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Learned feature variance is encoded in the target template and drives visual search

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Abstract

Real world visual search targets are frequently imperfect perceptual matches to our internal target templates. For example, the same friend on different occasions is likely to wear different clothes, hairstyles, and accessories, but some of these may be more likely to vary than others. The ability to deal with template-to-target variability is important to visual search in natural environments, but we know relatively little about how feature variability is handled by the attentional system. In these studies, we test the hypothesis that top-down attentional biases are sensitive to the variance of target feature dimensions over time and prioritize information from less-variable dimensions. On each trial, subjects were shown a target cue composed of colored dots moving in a specific direction followed by a working memory probe (30%) or visual search display (70%). Critically, the target features in the visual search display differed from the cue, with one feature drawn from a distribution narrowly centered over the cued feature (low-variance dimension), and the other sampled from a broader distribution (high-variance dimension). The results demonstrate that subjects used knowledge of the likely cue-to-target variance to set template precision and bias attentional selection. Moreover, an individual's working memory precision for each feature predicted search performance. Our results suggest that observers are sensitive to the variance of feature dimensions within a target and use this information to weight mechanisms of attentional selection.

Keywords

Template; Visual Attention; Feature Based Attention; Variability

Introduction

Visual attention helps us identify objects that are relevant for goal-directed behavior, but the world we live in is highly dynamic and the features of target objects can vary over time. For example, imagine going to meet your friend in a park on a summer afternoon. As you search, you may recall the way she looked the last time you saw her, but this will not perfectly predict her appearance today. She may be wearing different clothes, have a

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Data Availability

These data are available on Open Science Framework (OSF) at this location: <https://osf.io/ep9sa/>

different hairstyle or accessories, and you may not know what she will be doing (e.g., walking or sitting). This means that your attentional template, or the representation of the target held in memory (Desimone & Duncan, 1995; Duncan & Humphreys, 1989; Geng & Witkowski, 2019; Olivers, Meijer, & Theeuwes, 2006), may be imprecise, impairing your ability to locate your friend. The attentional system must deal with this target variability during visual search in natural environments, but how it does so is poorly understood.

Here, we examine how top-down knowledge about the variance of feature dimensions might change the construction of templates to ameliorate the effects of uncertainty. For example, as you search for your friend you may remember that some “dimensions” of your friend are less variable than others and knowing which dimensions are reliable over time can help you find her. If you know your friend normally wears bright red glasses, but is constantly changing her style of clothes, you can focus on information about your friend that is likely to be similar to the last time you saw her (i.e. the glasses) and down-weight information that is likely to change (i.e. her clothes) (Olivers, Peters, Houtkamp, & Roelfsema, 2011).

Previous research has found costs in visual search performance when templates are less precisely specified or fail to exactly match the target (Malcolm & Henderson, 2010; Schmidt & Zelinsky, 2009; Yang & Zelinsky, 2009). For example, Hout & Goldinger (2014) cued subjects to a subsequent target with an exact visual copy of the object, the same object in a different state (e.g., configuration or viewpoint), or a different exemplar from the same category. They found that cues that were visually more dissimilar from the target produced longer response times, scan paths to find the target, and dwell time on the target (see also, Malcolm & Henderson, 2009; Nako, Wu, Smith, & Eimer, 2014; Reeder & Peelen, 2013).

This is presumed to happen because the target information held within the template is used to set sensory gain and decide if an object is the target (Chelazzi, Duncan, Miller, & Desimone, 1998; Chelazzi, Miller, Duncan, & Desimone, 1993; Desimone & Duncan, 1995; Kastner & Ungerleider, 2000; Moore & Fallah, 2001). For example, when searching for a red colored object, mechanisms of gain enhancement will increase the response of sensory neurons encoding “red”, resulting in increased firing rate, larger amplitude ERPs, and increased BOLD activation to all red stimuli in the visual field (Andersen, Hillyard, & Müller, 2008; Giesbrecht, Woldorff, Song, & Mangun, 2003; Liu, Larsson, & Carrasco, 2007; Ruff et al., 2006; Serences, Saproo, Scolari, Ho, & Muftuler, 2009; Treue & Trujillo, 1999; Zhang & Luck, 2009). These changes lead to better target selection. However, when the template-to-target correspondence is poor, then gain enhancement will be inaccurate and lead to longer search and decision times.

While there is good evidence for why there are performance costs when the template-to-target match is inaccurate, it remains unclear how the attentional system copes when there is uncertainty about target features. How are priority signals set when the target features themselves are variable? Dimension weighting provides evidence that it is possible to selectively enhance specific feature dimensions (e.g. color, orientation, size), even when the exact features of the target are unknown (Found & Müller, 1996; Müller, Heller, & Ziegler, 1995; Müller, Reimann, & Krümmenacher, 2003; Müller & Krümmenacher, 2006; Pollmann, Weidner, Müller, & von Cramon, 2006; Reshanne R. Reeder, Hanke, & Pollmann,

2017). These studies find that information from an entire dimension can be “weighted” if that dimension reliably distinguishes the target from distractors. For example, in Müller et al. (1995) subjects searched for a singleton target in one dimension (e.g., color) amongst distractors from another dimension (e.g., orientation, size). When the dimension that distinguished targets from distractors could be predicted, subjects were equally good at finding the target as control subjects who knew the exact target feature. Similar to single feature enhancement, dimension weighting appears to increase sensory gain for task-relevant dimensions (Gramann, Toellner, Krümmenacher, Eimer, & Müller, 2007; Pollmann et al., 2006; Reshane R. Reeder et al., 2017; Töllner, Zehetleitner, Gramann, & Müller, 2010; Wei, Yu, Müller, Pollmann, & Zhou, 2018).

Evidence from visual search (Kerzel & Witzel, 2019) and retro-cueing paradigms (Hollingworth & Hwang, 2013; Niklaus, Nobre, & Van Ede, 2017; Rajsic, Ouslis, Wilson, & Pratt, 2017; Rajsic & Woodman, 2019) have shown that task-relevant dimensions are also represented with greater precision compared to non-relevant dimensions in working memory. For example, in Niklaus, Nobre, & Van Ede (2017), showed participants an array of three colored arrows that were to be held in memory until subjects were probed to report the color or orientation of one arrow. During the interval between viewing the array and the probe response, subjects were cued with 75% validity as to which dimension would be probed. Critically, the cue did not indicate a specific arrow, and consequently, subjects did not know exactly which feature value would be probed. The results showed greater precision for the retro-cued dimension compared to the un-cued dimension. This demonstrates that multiple features within a dimension can be sharpened in working memory when they are believed to be task-relevant.

In the current studies, we examine how template specificity is shaped by top-down knowledge of the variance in different feature dimensions. To test this hypothesis, we use a novel paradigm in which target feature values change between the target cue and the actual target within the visual search display. Importantly, the changes in the two feature dimensions are governed by distributions such that the variance of one dimension is smaller than the other. We hypothesized that the expected variance of each feature would be 1) reflected in the contents of the target template because it is task-relevant and 2) be used to weight attentional priority towards the feature with less variance during visual search. Further, we directly compared the effects of template-to-target similarity on visual search performance against other known metrics of search difficulty including target-distractor similarity and distractor-distractor similarity (Chetverikov, Campana, & Kristjánsson, 2017; Duncan & Humphreys, 1989).

Experiment 1

The purpose of this first experiment was to test the hypothesis that the target template will reflect task-relevant expectations of the cue-to-target feature variance and predict the effect of each feature on visual search. We do this by using an experimental procedure in which participants are shown a cue stimulus on every trial composed of color and motion. The cue is followed by one of two tasks, interleaved across trials: One is a probe task that assesses the memory precision of each of the two cued features using color and direction wheels; the

second is a visual search task to measure how cue-to-target variance in each feature dimensions affects RT and decision times. Use of the two tasks is critical to acquiring separate measurements of the contents of the target template created from the cue stimulus, and the use of that information during visual search with distractor competition.

Methods

Participants: Forty students (females = 28, mean age = 20.35 years) from the University of California, Davis were recruited to participate in the study. This sample size was calculated from pilot data with G*power (<http://www.gpower.hhu.de/>) showing that it would give us at least 80% power in an ANOVA comparing template precision, at a partial eta-squared of .015. All participants had normal or corrected-to-normal vision, normal color vision, and received course credit for participating in the experiment. Thirty-Nine subjects were right-handed.

Procedure: Trials began with the presentation of a centrally presented cue, a random-dot-kinematic (RDK) of colored dots moving in a specific direction with 100% coherence, for 1000ms (Fig.1a). This was followed by a jittered ISI between 2000–3000ms and then one of two tasks. On 70% of trials, the cue was followed by a visual search display in which subjects we instructed to report the location of the target that most closely matched the cue by clicking on it with a mouse. Subjects were told to respond as rapidly as possible without sacrificing accuracy. The stimuli were RDKs viewed within an outline of a circle aperture 3.5° of visual angle in radius. Each RDK was 3.88° of visual angle from the central fixation cross on both the horizontal and vertical axis, and one stimulus was presented in each quadrant of the screen. All RDKs disappeared after 1000ms, but there was no limit on the time to respond. The circle outline bounding the RDKs remained visible on screen until the response.

Critically, on visual search trials, the target features changed from the cue systematically, creating variance in cue-to-target similarity between trials. Cue-to-target similarity was defined as the difference between the feature values of the cue and the target for each dimension independently. Each target feature was drawn from one of two Gaussian distributions, that were centered at zero (Fig.1b). However, the low-variance distribution had a standard deviation of 3.8°, bounded at –15 to 15 degrees from the cue. The high-variance distribution had a standard deviation of 38 degrees, bounded at –70 and 70 degrees from the cue. Half of all subjects had motion as the low-variance dimension and color as the high-variance dimension (i.e., the “motion” group), while the other half had color as the low-variance dimension and motion as the high-variance dimension (i.e., the “color” group). Distractors were pulled from a uniform distribution between –135 and 135 degrees, although all distractors were required to be at least 30 degrees further from the cue than the target feature in the same dimension. This was done so that the target features in each dimension were closer to the cue than any another object within the visual search array. Thus, either dimension could be used to find the target, but the task-relevance of each dimension was defined by its expected variability because weighting the less-variable dimension could lead to more efficient target selection.

On the other 30% of trials, the cue stimulus was followed by a color wheel or a motion-direction wheel on which subjects indicated the remembered color or motion-direction of the cue. These trials served as a direct measurement of the template representation of the two cued target features in working memory.

The experiment progressed in two parts. The first part consisted of 220 training trials, in which subjects were “trained” on the distributions through repeated exposure to search displays. Probe Trials were included here to prevent subjects from noticing any changes when the test session began. This was followed by 220 test trials, which were identical to the training trials, but now included “switch” trials on 15% of trials. On switch trials, each target feature was drawn from the opposite distribution (i.e., the high-variance feature was now the low-variance feature). This increased the observed variance of the low-variance distribution and decreased the observed variance of the high-variance dimension, allowing us to measure the effect of unexpected cue-to-target similarity values. Inclusion of these trials did not change the center of the distributions (both remained at zero) but increased the overall observed variance of the low-variance dimension to a standard deviation of 12.88 and the high-variance distribution to a standard deviation of 22.5. Only data from the test trials were analyzed. In total, subjects completed 420 trials with a short break every 60 trials. Once subjects made a response, there was a 2000–3000ms inter-trial-interval before the next trial began.

Apparatus and Stimuli: Stimuli were presented on an ASUS MG279Q monitor with a screen resolution of 1920×1200 pixels and a refresh rate of 60Hz. A computer running PsychoPy (Peirce, 2007) controlled all stimulus presentation and the recording of response variables. All participants were seated 60cm from the screen.

Stimuli were colored RDKs subtending 3.5 degrees of visual angle, with coherence set to one. Each RDK consisted of 20 dots that were .21 degrees of visual angle in diameter and moved at a speed of 2.4 degrees of visual angle per second. Motion and color were both randomly selected on each trial from a uniform distribution of motion directions in a 360-degree circle, and colors from CIE space (Bae, Olkkonen, Allred, & Flombaum, 2015) with one-degree increments.

Baseline experiment: In order to establish any inherent differences in representing the two feature dimensions (color, motion), a “baseline experiment” was run in which subjects only performed the memory probe task for a cued stimulus (Fig. 1a), without interleaved visual search trials. The baseline experiment was used to establish the default precision of representing each feature dimension, irrespective of our manipulation of cue-to-target variance.

Twenty different students (females = 11, mean age = 21.37 years) from the University of California, Davis were recruited to participate in the study. Seventeen of these subjects were right-handed. The results showed that motion probe responses ($M=11.05$, $SD=4.69$) were significantly more precise than color probe ($M=17.25$, $SD=7.05$) responses ($t(19)=-6.19$, $p<.001$, $BF_{10}>300$). This suggests that representation of motion direction in our stimulus space was more precisely represented at baseline.

Results: We first looked at the response error on probe trials as a measure of the precision of template representations for the target. Subjects' mean absolute response errors were normalized with respect to baseline response errors. We did this by calculating the deviation of each subjects mean response from baseline responses, weighted by the variance in baseline responses. We then recoded the probes so that it reflected whether the dimension was the low-variance or high-variance dimension for each subject and compared the response errors in a 2 (group) x 2 (dimension) ANOVA (Fig.2). The results showed no main effect of group ($F(1,38)=.51$, $p=.48$, $BF_{10}=.36$) nor an interaction between group and dimension ($F(1,38)=1.79$, $p=.19$, $BF_{10}=.6$). Importantly, there was a significant effect of dimension such that the low-variance dimension was represented with lower error (i.e., more precisely) than the high-variance dimension ($F(1,38)=5.46$, $p<.05$, $BF_{10}=2.8$). This confirms our hypothesis that the variance of a feature dimension was encoded in the precision of the template for each cue feature.

Overall rates of correct responses on visual search trials were high for the motion group ($M=.95$, $SD=0.48$) and the color group ($M=.93$, $SD=0.36$), and no difference was detected between groups ($t(35.18)=-1.04$, $p=.35$, $BF_{10}<.45$). Due to near ceiling performance on accuracy and our a priori hypothesis that these effects would be more prominent in response times (RTs), we focused all subsequent analyses on RTs from trials where subject responded correctly. Response times were measured as the difference between stimulus onset and mouse click. Mean RTs were overall shorter when expectations of cue-to-target variance were met (Mean= 1.08 seconds, $SD=.37$) compared to when they were violated (Mean= 1.44 seconds, $SD=.21$), ($t(39)=7.05$, $p<.001$, $BF_{10}>100$). More importantly, we analyzed RTs as a function of the relationships between stimuli during search in each trial. We hypothesized that trial by trial RT would increase as the similarity between the cue and the target features decreased. Further, cue-to-target similarity in the low-variance dimension would have a greater effect on RT than the high-variance dimension, because subjects will expect the target be more similar to the cue in this dimension and rely on it more. To test these predictions, we fit a hierarchical linear model with gamma-distributed residuals (Lo & Andrews, 2015) to subject response data with six fixed effects. We used two separate regressors for the cue-to-target similarity of features in the low-variance and high-variance dimensions in each trial (lvCT and hvCT). We also included regressors for target-distractor similarity (TD) and distractor-distractor relationships (DD). More specifically, for target-distractor similarity we took the absolute value of the differences between the target and each distractor and averaged them together for the low-variance and high-variance dimensions separately (lvTD and hvTD). For distractor-distractor similarity, we calculated the difference between each distractor and averaged those values for each dimension independently (lvDD and hvDD). All regressors were normalized before model-fitting due to large differences in the scale of each metric and we included all corresponding random-effects for each subject.

The results of this analysis (Fig. 3) showed no interactions between group and any of the regressors ($\chi^2(1)<2.08$, all p 's $>.14$, all BF_{10} 's $<.05$), and no main effect of group ($\chi^2(1)=.46$, $p=.5$, $BF_{10}<.05$), suggesting that any effects on RT did not differ between groups. The model showed a significant fixed-effect of cue-to-target similarity in both the

low-variance ($\beta=.121$, $\chi^2(1)=28.21$, $p<.001$, $BF_{10}>200$) and high-variance dimensions ($\beta=.06$, $\chi^2(1)=10.43$, $p<.001$, $BF_{10}>15$). All other main effects were non-significant and in favor of the null ($\chi^2(1)$'s >3.72 , all p 's $>.05$, all $BF_{10}<.01$). We tested for a difference between these coefficients by fitting a separate model where low-variance and high-variance cue-to-target similarity were fixed to have the same effect size ($H_0:lvCT= hvCT$), and compared it to the original model where the parameters were free to differ ($H_1:lvCT \neq hvCT$). If the constrained model was an equally good or better fit for these data, this would suggest no difference in the magnitude of the coefficients. The results showed significant evidence in favor of the original model ($\chi^2(1)=11.652$, $p<.001$, $BF>3$), indicating that low-variance cue-to-target similarity coefficient was significantly larger than that for high-variance cue-to-target similarity. The pattern was confirmed by a Wald-test using the pooled variance of the regression estimates ($Z=3.69$, $p<.001$). These results show that RTs varied as a function of the cue-to-target similarity, but the strength was modulated by the dimension's expected variance: the low-variance feature was a stronger predictor of RT than the high-variance feature, consistent with the probe results showing a greater precision for the feature with lower expected variance.

To further test the relationship between cue-target similarity and visual search RT, we created a "difference in memory precision" score for each subject, calculated as the difference in probe precision between the high-variance dimension and the low-variance dimension (high-variance minus low-variance), which was then regressed against each individual's corresponding coefficient for cue-to-target similarity from the response time regression models (Fig.4). This was done separately for the low- and high-variance dimensions separately. For the low-variance dimension, we found no main effect of group ($\beta=.33$, $t(38)=.964$, $p=.34$, $BF_{10}<.3$) nor an interaction between the difference in memory precision and group ($\beta=.25$, $t(38)=.997$, $p=.49$, $BF_{10}<.25$). The results did show an effect of the difference in memory precision ($\beta=.45$, $t(38)=3.07$, $p<.01$, $BF_{10}>10$), indicating that individuals with larger precision indices also showed a larger effect of cue-to-target similarity in the low-variance dimension. This suggests that subjects who held a sharper template for the low-variance dimension were also more affected by this dimension during search when it mismatched the cue. An identical model fit for coefficients from the high-variance dimension showed the opposite effect. These results showed no interaction between the difference in memory precision and group ($\beta=.38$, $t(38)=1.07$, $p>.29$). However, we did find a main effect of group ($\beta=.88$, $t(38)=2.52$, $p<.05$, $BF>3.75$) and an effect of the difference in memory precision ($\beta=-.42$, $t(38)=-2.38$, $p<.05$, $BF=2.74$). This shows that subjects who maintained more precise representations of the low-variance dimensions prior to search weighted that information more during search and down-weighted the less precise, high-variance dimension making it less useful during search.

Eye data: To obtain a finer grained understanding of how cue-to-target similarity influenced the scan time (i.e., time to first fixate the target) and decision time (i.e., duration of looking at the target before response) of visual search, we turned to eye-tracking data. One subject was removed from these analyses due to technical issues that occurred during data collection.

First, we fit a hierarchical regression model with normally distributed residuals predicting scan time (i.e., time to first fixate the target) using cue-to-target variance, target-distractor similarity, and distractor-distractor similarity in each feature dimension as predictors (Fig.5a). Group was not included as a predictor in this model to reduce model complexity given that it had no effect on response times for search. We found that both the low-variance feature dimension ($\beta=30.47$, $\chi^2(1)=22.04$, $p<.001$, $BF_{10}>150$) and the high-variance feature dimension ($\beta=24.37$, $\chi^2(1)=11.05$, $p<.001$, $BF_{10}>3$) predicted scan times. Again, we tested the difference between these coefficient by fitting another model in which they were artificially constrained to be equal and found evidence in favor of the constrained model, suggesting that there was no significant difference in the strength of these two coefficients on scan time ($\chi^2(1)=.61$, $p=.435$, $BF_{10}<.2$; Wald-test: $Z=.785$, $p=.216$). We also found an effect of low-variance target-distractor similarity ($\beta=-14.63$, $\chi^2(1)=11.02$, $p<.001$, $BF_{10}>3$). To test whether this was different from either the cue-to-target similarity effects we flipped the sign of the coefficient (to have an unbiased estimate of absolute magnitude) then fit two independent models where the low-variance target-distractor coefficient was set to be equal to the low-variance or high-variance cue-to-target similarity coefficient. This allowed us to test whether the magnitude of the coefficient for the low-variance target-distractor similarity – independent of the sign – was different from the two cue-target effects. The model comparisons revealed a difference with the low-variance cue-target similarity ($\chi^2(1)=6.35$, $p<.05$; Wald-test: $Z=1.96$, $p<.05$), although the Bayes factor was ambiguous ($BF_{10}=.37$), and no difference with high-variance cue-to-target similarity ($\chi^2(1)=1.45$, $p=.23$, $BF_{10}<.01$; Wald-test: $Z=1.18$, $p=.12$). This suggests scan times increased similarly when the target differed more from the cue in either feature dimension and decreased when target and distractor features in low-variance dimension were dissimilar. However, cue-to-target similarity in low-variance dimension had a larger effect on scan times than target-distractor similarity.

A second model with identical regressors was fit to predict decision time (i.e., total dwell time on the target before response) (Fig.5b). The results were significant for cue-target similarity in the low-variance feature ($\beta=27.31$, $\chi^2(1)=20.43$, $p<.001$, $BF_{10}>20$), but not the high-variance feature ($\beta=9.87$, $\chi^2(1)=2.56$, $p=.1$, $BF_{10}<.05$). All other regressors had a null effect (all $\chi^2(1)$'s < 1.4 , all p 's $> .24$, all $BF_{10}<.05$). These results extend the RT and scan time analyses showing that cue-target similarity in the low-variance dimension was the primary source of information used to search for and decide if an object is the target. This suggests that statistical regularities in each feature dimension contributed to information processing at different stages of visual search. Higher attentional priority was given to information from low-variance dimension resulting in more precise encoding of that dimension and more reliance on the dimension guide search and make target decisions.

Discussion: The purpose of Experiment 1 was to test the hypothesis that statistical regularities governing cue-to-target similarity in two feature dimensions would be reflected within the target template and have a concomitant effect on visual search efficiency. The data were consistent with these hypotheses, showing that on probe trials there was a smaller response error for the low-variance feature compared to the high-variance feature; on visual search trials, RT was better predicted by the cue-to-target similarity on the low-variance than

the high-variance feature dimension. Moreover, individuals with a greater precision for the low-variance dimension were more affected when the low-variance target feature was distant from the cue. This suggests a direct relationship between the precision of the template representation on each dimension and the effect of cue-to-target similarity in a feature dimension during visual search.

In addition to overall RT, the eye data demonstrated that the effect of cue-target variance on visual search could be broken down into two components: search duration, indicated by scan time and decision duration, indicated by the fixation time on the target. Interestingly, scan time was influenced by both feature dimensions, but decision time was predicted only by the low-variance feature. This suggests that the dimension with lower variance was the primary information source for deciding if an object is the target, but both dimensions affected the time to locate the target. Together, these results demonstrate that subjects maintain a more precise representation of low-variance dimension and correspondingly relied on information from low-variance during visual search.

Experiment 2

The purpose of Experiment 2 was to provide a conceptual replication of Experiment 1 and test if stronger distractor competition would reduce the effect of cue-to-target variance on visual search. Distractor competition is hypothesized to be a core precondition for attentional selection (Desimone & Duncan, 1995; Duncan & Humphreys, 1989). It was therefore somewhat surprising in Experiment 1 to find that target-distractor similarity and distractor-distractor similarity did not predict RT. One reason for this may be that distractors were sufficiently distant from targets in Experiment 1 (i.e., at least 30 degrees from the target, sampled from a uniform distribution) that they produced very little competition for attention (Duncan, 1989; Wolfe et al. 1989; Wolfe, 1992). In this experiment, we increased distractor similarity, and therefore competition for attention, by focusing distractor distributions much closer to the target distributions. We expected the increase in search difficulty to increase RTs overall. The critical question was whether doing so would also lead to the emergence of target-distractor similarity and distractor-distractor similarity as predictors of visual search RT and scan times. However, we predict that the manipulation will not change the effect of cue-to-target similarity decision times, given that decisions are more purely based on matching the current stimulus to the target template.

Participants—Forty students (Females = 24, Age = 20.9) from the University of California, Davis were recruited to participate in the study. All participants had normal or corrected-to-normal vision, normal color vision, and received course credit for participating in the experiment. Thirty-six subjects were right-handed.

Procedure—All methods were identical to Experiment 1, except for the feature distributions used. New distributions were used to increase the likelihood that distractors would be highly similar to a given target object and create more competition. To do this, both motion and color distractors were drawn from bimodal distributions centered on -45 and 45 degrees with SD's of 5 degrees (Fig.6). However, when color was the low-variance dimension (in the color group) color distractors were drawn from distributions centered on

–25 and 25 degrees with SD's of 5 degrees – this was necessary to ensure competition given that 25 degrees is the average distance between the category boundary and category center for all colors (Bae, Olkkonen, Allred, & Flombaum, 2015).

The target features from the high-variance dimension were drawn from a bimodal distribution with centers at –35 and 35, and SD's of 3.8 (Fig.6). This ensured that the distractor features were always near target features, while still maximizing the distance of the high-variance target feature from the cue. The low-variance target distribution was the same as in Experiment 1. Because the high-variance target distributions were non-overlapping with the low-variance target distributions, target features in each dimension were always inversely correlated with each other – when one feature was sampled from the low-variance distribution, the other was sampled from the distributions centered 35 degrees away, and vice versa on switch trials. This meant that the overall distribution for the low-variance features had standard deviation of 12 degrees and the high-variance distribution had a standard deviation of 33 degrees. Because of this covariation in the two target features, we used a single metric of feature similarity in our analyses that combined both features dimensions together in this experiment. The combined regressor represents the impact of the expectation that the low-variance dimension will have feature values more similar to the cue than the high-variance dimension.

Results—We again first looked at the error in probe responses as a measure of the precision of the template representation for the cue. The response errors were first normalized with respect to baseline error data and then compared in a 2 (group) x 2 (dimension) ANOVA. Replicating results from Experiment 1, we found no effect of group ($F(1,38)=.114, p<.737, BF_{10}=.3$) nor an interaction between group and dimension ($F(1,38)=.878, p=.35, BF_{10}=.47$). Only main effect of dimension ($F(1,38)=6.38, p<.01, BF_{10}>3$) was significant, showing that the low-variance dimension was more precisely represented compared to the high-variance dimension. This result replicates the probe data from Experiment 1.

Overall accuracy rates were lower for both motion (Mean = .69, SD=.07) and color groups (Mean = .65, SD=.08), compared to Experiment 1, but no differences were found between groups ($t(39)=1.73, p=.09, BF_{10}=1$). The change in accuracy reflects our success in increasing the difficulty of search through increased distractor competition. Similarly, mean RT's were longer in Experiment 1 (M=1.46s, SD=.18) than Experiment 2 (M=1.14s, SD=.2), ($t(76.43)=7.43, p<.001, BF_{10}>200$), suggesting that increasing distractor competition did indeed make the visual search task more difficult (Fig.8).

Next, we fit regression models in the same way as Experiment 1, with the exception that now the cue-to-target similarity in both dimensions were combined into a single regressor representing the overall cue-to-target similarity. This was done by subtracting the high-variance cue-to-target similarity from the low-variance cue-to-target similarity. Negative values mean that the low-variance target feature was closer to the cue on that trial; positive values mean that the low-variance target feature was more distant from the cue on that trial (which occurred infrequently). We coded it this way so that larger positive coefficients

would correspond to longer RTs in response to target stimuli that mismatched the anticipated target values.

Mean RTs were again shorter when expectations of cue-to-target variance were met (Mean= 1.41 seconds, SD=.18) compared to when these expectations were violated (Mean= 1.67 seconds, SD=.27), ($t(39)=6.89, p < .001, BF_{10} > 100$). The results showed a positive effect of cue-to-target similarity ($\beta=.048, \chi^2(1) = 7.89, p < .001, BF_{10} > 100$). This finding replicates Experiment 1 by showing that violations of the expected cue-to-target similarity increased RT (Fig.9) and suggesting that subjects relied on task-relevant expectations of target feature variance to guide attention during visual search. There was also an effect of distractor-distractor similarity in the low-variance dimension ($\beta=.016, \chi^2(1)=6.45, p < .05$), although this result should be interpreted with caution as the Bayes Factor indicated marginal evidence in favor of the null ($BF_{10} < .4$). Further, the magnitude of the coefficient was significantly smaller compared to the combined coefficient for cue-to-target similarity ($\chi^2(1) = 7.21, p < .01, BF_{10} = 1.6$; Wald-test: $Z=4.98, p < .001$), suggesting that expectations about the target features had a larger effect on RTs than distractor similarity. There were no significant main effects associated with group ($\chi^2(1) = .46, p = .5, BF_{10} < .05$) or any other conditions ($\chi^2(1)'s < 3.72$, all $p's > .05$, all $BF_{10} < .01$). There were also no interactions between group and any regressor ($\chi^2(1)'s < 2.08$, all $p's > .14$, all $BF_{10}'s < .05$), except for distractor-distractor differences ($\chi^2(1) = 6.2, p < .05$), suggesting a larger effect of distractor-distractor similarity for the color group. However, analysis of the Bayes Factor indicated evidence in favor of a null effect ($BF_{10} < .2$).

Finally, we correlated the subject specific slopes from the regression model to each subject's difference in memory precision, calculated by subtracting the probe error in the low-variance dimension from the high-variance dimension (Fig.10). We again found a positive correlation between these variables ($\beta=.46, t(38)=2.55, p < .05, BF > 10$), replicating Experiment 1. This shows that the bias in the precision of the subject's template representations in memory towards the low-variance dimension directly relates to visual search performance.

Eye Tracking—Next, we analyzed eye-tracking data by fitting a hierarchical model with normally distributed residuals to data predicting scan time using the same regressors as in Experiment 1 (Fig. 11a). A single subject was removed from these analyses due to issues during data collection. We found a null effect of cue-to-target similarity ($\beta = .04, \chi^2(1)=0.027, p=.87, BF_{10} < .05$), and null effects for target-distractor similarity ($\chi^2(1)'s < 1$, all $p's > .4$, all $BF_{10}'s < .05$). However, we found commensurate effects of distractor-distractor differences in both the low-variance ($\beta = 16.23, \chi^2(1)=10.79, p < .01, BF_{10} > 3$), and the high-variance dimensions ($\beta=14.73, \chi^2(1)=8.65, p < .01, BF_{10} = 1.2$). In addition, we found no difference in the magnitude of these coefficients ($\chi^2(1) = .049, p = .82, BF_{10} < .02$; Wald-test: $Z=.22, p=.41$). These suggest that in this task, attention was guided via perceptual grouping and rejection of distractors. However, cue-to-target similarity continued to be the only significant predictor of dwell time on the target ($\beta = 25.69, \chi^2(1)=10.67, p < .01, BF_{10} > 3$; Fig.11b). All other effects in both models were null (all $\chi^2(1)'s < 1$, all $p's > .4$, all $BF_{10}'s < .05$). These data suggest that cue-to-target similarity continued to have a unique effect on the time subjects needed to decide whether the target matched their template, but that the effect on scan time was reduced when distractor competition was increased.

Experiment 2 Discussion—Experiment 2 provides a conceptual replication of Experiment 1, again showing that expectations of cue-to-target similarity are the strongest predictor of variation in RT even when distractor competition has made the task overall more difficult. In this experiment we also increased distractor competition and show that under these conditions overall response times are longer, with increases in the effect of distractor-distractor similarity on search and scan time. This suggests that even though scan times may be influenced more by distractor properties when distractor competition is high, decisions about the target depend more purely on how well the stimulus matches the target template.

General Discussion

The purpose of these experiments was to test hypotheses of how expected variability in target features shape the target template and visual search performance. We introduced a new paradigm that uses systematic variation between the cue and target stimuli to ask whether the level of variation would predict the quality of the target template and visual search performance. The contents of the target template (i.e., what is remembered about the cue stimulus) was measured through probe trials that asked subjects to recall each cue feature using a color or motion wheel. These trials did not require attentional processes engaged in selection and therefore served as a direct measurement of the target representation uncontaminated by competition for attention. Target selection was measured through visual search trials that included distractors that differed in target similarity (Experiments 1 and 2). Eye-tracking data during the search display allowed us to dissociate the consequence of expected variability on the scan time to locate the target and the decision time to determine that an object is the target once it was fixated.

In the first experiment we manipulated the cue-to-target variance using two distributions, both centered on the cue feature value. They differed in that the “low-variance dimension” target feature was typically sampled from a narrower distribution than the “high-variance dimension” feature. We found that features of the low-variance dimension were represented more precisely in the target template and cue-to-target similarity along this dimension was significantly better predictor of visual search RT. Moreover, the low-variance feature predicted both scan times and decision times, while the high-variance feature only predicted scan times.

This pattern of results indicates both target features were used to locate target, but only the more precise one was used to make the final decision regarding whether the selected object was indeed the target. Subjects clearly used the task-relevant expectations of cue-to-target variance to bias the target template towards the more reliable feature, but this bias was not all-or-none: the high-variance feature was still maintained and used to constrain search for the target, as indicated by the significant coefficient for high-variance cue-to-target similarity. This latter finding is in line with those from Foerster & Schneider (2018) showing that the task-irrelevant color of a cue object biased the direction of first saccades during search. More generally, others have found evidence that templates in working memory are maintained as bounded features (Luck & Vogel, 1997; Vogel, Woodman, & Luck, 2001), but attentional biases toward each feature are weighted toward their task-relevance (Müller et al., 1995; Reshanne R. Reeder et al., 2017). Thus, our data are consistent with previous work

showing attentional guidance from task-irrelevant features and go further to show that learned variance is used to define the task-relevant dimension even both dimensions could be used to identify the target. Specifically, these data show that when target features are uncertain, the low-variance dimension is used to make target-match decisions.

In Experiment 2 we increased distractor competition in order to see if doing so would reduce the importance of cue-to-target variance on search processes. To do so, selection of distractor features was constrained to distributions that increased distractor similarity to the target. Following the literature (Duncan & Humphreys, 1989), this manipulation made search harder, resulting in overall longer visual search RTs and lower accuracy compared to Experiment 1. Despite this change, cue-to-target variance was still the strongest predictor of behavior overall. However, the eye-data now showed that distractor-distractor similarity predicted scan times. It took longer to fixate the target when distractor heterogeneity was greater. This suggests that scan times were influenced by distractor properties when the distractors were overall more similar to the target. Interestingly, cue-to-target similarity was still the only predictor of decision times once the target was fixated, replicating Experiment 1. The eye data suggests that different components of visual search (scan time, decision time) are informed by different stimulus properties (Malcolm & Henderson, 2010).

Together, these experiments show that target feature variability is reflected in the attentional template and has direct consequences on visual search. Task-relevant visual dimensions that are expected to be less variable are held in working memory with greater precision compared to those that are expected to be highly variable. The efficiency of search is similarly determined by expected variance of the task-relevant dimensions, presumably because search times are determined by how well the template matches targets. It is worth noting that in our studies, learned expectations were for task-relevant stimulus properties and therefore we cannot disentangle contributions from stimulus expectations devoid of relevance in our data. In recent years, stimulus expectations have been shown to be separable from task-relevance (Summerfield & Egnor, 2009), but in the current paradigm, the expectation of the variance of the distribution defines the task-relevance of each target feature. It is possible that subjects are estimating the perceived relevance of each feature dimension (i.e. how likely is it that they can use that dimension to identify the target) as opposed to estimating the expected features values of the target, *per se* (i.e. the likelihood that the target feature will have some value). Future work is needed to determine how expectations of stimulus values vs. their utility for target selection differ in guiding attention.

Taken together, these results illustrate that attention is sensitive to the reliability of different target feature dimensions and will adaptively encode less-variable features and use them to guide search. When subjects expect a feature dimension will be a reliable source of information about how the target will appear, they represent this information in the attentional template with greater precision and rely on this information more during search. In contrast, when a target feature is more likely to be dissimilar to the cue, it is likely to have a less precise representation and have less of an effect on search. In addition to illuminating the importance of expected variance of different target features on attention, the data suggest that visual search involves multiple stages of processing that differentially weight sources of information. In sum, these studies confirm the hypothesis that the attentional templates are

sensitive to variation in specific target features and actively weights information from low-variance dimensions compared to high-variance dimensions during visual search but also suggest that information from both dimensions are preserved during search for the target.

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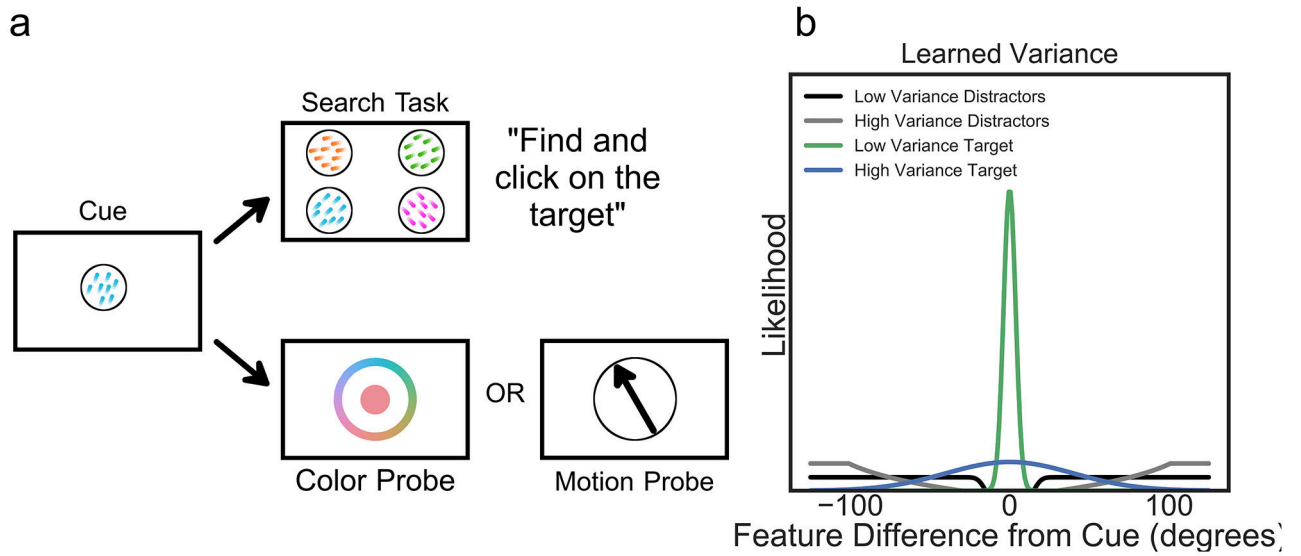


Figure 1:

a) Schematic of task. Subjects were given a cue object at the beginning of each trial defined by a randomly selected color and direction of motion. On 70% of trials, this was followed by a visual search display. On 30% of trials, they were asked to report the remembered color or motion of the cue object. b) Distributions of target and distractor features for Experiment 1. Zero represents no difference from the cue. Half of the subjects saw motion follow the “low-variance target” distribution and color follow the “high-variance target” distribution. The other half of subjects experienced the reverse.

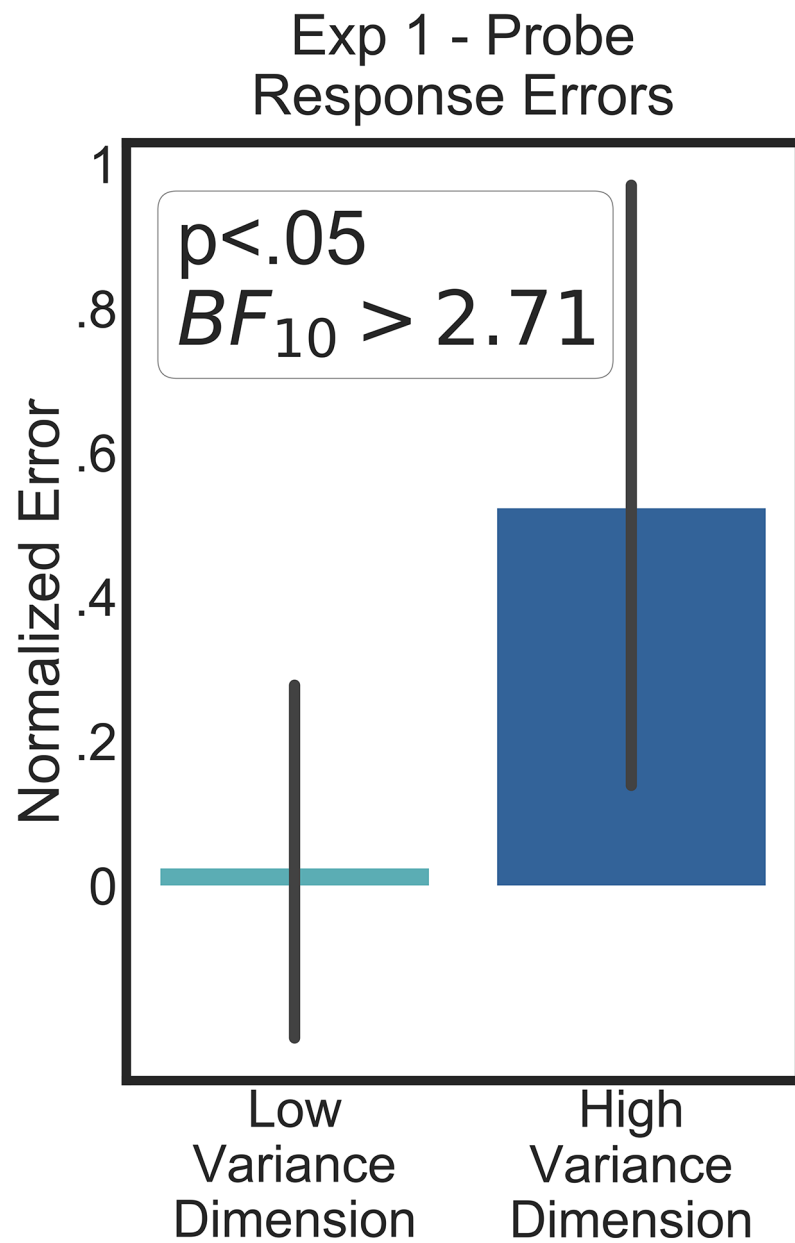


Figure 2: Response errors from probe trials. Errors were normalized to baseline values and compared. The representation of the low-variance dimension was more precise than that of the high-variance dimension.

Exp 1 - Effect of Stimulus Properties on Response Time

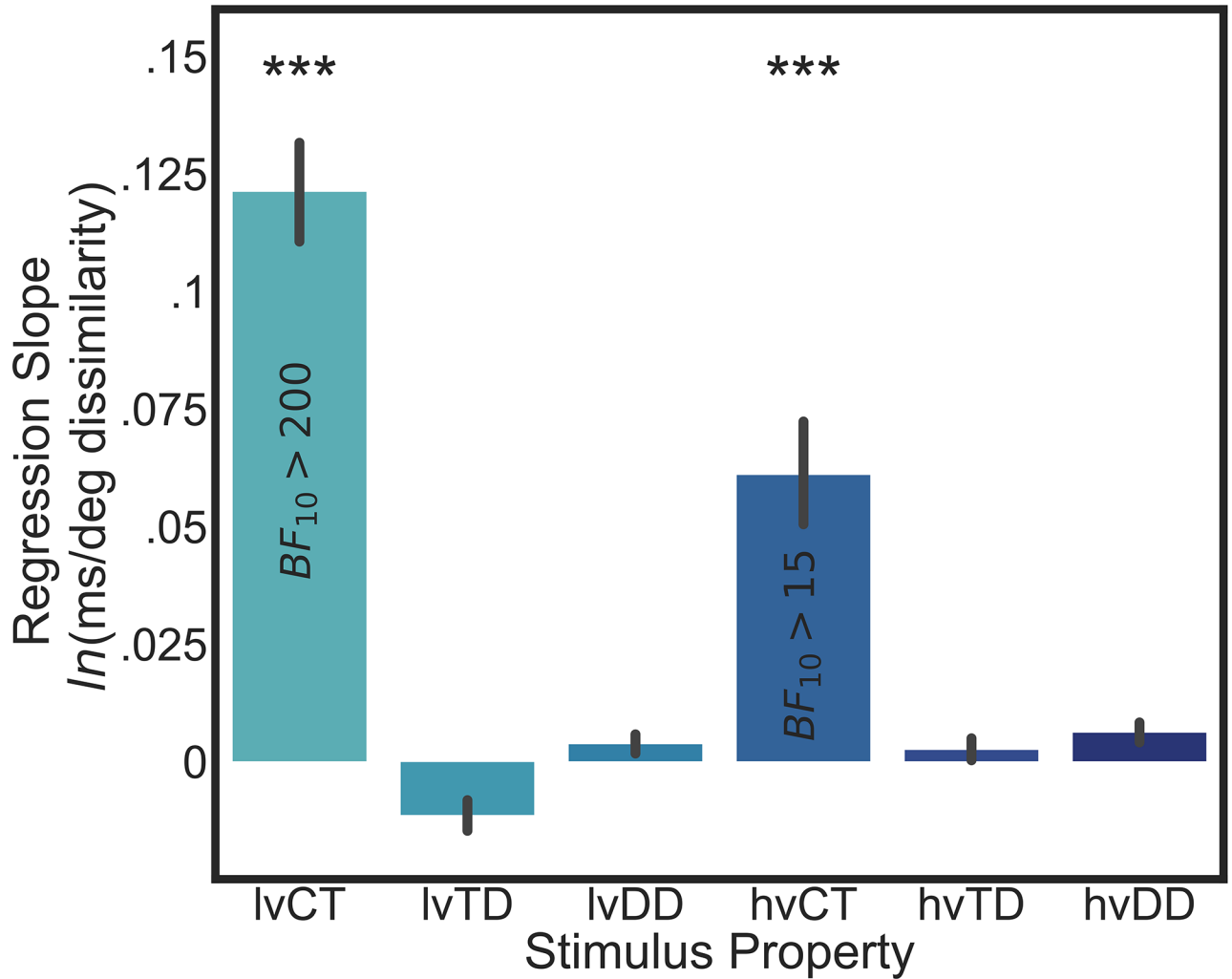


Figure 3:

Regression slopes from a multilevel model measuring the effect of stimulus properties on response time. Bar heights show the size of the fixed effect while error-bars show the variance of the subject specific random effects. The model tested the effects of cue-to-target similarity (CT), target-distractor similarity (TD) and distractor-distractor similarity (DD) for the low-variance (lv) and high-variance (hv) dimensions separately. The model showed significant effects of lvCT and hvCT only, with more of the variance in RT explained by lvCT.

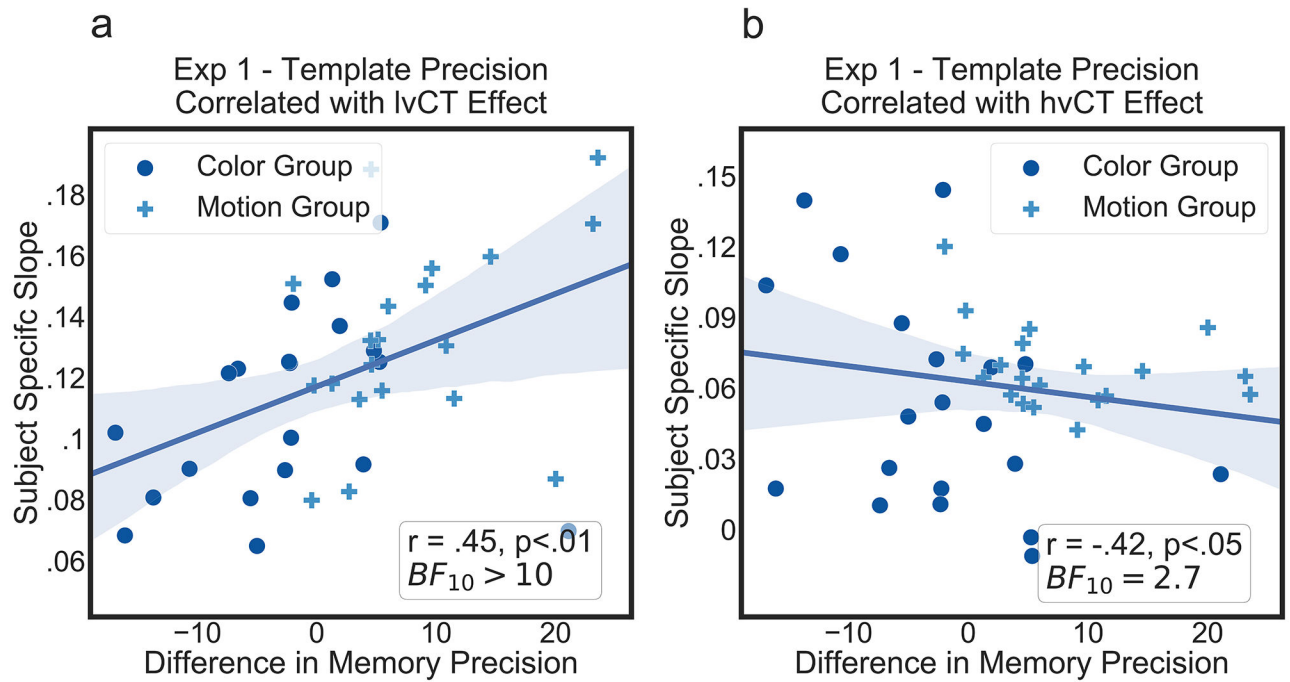


Figure 4:

Correlations between individual coefficients from the RT regression models with the difference in memory precision between feature dimensions. The difference in memory precision score was calculated for each subject by subtracting the mean response error of the low-variance dimension from that in the high-variance dimension. High values of the difference in memory precision indicate subjects had a more precise template for the low-variance dimension relative to the high-variance dimension. (a) The difference in memory precision positively correlated with lvCT and (b) negatively with hvCT, suggesting that subject with templates biased towards the low-variance dimension used that dimension more during visual search.

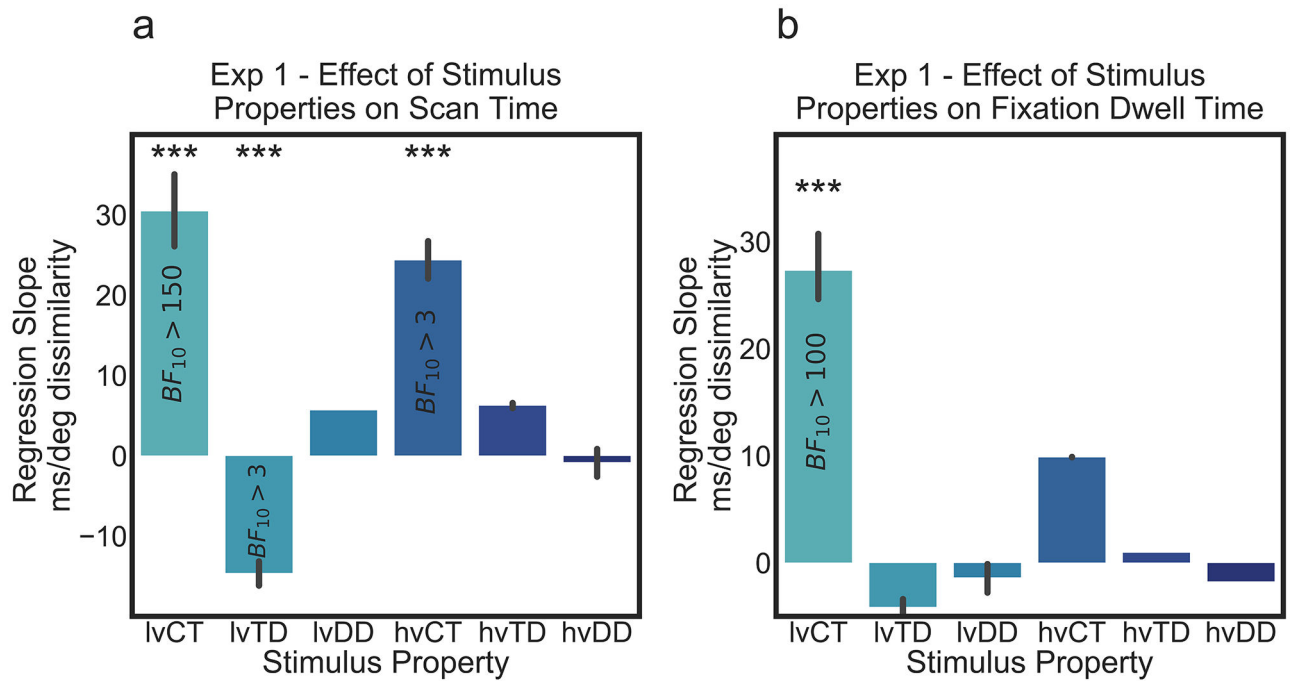


Figure 5:

Regressions slopes measuring the effect of stimulus properties on (a) scan time and (b) fixation dwell time on the target, from a multilevel regression model. Bar heights show the size of the fixed effect while error-bars show the variance of the subject specific random effects. The model tested the effects of cue-to-target similarity (CT), target-distractor similarity (TD) and distractor-distractor similarity (DD) for the low-variance (lv) and high-variance (hv) dimensions separately. Results show that while there was a small effect of lvTD, lvCT and hvCT had greater effects on scan time, indicating that the cue-to-target similarity dominated scan times. However, only lvCT influenced fixation dwell times, suggesting that the similarity of the cue-to-target in the low-variance dimension played a unique role in deciding if the stimulus matched the target.

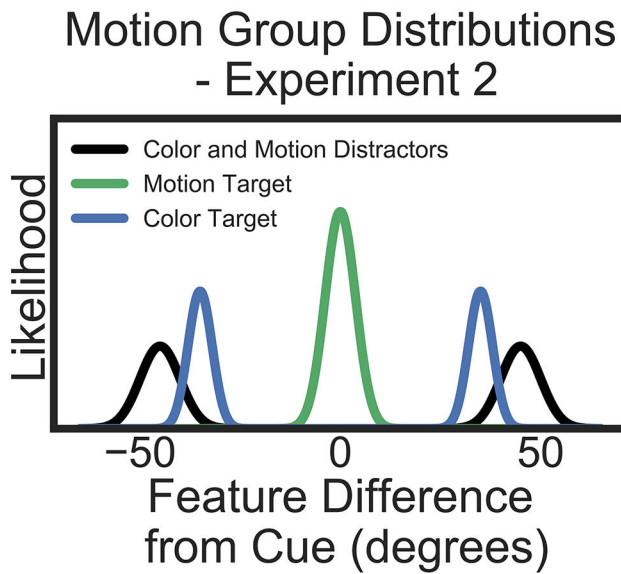
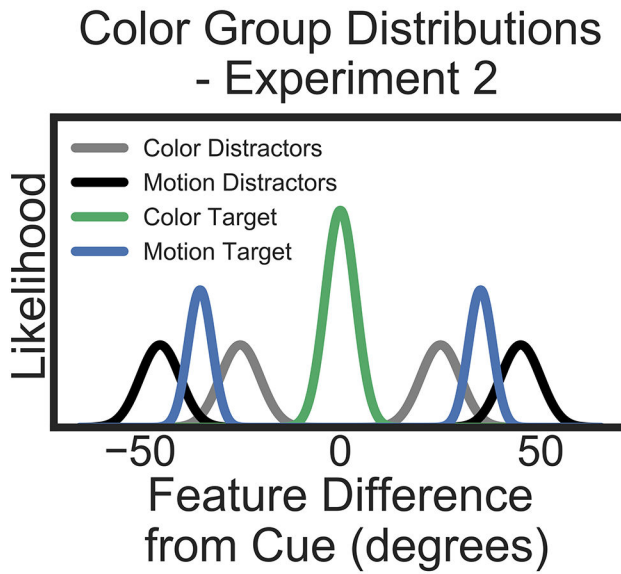


Figure 6: Distributions of target and distractor features for Experiment 2 for the “color group” and the “motion group”. Zero represents no difference from the cue. The distractor distributions were generated around category boundaries to increase distractor competition.

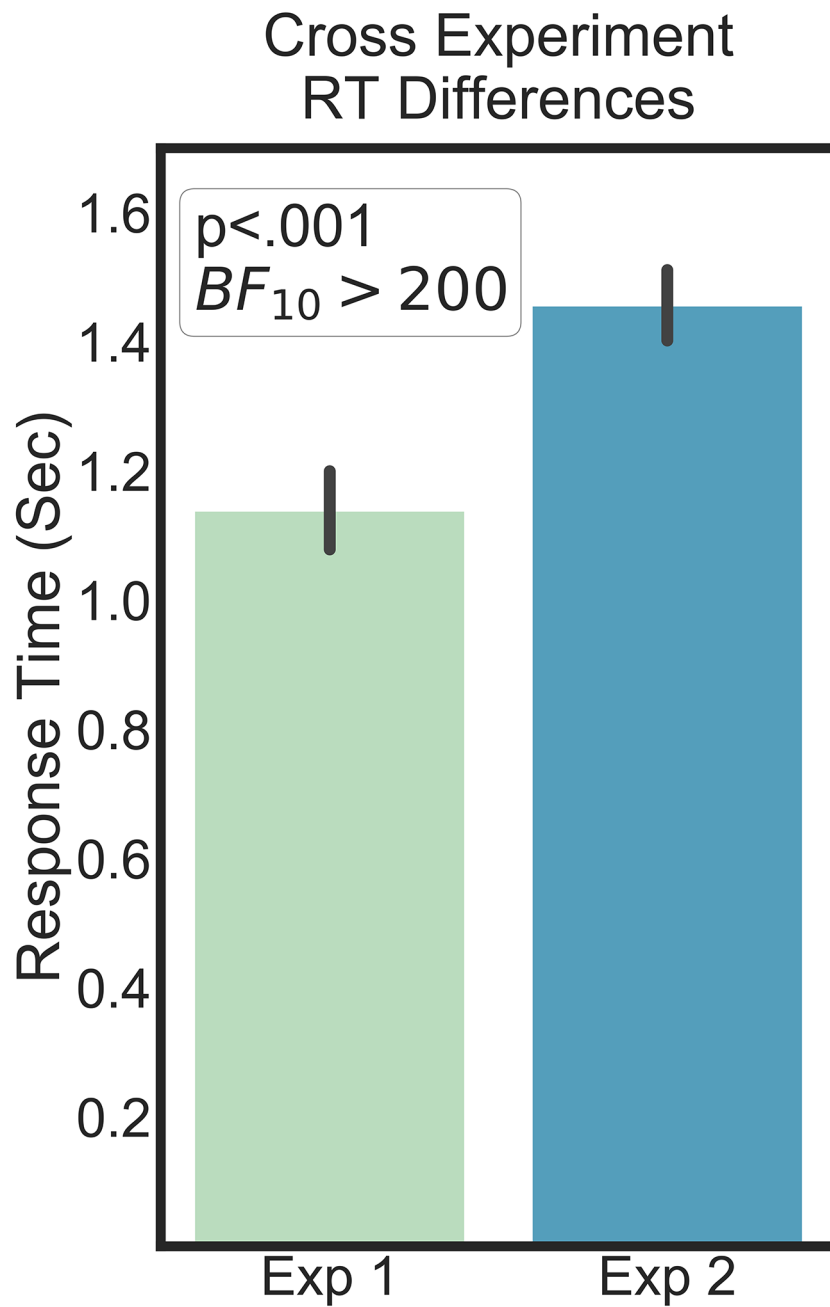


Figure 7: Response errors from probe trials normalized with the baseline measures (see Methods, Experiment 1). These data replicate Experiment 1 showing representations of the low-variance dimension were more precise than those of the high-variance dimension.

Exp 2 - Probe Response Errors

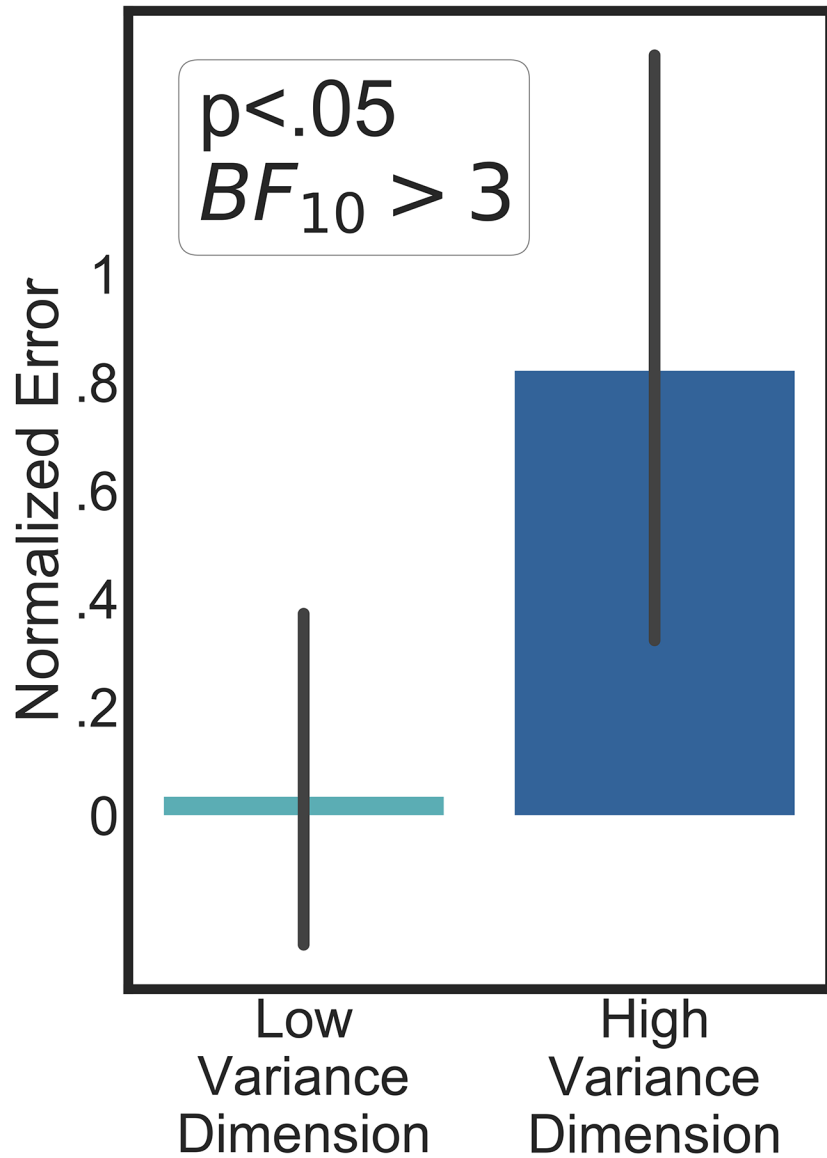


Figure 8: Comparison of RT from Experiments 1 and 2. These data show that correct RTs in Experiment 2 were significantly longer than in Experiment 1, suggesting the overall difficulty of Experiment 2 was successfully increased by distractor competition.

Exp 2 - Effect of Stimulus Properties on Response Time

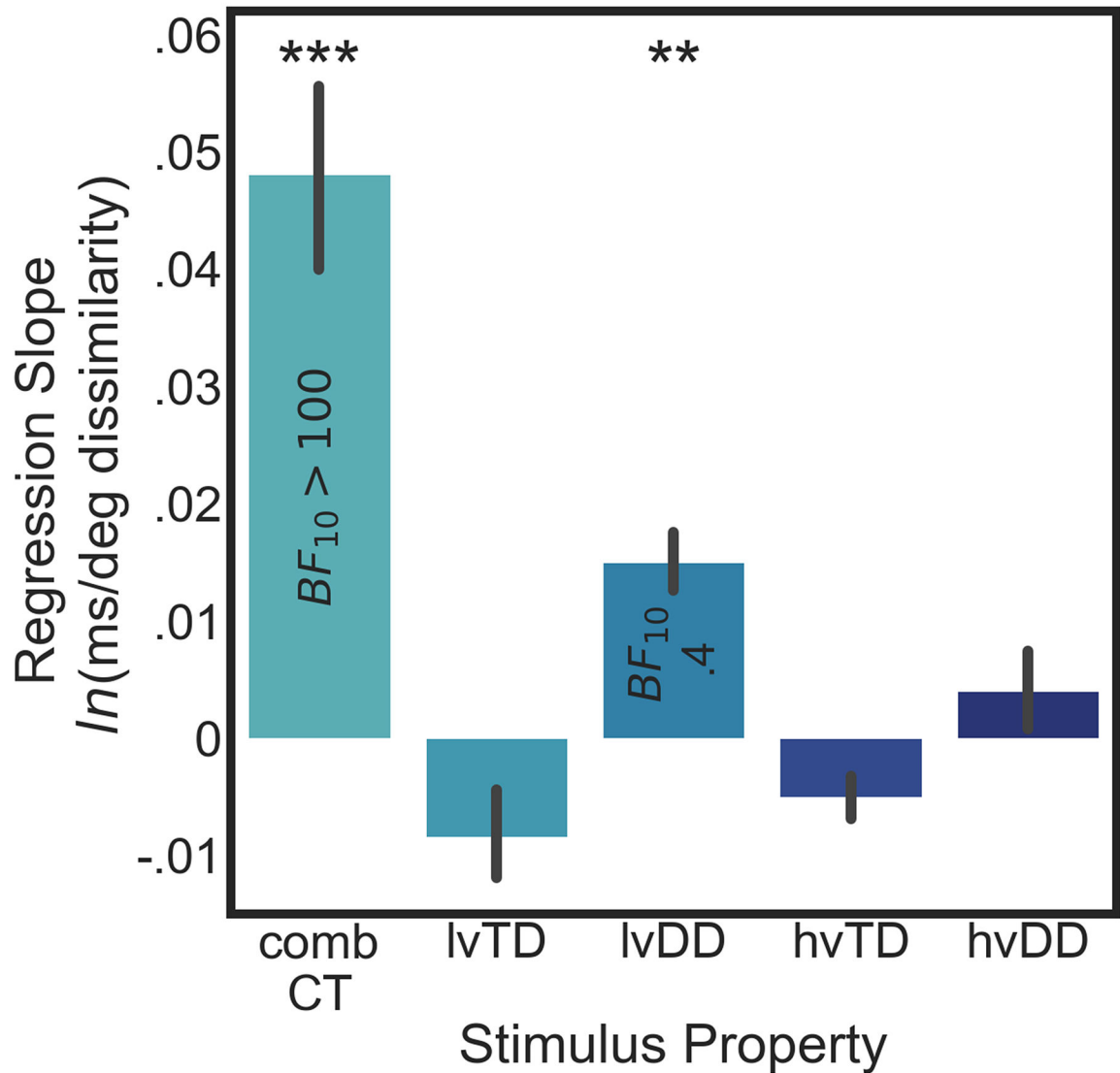


Figure 9:

Slopes measuring the effect of stimulus properties on response time from a multilevel regression model. Bar heights show the size of the fixed effect while error-bars show the variance of the subject specific random effects. The model tested the effects of cue-to-target similarity (CT) combined from both dimension, and target-distractor similarity (TD) and distractor-distractor similarity (DD) for the low-variance (lv) and high-variance (hv) dimensions separately. Results show that while there was a small effect of lvDD, the combined effect of CT – the difference between the target and the way it was expected to appear – was again the primary predictor of response time variation.

Exp 2 - Template Precision Correlated with combCT Effect

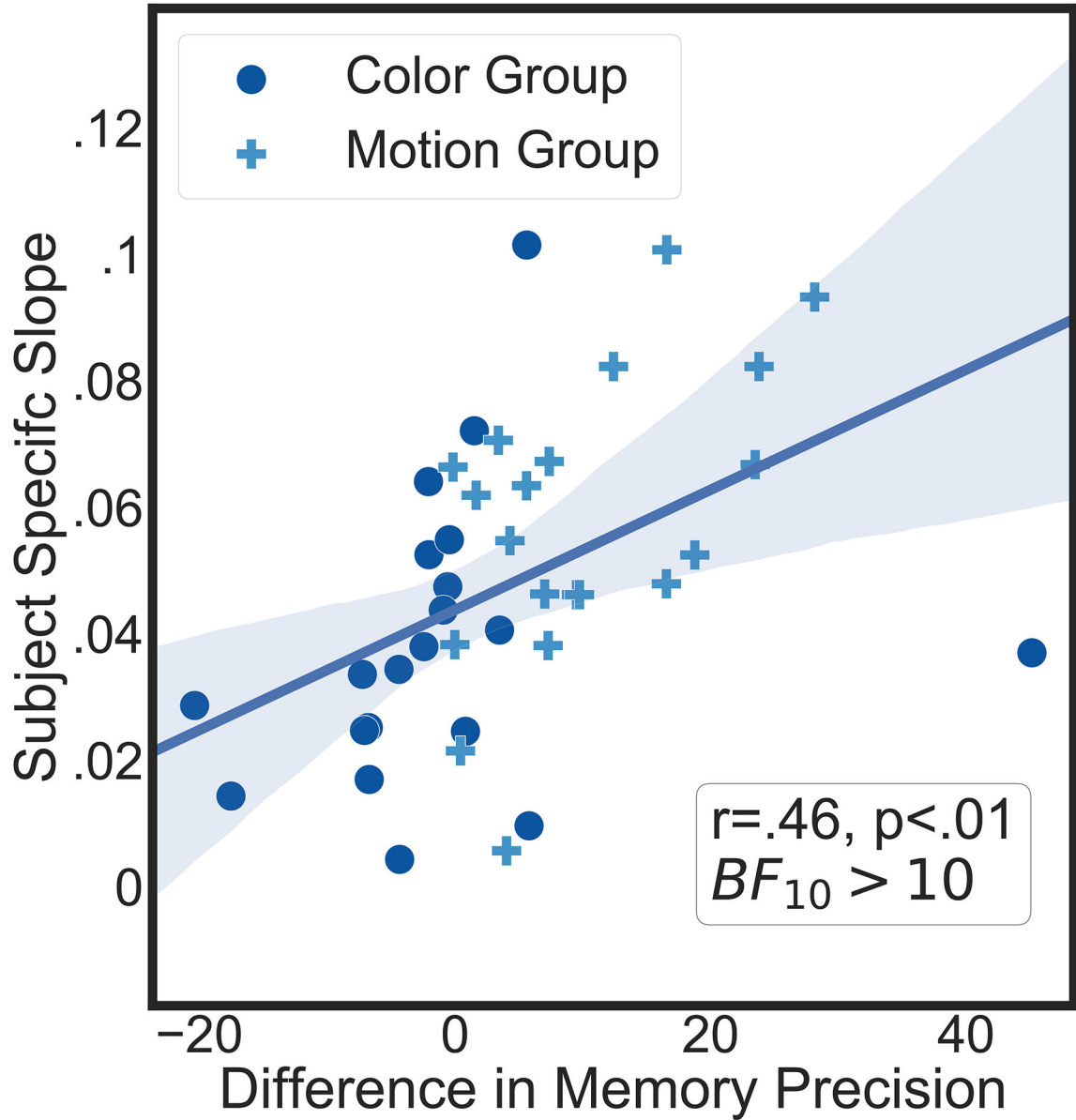


Figure 10: Subject specific coefficients from the regression models were correlated with each subject's difference in memory precision.

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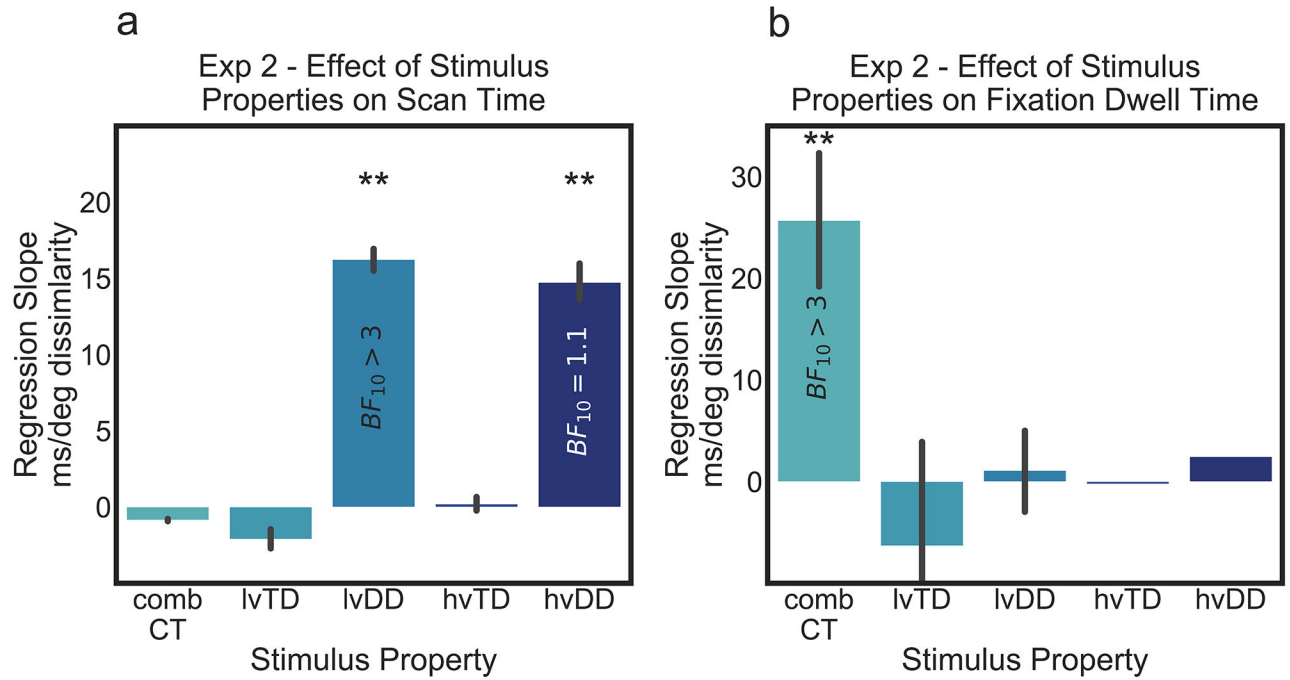


Figure 11:

Slopes measuring the effect of stimulus properties on scan time (**11a**) and fixation dwell time on the target (**11b**), from a multilevel regression model. Bar heights show the size of the fixed effect while error-bars show the variance of the subject specific random effects. The models show that while variation in scan time was primarily a function of distractor-distractor differences, CT was still the only regressor that explained variation in dwell time.