigated the role of predictive representations in the target template when the identity of upcoming targets is uncertain. We did this by using a visual search paradigm in which target features were stochastically determined, creating uncertainty in the target’s appearance. Our main hypothesis was that observers would use predictions about the variability of upcoming target features to set attentional priority and encode these predictions into the target template prior to search. To anticipate, we found that attentional priority is set by explicit predictions about the variability of upcoming target features, and not by the precision of memory for specific cues. Our results suggest that predictive representations are a key element in determining attentional priority and illuminate how attentional systems mitigate feature uncertainty inherent to the natural world.

## Experiment 1

In Experiment 1, we tested if predictions about the distribution of possible target features underlie changes in attentional priority. We used a visual search task in which target features were drawn from distributions that change in standard deviation (STDEV) over time without notice, requiring participants to actively maintain predictions about the distribution of possible features to know which feature dimension should be prioritized on each trial. If participants use these predictions to set attentional priority, we should see that response times (RT) to select targets is modulated by the STDEV of underlying target feature distributions.

## Methods

We recruited a sample of 60 participants (self-reported females=47, males=13; mean age =19.05) from the University of California, Davis SONA system. This sample size was calculated to have 90% power to detect the desired RT effect based on simulations from

pilot data. All procedures were approved by the University of California, Davis Internal Review Board (IRB). The experiment was completed online using the Testable platform ([www.testable.org](http://www.testable.org)), and all participants were required to calibrate their screens before beginning the experiment so that search stimuli were a constant size (approximately 2.5 degrees of visual angle). Participants did so by holding a standard credit card up to the screen and adjusting a line so that it matched the size of the card.

At the beginning of each trial participants were given a “cue” object composed of a colored circle with a bar that indicated orientation (Fig. 1). On each trial, the cue was randomly selected to have one of three colors (RGB values: (194.9, 156.4, 226.8), (210.2, 160.9, 104.0), (56.9, 190.3, 180.7)) and one of three orientations (35, 155, 275-degrees) for a total of 9 possible combinations. The same cues were used throughout the experiment, irrespective of the current STDEV. Cues were shown for 500ms and followed by a 1000–3500ms interstimulus-interval (ISI). The ISI was followed by a visual search display during which participants were asked to report the location of the target as quickly and accurately as possible by pressing “j” if it was on the left and “k” if it was on the right. The target was defined as the item that was *most similar* to the cue. Calibration for color on individual monitors was not possible. The search display was visible for 500ms, after which the stimuli disappeared, but participants had an unlimited time to respond. Each trial ended with feedback about whether or not they correctly identified the target (“Correct”, “Incorrect”), followed by a randomly jittered 500–2500ms intertrial-interval. Each participant completed 160 trials in total during the experiment.

Both target orientation and target color were drawn from t-distributions centered on the cued feature (Mean=0) on each trial, but the variability of the distribution randomly changed without warning throughout the experiment (Fig. 2a). Thus, while there were only nine possible cue values, there were over 180 possible targets. However, each feature had a particular variability that was consistent across cues and could be utilized to reduce the uncertainty of the upcoming target features. Target distributions were bounded such that the cue-to-target feature difference could never be greater than 90-degrees to minimize correlations between target and distractor values. Since distractors were required to be more dissimilar from the cue than the target, trials with large cue-to-target differences were also more likely to have small target-to-distractor differences, making it difficult to dissociate their influence on the search process. However, bounding the target distribution minimized these correlations (Pearson  $r=.05$ ) allowing us to capture the unique influence of target variability and distractor features on search.

At seven predetermined “change points” during the experiment, the variability of orientation and color abruptly shifted. These “change points” in the STDEV of both target features occurred every 25 to 50 trials and followed a fixed schedule: STDEV=25,10,65,45,40,25 for orientation and STDEV=40,10,20,15,45,60 for color. Values of STDEV for each feature distribution were chosen such that they produced noticeable shifts in feature variability over time based on simulations and independent pilot experiments. All participants experienced the same transitions in STDEV. Notably, participants were not given any prior information about the variability of each feature, how the variability would change, nor which feature would be most similar to the cue on the upcoming trial. Thus, participants had to predict the

distribution of possible target features in the upcoming trial based on recent experiences in order to determine which feature would be the most useful to prioritize in order to maximize the efficiency of target selection.

Finally, distractors in each trial were randomly selected from a uniform distribution between  $-179$  degrees and  $180$  degrees away from the cue. The only constraint on the distractor features were that distractors must be at least  $20$  degrees more distant from the cue than the target. All stimuli that appeared on the screen had colors taken from a CIE color space color wheel, which contained  $360$  colors of equal luminance separated by one degree units (Bae, Olkkonen, Allred, & Flombaum, 2015).

**Bayesian Modeling of Predicted Variability**—To understand if participants used predictions about the distribution of target features to set attentional priority, we created a Bayesian learning model that allowed us to estimate feature predictions based on previously seen targets, without assuming perfect knowledge of the new distribution at each change point. We modeled predictions about the distribution of target features as beliefs about the STDEV of the target distribution for the upcoming trial, given the history of observed targets. We used a normative Bayesian learning model (O'Reilly et al., 2013; Summerfield et al., 2011). On each trial  $t$ , the probability of observing a specific target feature (for orientation and color separately)  $y$  given the variance of the feature distribution was written as:

$$(y_t | \sigma_t) \sim N(\mu = 0, \sigma_t) \quad (1)$$

where  $\mu$  is the mean and  $\sigma$  is the STDEV of the feature distribution. The range of  $\sigma$  was bounded between  $\text{STDEV} = 2$  and  $\text{STDEV} = 80$ . Each new target revealed information that participants could use to update their beliefs about the STDEV of each feature for the next trial. The true STDEV of each distribution (Fig. 2a, gray lines) stayed constant until a change point occurred. Thus, prior beliefs in the STDEV of the underlying distribution were modeled as the following:

$$p(\sigma_t | \sigma_{t-1}, J_t) = \begin{cases} \delta(\sigma_t - \sigma_{t-1}) & J_t = 0 \\ U(2, 80) & J_t = 1 \end{cases} \quad (2)$$

This equation states that the estimated standard deviation of the feature distribution ( $\sigma$ ) on trial  $t$  stayed the same as the previous trial if a change point was not estimated to have occurred ( $J_t = 0$ ) or switched to any value between  $2$  and  $80$  with uniform probability if a change point was estimated to have occurred ( $J_t = 1$ ). This allows the model to down-weight the influence of trials after a change point occurs. Change points were estimated to have occurred by  $v$ , based on the likelihood that the current feature value was more likely to have been sampled from a distribution with a different standard deviation:

$$v = p(J_t = 1) \quad (3)$$

Where  $p(J_t = 1)$  is the marginalized probability that  $\sigma$  has changed, over all values of  $\sigma$ . The conditional prior for  $\sigma_t$  can be written as:

$$p(\sigma_i | \sigma_{i-1}, v) = (1 - v)[\delta(\sigma_i - \sigma_{i-1})] + vU(2,80) \quad (4)$$

Importantly, integrating the change probability,  $v$ , allows the model to quickly switch beliefs about the STDEV of each feature distribution when the evidence changes dramatically. At these same points, participants would be expected to rapidly change their beliefs given new observations. The generative model can then be inverted using Bayes rule and written as:

$$p(\sigma_i, v | y_{1:t}) = \frac{p(y_i | \sigma_i)p(\sigma_i, v | y_{i-1})}{\iint p(y_i | \sigma_i)p(\sigma_i, v | y_{i-1})d\sigma_i dv} \quad (5)$$

The model's predicted variability estimates for color and orientation (Fig. 2a) reflect an "optimal observer's" prior belief in the STDEV of each feature distribution *on the next trial* ( $t + 1$ ). That is, each estimate of the feature distribution contains information learned from previous trials and are applied *prior* to the next trial before the true target features have been observed.

We then used these estimates to compute the *difference in predicted variability* of each feature. The *difference in predicted variability* is positive when color is more predictive, and it is negative when orientation is more predictive. If participant RT follows the *difference in predicted variability*, it would mean that they use predictions about the distribution of possible target features to weight attentional priority towards the feature with lower variability on the upcoming trial.

**Regression Modeling of Response Time Data**—To estimate the effect of feature predictions on attentional priority, we used a linear regression model to test how *the difference in predicted variability*, derived from the model, moderates participant RT search costs for targets over-and-above cue-to-target similarity alone. Specifically, we hypothesized that the effect of cue-to-target similarity in each feature dimension would be modulated by expectations about which of the two features was currently less variable (and therefore more reliable). For example, the expected RT cost for a target with an orientation that is 45-degrees from the cue is expected to be large when the *difference in predicted variability* indicates that orientation is the less variable feature (i.e., orientation is more reliable); in contrast, the RT cost for the same target orientation should be smaller when the *difference in predicted variability* is positive, indicating that color is the less variable dimension. This outcome would lead to a statistical interaction in RT between the *cue-to-target difference for each feature dimension and the Bayesian model generated estimates of the difference in predicted variability*. Such an interaction would suggest that participants maintain learned predictions about the distribution of each feature and use those predictions to weight attentional priority during search.

We tested this hypothesis by fitting RT data from trials with correct responses to a gamma-distributed hierarchical regression model (Lo & Andrews, 2015), using the lme4 package in R. Trials with incorrect responses or RTs greater than 3 times the interquartile range (IQR) from the median RT were excluded from the analysis (Mean=14 trials total per participant). The regression model had one regressor for *orientation cue-to-target difference* and one

for *color cue-to-target difference*. Each regressor reflects the number of milliseconds added to RT for each degree of difference between the cue and the target (ms/degree). In other words, each regressor reflects the slope of RT increase as the target becomes more dissimilar from the cue along one feature dimension. Importantly, there was also a regressor for the *difference in predicted variability* from the Bayesian model (see above). This regressor represents a prediction of how much more reliable orientation is than color, or vice versa. If observer's are sensitive to this difference in predicted variability of the upcoming target, attentional priority should be biased towards the feature with lower variability (Fetsch et al., 2012; Foley et al., 2017; Hillis et al., 2004). We therefore hypothesized that the *difference in predicted variability* would interact with *orientation cue-to-target difference* and with *color cue-to-target difference*. Because of the way in which the *difference in predicted variability* is calculated (see above), the sign of the interaction will be negative for orientation and positive for color. Nevertheless, both interactions reflect change in RT (ms) per degree of *cue-to-target* similarity as a function of the degree of *difference in predicted variability* (ms/deg/deg). This will only occur if participants maintain a representation of the predicted distribution of both target features. Finally, we included two regressors for the target-to-distractor difference in each feature dimension, *orientation target-to-distractor difference* and *color target-to-distractor difference* (Duncan & Humphreys, 1989; Wolfe & Horowitz, 2017). The random effects structure included random intercepts for each participant and random by-subject slopes for each of the fixed effects explained above.

All significance testing was done using likelihood-ratio tests between the full model and models with the relevant fixed effect removed, as is appropriate for hierarchical models (Luke, 2017). For example, the significance of the interaction between *orientation cue-to-target difference* and *difference in predicted variability* was tested by fitting a model with and without the fixed-effect of the interaction, then comparing the difference in likelihoods. The HDI (Bayesian confidence interval) of each parameter was determined by fitting the full model in PyMC3 with uninformative priors over parameter values.

## Results

Mean accuracy was high across all participants (Mean=.935, SD=.045). We observed the hypothesized interaction between *orientation cue-to-target difference* and *difference in predicted variability* ( $\beta = -.024\text{ms/deg/deg}$ ,  $\chi^2(1)=11.76$ ,  $p<.001$ , HDI 95% [-.024, -.001]) (Fig. 2C). Greater *orientation cue-to-target* differences led to longer RTs as expected, but this effect proportionately decreased as target orientation became more variable relative to target color. Similarly, we found a positive interaction between *color cue-to-target difference* and *difference in predicted variability* ( $\beta = .040\text{ms/deg/deg}$  difference,  $\chi^2(1)=15.35$ ,  $p<.001$ , HDI 95% [.026, .058]). This shows that participants responded slower with increasing *color cue-to-target differences* when color was less variable than orientation. Together, these results indicate that predictions about the distribution of possible target features were used to bias attentional priority. When the predicted variability in one dimension (e.g., orientation) was higher than the other (e.g., color), dissimilar targets in that dimension (e.g., orientation) did not slow RT as much as when predicted variability is lower than the other dimension (e.g., color) and the dissimilar target feature was more surprising.



In addition to looking at cue-to-target similarity, we also looked at the effect of target-to-distractor similarity on search RT. There was a significant interaction between *difference in predicted variability* and *orientation target-to-distractor difference* ( $\beta = .006\text{ms/deg/deg}$  difference,  $\chi^2(1) = 11.59$ ,  $p < .001$ , HDI 95% [.004, .011]), and a weaker opposite interaction with *color target-to-distractor difference* ( $\beta = -.004\text{ms/deg}$ ,  $\chi^2(1) = 6.25$ ,  $p = .012$ , HDI 95% [-.006, .003]). RTs were longer when distractors had features close to the target, but this effect was bigger in the dimension with lower predicted variability. That is, distractor features interfered with search more when they were similar to the less variable target feature, presumably because that dimension was prioritized for finding the target.

## Experiments 2a and 2b

Experiment 1 found that observers readily used predictions about the distribution of possible target features to bias attentional priority towards the low-variability feature. However, it is still unclear how these predicted distributions are encoded by the target template. One possibility is that the target template holds only a single memory of the most likely target and adapts the precision of this working memory representation to reflect the predicted STDEV (Grubert & Eimer, 2013; Hout & Goldinger, 2015; Olivers et al., 2011). For example, the memory representation of the current cue may degrade if the participants do not expect the target to match perfectly, leading to less precise memories for the cue as target variability increases. If true, this would mean that the expected variability of a distribution is not encoded directly but interacts with working memory precision to produce behavior. Another possibility is that observers directly encode a distribution of predicted likelihoods for each feature that is separate from the memory of the cue (Knill & Pouget, 2004; Ma & Jazayeri, 2014). If true, the memory representation may remain precise but there would be additional information regarding variability in the predicted target. Such a result would be evidence for the hypothesis that predictions are distinct from memories of the cue and that attentional priority is more related to predictions about target variability than memory precision. We test these alternative possibilities in Experiments 2a and 2b using probe trials interleaved amongst visual search trials.

## Methods

We recruited two independent samples of 240 participants for Experiments 2a (self-reported females=185, self-reported males=55; mean age=20.0 years) and 2b (self-reported females=184, self-reported males=56, mean age=19.67 years) from the University of California, Davis undergraduate SONA system. This sample size was calculated to have 90% power to detect the desired RT effect in each experiment alone, based on simulations from pilot data. All procedures were approved by the University of California, Davis IRB prior to the study.

All methods were the same as in Experiment 1 with a few key differences. To simplify the design, we only manipulated the variability of orientation, while color variability was kept constant. Participants in each experiment were split into three *predicted variability* conditions (N=60 per condition per experiment) defined by the STDEV of the target orientation distribution (Fig. 3AB). As in Experiment 1, all cues had a

randomly selected combination of color (RGB values: (194.9, 156.4, 226.8), (210.2, 160.9, 104.0), or (56.9, 190.3, 180.7)) and orientation (35, 155, or 275-degrees) and this was true for all groups. Target orientations were drawn from t-distributions centered on the cue (mean=0) and had a standard deviation of 10, 25 or 40 degrees. These corresponded to low-variability (STDEV=10), medium-variability (STDEV=25) and high-variability (STDEV=40) conditions, respectively. Splitting participants into groups with a stable STDEV allowed us to probe representations of specific learned distributions more accurately. In all variability conditions, color was drawn from a high-variability distribution (STDEV=55). Finally, all distractor features were sampled from a uniform distribution but were restricted to values that were at least 20 degrees more distant from the cue than the target.

An additional 60 participants per experiment were assigned to a *control condition*, in which both color and orientation were drawn from identical low-variability distributions (STDEV=10). This established a “baseline” in which expectations of the feature distributions were matched and any differences in memory or prediction probe responses could only reflect pre-existing differences in each dimension. The data from this control group were used to normalize probe responses from the other conditions following the procedures in Witkowski and Geng (2019). Specifically, we calculated the difference of each participants mean responses from the control group responses, divided by the standard deviation in control responses. This gave us a normalized measure of the change in working memory precision or predictions in response to the variability conditions.

In Experiment 2a, 14 memory probe trials (7 orientation/7 color) were interleaved between 40 search trials, following 54 initial “training” visual search trials. On memory probe trials, participants were shown either a color wheel or an orientation wheel. Each wheel contained 24 feature segments of different colors or orientations, respectively, split into 15-degree bins. Each feature segment was associated with a number, and participants were asked to report the number next to the remembered cue feature. In Experiment 2b, the 14 interleaved prediction probe trials asked participants to rate the likelihood that a subsequent object would be the target. Participants made their responses on a 1 to 9 scale with 1 being “very unlikely” and 9 being “very likely”.

Probe objects spanned the distribution of all possible cue-to-target differences (–90 to 90 degrees) in 15-degree intervals, with color and orientation being randomly combined such that there was no correlation between features. Importantly, although a single participant only saw 14 probes, all the possible cue-to-target differences for color and orientation were probed across participants. Both probe types were then fit to Gaussian functions using maximum likelihood to make these data commensurate with the stimuli generated in search, however, see supplementary figure S1 for results with alternative distributions. For prediction probes, we allowed amplitude of the Gaussian function (i.e., the height of the peak) to range from 1 to 9, so that ratings about the likelihood of target features could be directly mapped to predictions about the distribution of possible features.

## Results

### Search behavior is determined by the predicted variability of target features

—We used the same regression model to analyze RT data in Experiments 2a and 2b as in Experiment 1, except that the three *predicted variability* conditions were manipulated between-subjects. We expected the RT data to be identical given in these experiments that the visual search trials were identical. Accuracy was overall high in both experiments (Experiment 2a Mean=0.918, SD=0.062; Experiment 2b Mean=0.921, SD=0.060), but decreased significantly as orientation variability increased (Exp2a:  $\chi^2(1)=37.11$ ,  $p<.001$  HDI 95% [−0.507, −0.288]; Exp2b:  $\chi^2(1)=14.36$ ,  $p<.001$  HDI 95% [−0.405, −0.127]); this was consistent with the idea that the task became more difficult as orientation variability increased (and color variability did not change). Again, we excluded trials where responses were incorrect or greater than 3 IQRs from the median RT (mean=9 trials per subject in both experiments).

Consistent with Experiment 1, the RT results from Experiment 2a showed a negative interaction between *orientation cue-to-target difference* and *predicted variability* ( $\beta = -.98\text{ms/deg/group}$ ,  $\chi^2(1)=7.49$ ,  $p=0.006$ , HDI 95% [−1.924, −0.769], Fig. 4B). The interaction was due to *orientation cue-to-target difference* having a weaker effect on RT as the variability of the feature distribution increased. We found no significant interaction between *color cue-to-target difference* and *predicted variability* ( $\beta = .18\text{ms/deg}$ ,  $\chi^2(1)=1.65$ ,  $p=0.20$ , HDI 95% [−0.064, 0.31]), although the sign of the interaction was the same as in experiments 1 and 2b (see below). Finally, the model showed a significant effect of *orientation target-to-distractor difference* on search time ( $\beta = -.11\text{ms/deg}$ ,  $\chi^2(1)=4.82$ ,  $p=0.028$ , HDI 95% [−0.222, −0.056]), but not for color *target-to-distractor difference* ( $\beta = .09\text{ms/deg}$ ,  $\chi^2(1)=3.19$ ,  $p=0.074$ , HDI 95% [−0.058, 0.111]). The effect of distractor similarity is consistent with the overall attentional prioritization of target orientation over color given that orientation was always less variable than color.

Analysis of RT in Experiment 2b replicated these findings. There was a significant negative interaction between *orientation cue-to-target difference* and *predicted variability* ( $\beta = -.89\text{ms/deg/grp}$ ,  $\chi^2(1)=5.26$ ,  $p=0.022$ , HDI 95% [−1.93, −0.724], Fig. 4D). There was also a significant interaction between *color cue-to-target difference* and *predicted variability*, but in the opposite direction ( $\beta = .35\text{ms/deg/grp}$ ,  $\chi^2(1)=4.23$ ,  $p=0.040$ , HDI 95% [0.017, 0.437]), showing that as orientation variability increased, participants were more sensitive to the cue-to-target difference for color. Finally, the results replicated the significant effect of *orientation target-to-distractor difference* ( $\beta = -.16\text{ms/deg}$ ,  $\chi^2(1)=7.83$ ,  $p=0.005$ , HDI 95% [−0.242, −0.067]), and a null effect of *color target-to-distractor difference* ( $\beta = .01\text{ms/deg}$ ,  $\chi^2(1)=.17$ ,  $p=.718$ , HDI 95% [−0.123, 0.051]). These results provide further evidence that predictions about target feature distributions are used to set attentional priority; specifically, attentional priority for orientation decreased when it was predicted to be more variable, and priority for color increased.

### Predictions, but not memory for the cue, reflect knowledge about the learned target feature distribution

—We next analyzed differences in memory precision (Experiment 2a) and predictions about target features (Experiment 2b) across variability

conditions. First, we fit each participant's memory probe responses to a Gaussian function using maximum likelihood, separately for orientation and color. The resulting estimates of the standard deviation of memory responses were log-transformed to fit assumptions of a linear regression model. The model included regressors for *predicted variability* (low-variability, medium-variability, high-variability) and *feature dimension* (orientation, color), and their interaction. If the information about feature variability that is used to compute attentional priority is contained in the precision of cue memory, we should see an interaction between *predicted variability* and *feature dimension* similar to the pattern of results on search trials. Specifically, the precision of memory for orientation features should decrease with variability, and the precision of memory for the color feature should increase or stay the same.

The results revealed a marginal main effect of increasing memory precision across predicted variability conditions ( $\chi^2(1)=3.67$ ,  $p=0.055$ , HDI 95% [-0.263, -0.006]), suggesting that memory for both features slightly increased in precision when both features were highly variable, and the search task was overall more difficult. There was also a main effect of feature dimension ( $\chi^2(1)=6.04$ ,  $p=0.014$ , HDI 95% [0.027, 0.402]), suggesting that orientation was held more precisely compared to color (Fig. 5A) across all three variability conditions. However, we found no interaction between variability condition and feature dimension ( $\chi^2(1) = .94$ ,  $p=.33$ , HDI 95% [-0.313, 0.122],  $BF_{01}=14.28$ ), suggesting no link in the precision of memory to the pattern of attentional priority during search. The main effect replicates previous findings, showing that more reliable (i.e., low variability) features are encoded in working memory more precisely compared to low reliability features (Witkowski & Geng, 2019), but goes further to suggest that this overall benefit is not sensitive to the difference in the predicted variability of each target feature.

In contrast to the memory probes, in Experiment 2b we observed changes in the distribution of responses to the prediction probes commensurate with the specific standard deviation in each *predicted variability* condition. The same regression for prediction probe responses produced a significant interaction between *predicted variability* and *feature dimension* ( $\chi^2(1) = 23.56$ ,  $p<.001$ , HDI 95% [-0.864, -0.384]). Follow up comparisons with simple regression showed the distribution of prediction responses for orientation features became wider as a function of increasing predicted variability condition ( $\beta =.31$ ,  $\chi^2(1)=10.67$ ,  $p=0.001$ , HDI 95% [0.135, 0.503]), but became narrower for color ( $\beta =-.32$ ,  $\chi^2(1)=11.84$ ,  $p<.001$ , HDI 95% [-0.494, -0.130]). We then tested whether this pattern was significantly different from Experiment 2a by including both sets of data into a single model and adding an interaction term between experiments. The results showed that the pattern in Experiment 2b was significantly different from the pattern shown in Experiment 2a ( $\chi^2(1)=9.41$ ,  $p=.002$ , HDI 95% [0.792, 0.221]).

This pattern mirrors the pattern of attentional priority seen during search (Fig. 5B), showing that manipulations of the underlying feature distribution change both predictions about the likely target feature and attentional priority for each feature during search (see figure S2 for an exploratory analysis of this effect at the participant level). Even though the variability of color did not change across conditions, participants estimated the predicted variability as lower, presumably because perceived estimates of color variability were yoked to estimates

of the variability of orientation, paralleling attentional priority. This result indicates that predictions about the likelihood of target features, but not memories of the cue, are used to set attentional priority during visual search.

## Discussion

In the current experiments, we test whether observers learn the feature distributions of uncertain targets and we measure the consequences of this knowledge on attentional priority. We used a novel visual search paradigm in which target features were drawn from a distribution and participants learned the feature variability from observing targets over time. Search behavior showed that attentional priority for each feature tracked the predicted distribution of the feature distributions over time, such that low-variability features were prioritized over high-variability features in a push-pull manner. We then probed memory precision for cued features and explicit predictions about target features. Our results showed that the target-template dynamically encoded the variability as explicit predictions about target features, while memory for the cue remained static. These data suggest that observers use predictions about the likelihood of possible features to determine attentional priority when target features are uncertain.

The current studies provide novel evidence that attentional priority is tied to predictions about upcoming targets, and not memories of a cue. Previous research has generally focused on how the precision of memories determines attentional priority (Hout & Goldinger, 2015; Olivers et al., 2011; Schmidt & Zelinsky, 2009; Vickery et al., 2005) but have not examined how attentional priority is set when the target features are variable. Our results show that when faced with feature uncertainty, observers actively generate predictions about the distribution of possible features before the true target features can be observed. These predictions are then used to mitigate uncertainty by prioritizing features with the least variability. This predictive process is also highly flexible. When observers learn that the variability of the target has changed, they rapidly update priority settings for each feature. These findings directly connect feature distribution learning to information biases in the target-template and show how predictions are used by attentional systems to reduce uncertainty.

The results observed in search behavior also shed light on how target variability is translated into attention priority. Push-pull dynamics have been observed throughout the literature, showing that attending to one place or feature results in decreased encoding of an unattended feature (Kozyrev et al., 2019; Mehrpour et al., 2020). In Experiment 1, we observed that the attentional priority for both orientation and color were oppositely modulated by the *difference in the predicted variability* of each feature. Experiment 2b confirmed this finding by showing that attentional priority for color increased in response to manipulations of the orientation feature distribution, even though the color distribution remained the same. Although this effect did not reach significance in experiment 2a, we found the data across experiments 2a and 2b show substantially more evidence for this effect compared to the null ( $BF_{10}=6.3$ , Scheibehenne et al., 2016). This pattern of results is exactly what is expected if predicted variability was translated into attentional priority in a push-pull manner (Carandini & Heeger, 2012; Louie et al., 2013; Pinsk et al., 2004). These findings suggest that target-

templates help reduce uncertainty by optimally weighting features based on the relative predicted utility for identifying the target, rather than removing or adding features in an “all-or-none” fashion.

Knowledge about the variability of feature distributions also moderated distractor interference. Distractor similarity to targets is known to decrease the efficiency of search due to the competition that arises when distractors and targets have similar features (Driver, 2001; Duncan & Humphreys, 1989; Wolfe & Horowitz, 2017). RT analyses in all three experiments revealed that the effect of target-to-distractor difference on search was greater for prioritized feature dimensions (i.e., the low-variance feature). This shows that distractors only affect the search process when they share features used to identify the target.

Finally, in Experiments 2a and 2b we tested two possibilities for how predicted variability is encoded by the target template. One possibility was that the predicted distribution would only be reflected in the precision of a single feature encoded into working memory (i.e. the cue) (Grubert & Eimer, 2013; Olivers et al., 2011). The other possibility was that predictions were encoded as a likelihood distribution over possible target features - separate from cue memory. While our data showed that memory was more precise for low-variance features compared to high variance features (Boettcher et al., 2020; Kerzel & Witzel, 2019; Niklaus et al., 2017), we also found that only prediction probes were sensitive to changes in the actual distribution of target orientation. This suggests that separate representations are held for memories of the cue and for predictions about what the target will look like, with the latter being used to set attentional priority.

Interestingly, predictions about the target color, which did not change in variability in Experiment 2, became more precise as predictions about target orientation became more variable. This could be due to the fact that predictions about the reliability of target features are coded relative to each other (Foley et al., 2017; Horan et al., 2019). This would result in color seeming “less variable” because all target orientations became more variable. However, further experiments will be needed to confirm this interpretation. Nonetheless, the changes in both color and orientation revealed that feature predictions showed the same pattern of changes as visual search performance, suggesting that predictions about the target distribution, not specific memories of the average target, are linked to attentional priority. These results highlight the fact that when target features are uncertain, observers rely on predictions about possible target features rather than a single memory trace.

One outstanding question about the representation of target feature variability concerns whether the knowledge of variability is specific to targets or represented across targets. For example, it is difficult to tell with these data if there is a unique representation of variability for each target, which appear similar because all targets follow similar statistics. Or in contrast, if feature variability is coded in a common representation across targets. Future studies may address this question by using multiple targets which share features but differ in variability to test for target specific knowledge of the variability.

Furthermore, while our data suggest that predictions influence feature-based attentional priority, it is difficult to tell whether this change in priority is specific to changes in guidance

or target decisions. Previous work has shown that the initial guidance of attention is a distinct process from target-match decisions, and that these two processes may rely different information about target objects (Rajsic & Woodman, 2019; Wolfe, 2021; Yu et al., 2022). However, this study cannot determine how predictions influence attentional priority at each stage of visual search. Thus, we are agnostic to whether these results describe a change in the information being used for guidance or target-match decisions within a visual search cycle.

In conclusion, we have shown that the target template encodes detailed predictive knowledge that is vital to the search process and determines how attention is allocated in feature-based attention. Our work joins a growing literature that reframes the target template as an inherently prospective construct that seeks to maximize predictive information for the upcoming task and ignore information with little predictive value (Nobre & Stokes, 2019). These findings inform theories of attention by showing how attentional systems overcome the uncertainty of dynamic stimuli during goal directed processing, and by showing that predictive processes play a key role in setting priority for uncertain targets.

## Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

## Acknowledgements

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## Data Availability

These data are available on Open Science Framework (OSF) at this location: [https://osf.io/at5z4/?view\\_only=0419490d3f93433cbc71a317892d7614](https://osf.io/at5z4/?view_only=0419490d3f93433cbc71a317892d7614)

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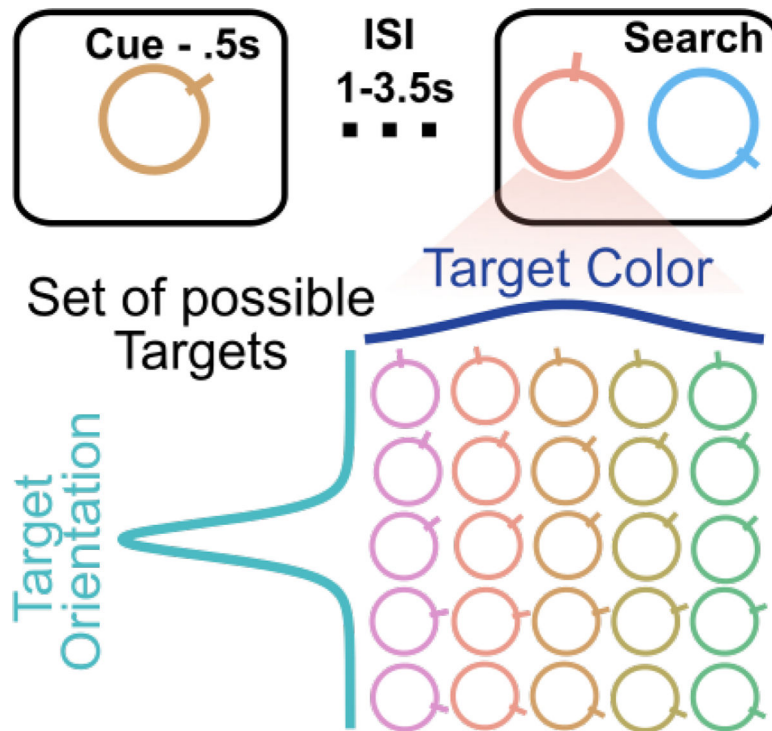


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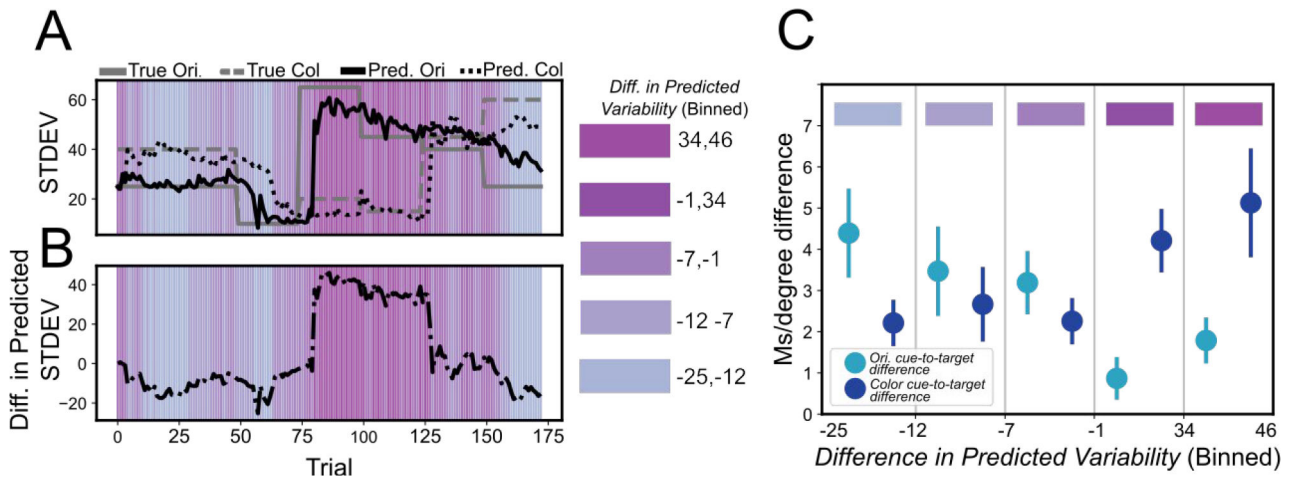
### Significance statement

Theories of attention and working memory posit that when we engage in complex cognitive tasks, our performance is determined by how precisely we remember task-relevant information. However, in the real world, properties of objects change over time, creating uncertainty about many aspects of the task. There is currently a gap in our understanding of how cognitive systems overcome this uncertainty when engaging in common behaviors like visual search. In two studies we show that when searching for target objects, observers readily learn the distribution of possible target features and leverage this information to make predictions about which features will best guide attention in the upcoming search. Further, we show that these predictions are distinct from memory, and uniquely influence attention when search targets are uncertain. These results help advance theories of attention and working memory by explaining how we use learning and prediction to overcome uncertainty in the environment.



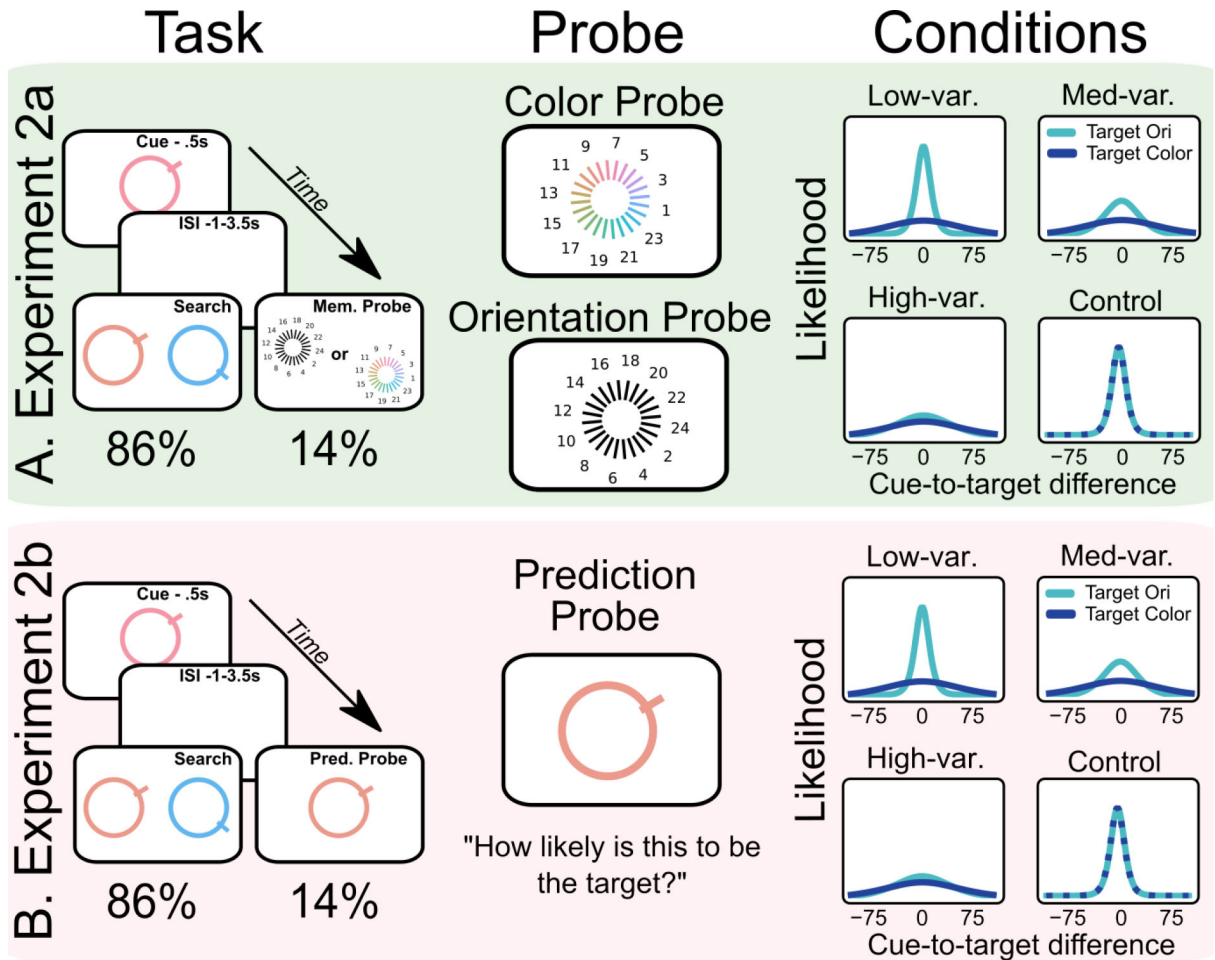
**Figure 1).**

Task schematic for Experiment 1 with example trial where orientation is the low-variability feature. Each trial began with the presentation of a cue, which lasted 500ms. After a short delay, participants were asked to search for the target most similar to the cue as quickly as possible and report its location. Stimuli were visible for 500ms. The set of targets illustrate possible target features for one example cue with particular color and orientation features. The actual distribution of features was continuous in 1-degree units over each feature space. The “Target Color” and “Target Orientation” distribution represent the relative likelihood with which a target object would have each feature in a case where color variability is high, and orientation variability is low, but these distributions changed overtime (see methods).

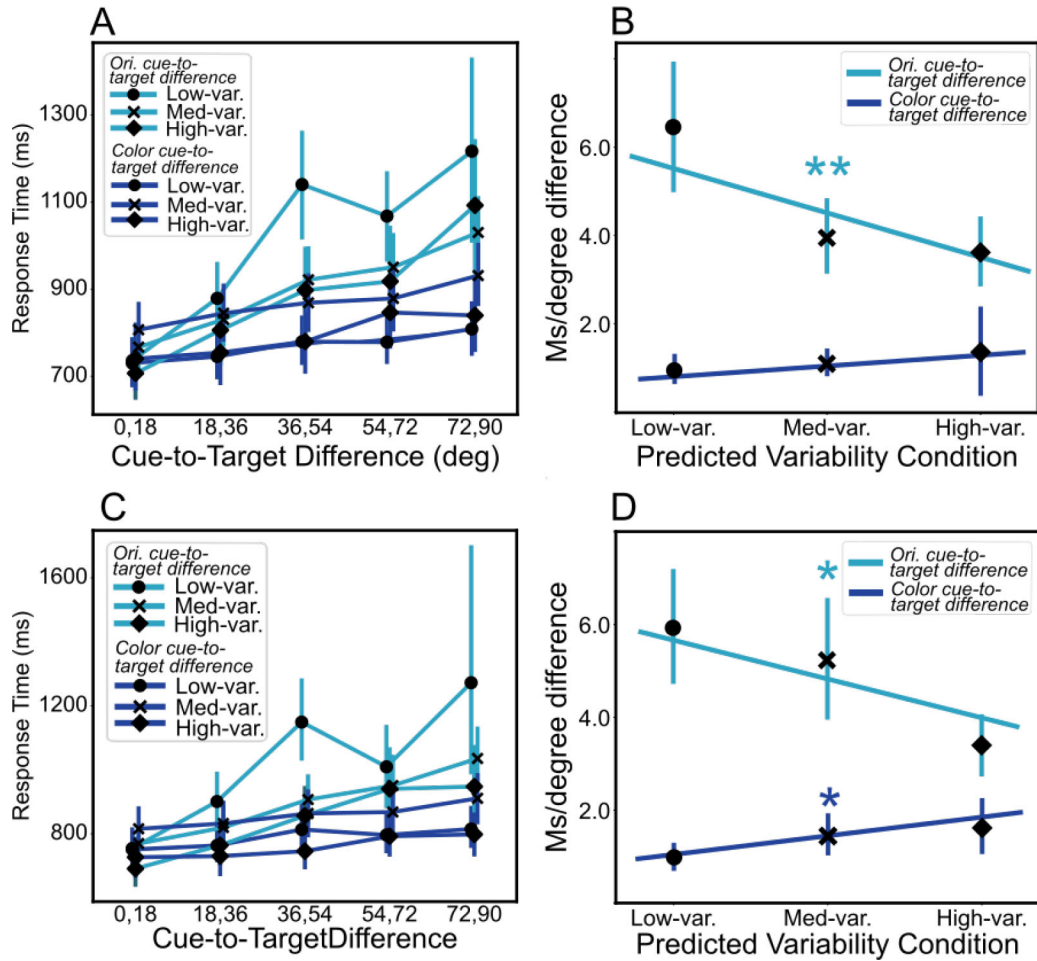


**Figure 2:**

A) Predicted variability estimates for each feature were derived from a Bayesian learning model that tracked changes in the STDEV of each target feature distribution given previously seen targets (Black lines). These estimates of STDEV were the same across participants. Estimated STDEV per trial are overlaid on the true STDEV of each feature distribution (Grey lines). Background hue (blue to purple) indicates the difference in predicted variability. Blue colors indicate trials when orientation STDEV is lower than color (i.e., orientation has lower predicted variability); purple colors indicate trials when color STDEV is lower (i.e., color has lower predicted variability). B) Same as A but shows the *difference in predicted variability* across trials used in the regression model. C) Illustration of the interaction between cue-to-target difference and difference in predicted variability for orientation (dark blue) and color (teal). Color bars at the top indicate the trials in A from which the data were taken. Bins were created such that there were approximately equal trial numbers in each bin per participant. The Y-axis indexes the change in RT (in milliseconds) per degree of cue-to-target dissimilarity for each feature. Error bars represent a 95% confidence interval.

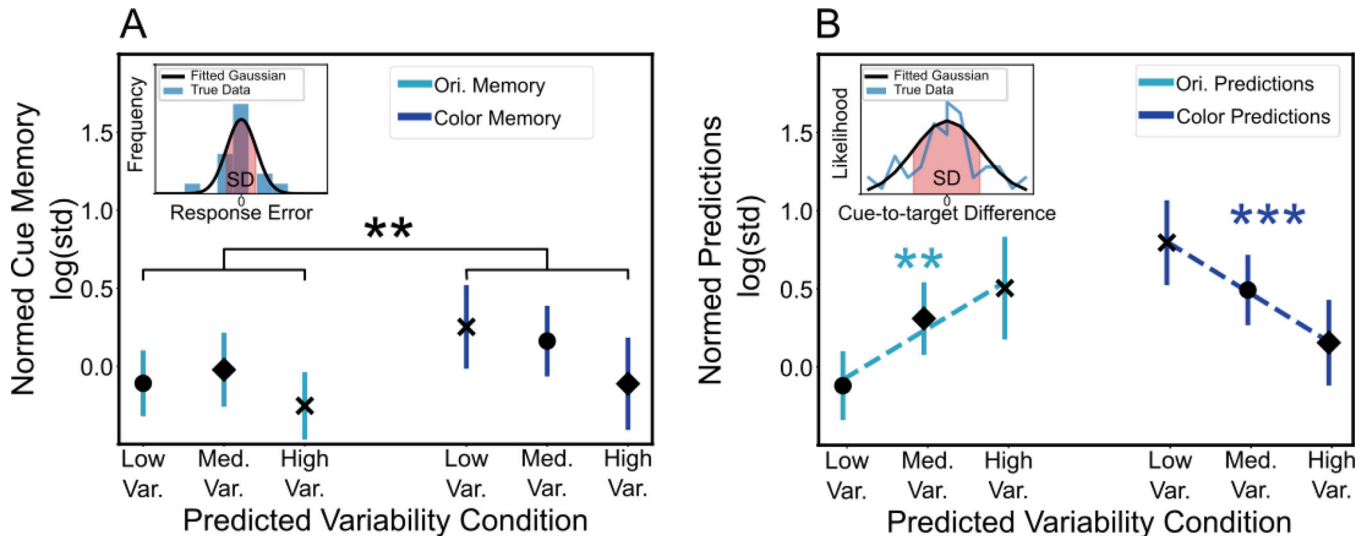
**Figure 3:**

A) Task schematic for Experiment 2a. Each trial began with the presentation of a cue, which lasted 500ms. On each trial, participants were asked to either search for the target object (86% of trials) or complete a memory probe task (14%) in which they reported the remembered features of the cue item by pressing the number associated with the remembered feature. Participants were split into 3 *predicted variability* conditions and 1 *control condition* defined by the distribution of target features (see Figure 1 for illustration of search target variability). B) Same as A but for Experiment 2b. In this experiment, participants completed a “prediction probe trial” by reporting the predicted likelihood of a possible stimulus being the target.



**Figure 4:**

A) Mean response time for binned values of *cue-to-target difference* in Experiment 2a for color and orientation separately. Bins were created by splitting the data into equally portioned quantiles. Each line represents the increase in response times due to a specific cue-to-target difference for orientation (light blue) or color (dark blue) in each *predicted variability* condition (denoted by marker points). B) Points represent the slopes from A for each *predicted variability* condition with error bars representing the 95% confidence interval. C) same as A but for Experiment 2b. D) Same as B but for Experiment 2b. \*= $p < .05$ , \*\* =  $p < .01$



**Figure 5:**

A) Fitted standard deviation of memory probe responses in each *predicted variability* condition for Experiment 2a. Error bars represent the 95% confidence interval around the mean of each group. Y-axis represents the difference in variability relative to the *control condition* B) Same as A but for prediction probe responses in Experiment 2b. The colored lines show the best-fit line for differences between variability conditions. \*\* =  $p < .01$ , \*\*\* =  $p < .001$

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