Probabilistic rejection templates in visual working memory

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1   **Abstract**

2   Our interactions with the visual world are guided by attention and visual working memory.

3   Things that we look for and those we ignore are stored as templates that reflect our goals and the

4   tasks at hand. The nature of such templates has been widely debated. A recent proposal is that

5   these templates can be thought of as probabilistic representations of task-relevant features.

6   Crucially, such probabilistic templates should accurately reflect feature probabilities in the

7   environment. Here we ask whether observers can quickly form a correct internal model of a

8   complex (bimodal) distribution of distractor features. We assessed observers' representations by

9   measuring the slowing of visual search when target features unexpectedly match a distractor

10   template. Distractor stimuli were heterogeneous, randomly drawn on each trial from a bimodal

11   probability distribution. Using two targets on each trial, we tested whether observers encode the

12   full distribution, only one peak of it, or the average of the two peaks. Search was slower when

13   the two targets corresponded to the two modes of a previous distractor distribution than when

14   one target was at one of the modes and another between them or outside the distribution range.

15   Furthermore, targets on the modes were reported later than targets between the modes that, in

16   turn, were reported later than targets outside this range. This shows that observers use a correct

17   internal model, representing both distribution modes using templates based on the full

18   probability distribution rather than just one peak or simple summary statistics. The findings

19   further confirm that performance in odd-one out search with repeated distractors cannot be

20   described by a simple decision rule. Our findings indicate that probabilistic visual working

21   memory templates guiding attention, dynamically adapt to task requirements, accurately

22   reflecting the probabilistic nature of the input.

23   Keywords*: attentional templates, visual working memory, probabilistic representations, visual*
24   *ensembles, summary statistics, visual search*.

25

26 **Probabilistic rejection templates in visual working memory**

27 Our senses are constantly bombarded with an overwhelming amount of information that needs to

28 be filtered by the brain to guide action. This information, however, is not completely chaotic. For

29 example, leaves on a tree usually have similar colors, and colors within a single leaf would be

30 more similar to each other than to another leaf. Probabilistic models of vision (Bejjanki, Beck,

31 Lu, & Pouget, 2011; Feldman, 2014; Girshick, Landy, & Simoncelli, 2011; Kersten, Mamassian,

32 & Yuille, 2004; Ma, 2012; Rao, Olshausen, & Lewicki, 2002) suggest that the brain utilizes

33 existing correlations in the environment and uses them in perception. However, some of the

34 incoming information is not relevant for current behavior, and it is important to reject it while

35 processing other stimuli in more detail. Traditionally, the rejection of irrelevant information

36 within a specific feature dimension (e.g., orientation) is thought to be based on specific feature

37 values (Woodman, Carlisle, & Reinhart, 2013). Here we ask whether such rejection can instead

38 be based on probabilistic templates and whether such templates accurately reflect the

39 probabilities of distractor features. If this is the case, then probabilistic inference in the brain

40 does not start with perception, but sooner, when to-be-rejected templates are formed (based on

41 previously encountered stimuli) to optimize the prioritization of what is perceived.

42 Imagine a radiologist looking for signs of tumor in x-ray scans. Malignant signs can take

43 many forms so the targets to look for are diverse. By many accounts, search in this and other

44 contexts is thought to be guided by templates held in visual working memory (Woodman et al.,

45 2013). These templates reflect what one should look for, but may also reflect what should be

46 ignored (Arita, Carlisle, & Woodman, 2012; Won & Geng, 2018). For example, distractors such

47 as the rib cage on a lung scan are salient but not informative and radiologists can therefore ignore

48 them. It is well known that information about to-be-ignored stimuli or features is kept in

49 memory, but the way they are represented is still unknown.

50 There are capacity limits in the amount of information that can be stored in visual

51 working memory templates (Bundesen, 1990; Grubert & Eimer, 2013; Vickery, King, & Jiang,

52 2005), with some authors even suggesting that only one template containing a single feature

53 value can guide attention at any given time (Oberauer, 2002; Olivers, Peters, Houtkamp, &

54 Roelfsema, 2011; van Moorselaar, Theeuwes, & Olivers, 2014). Alternatively, templates could

55 be conceptualized as probabilistic entities of varying precision (Bays, 2015) rather than matches

56 to exact feature values. While previous studies found some support for this, observers typically

57   reported features of single items (Ma, Husain, & Bays, 2014). However, in the real world such

58   isolated features practically never occur. Furthermore, with a few exceptions (Arita et al., 2012;

59   Won & Geng, 2018), templates for ignored information are rarely studied. For any inference

60   based on the probabilistic representations, it is crucial that the internal model used by observers

61   accurately reflects the environment. Here, we provide strong evidence for the probabilistic

62   template view by showing that visual working memory templates for rejection mirror the

63   probability distribution of distractor features.

64   Our observers searched for two oddly oriented targets among distractors randomly drawn

65   from a bimodal orientation distribution. To expose observers' templates, after a sequence of

66   *learning* trials with distractors randomly drawn from a bimodal distribution, targets on *test* trials

67   could either correspond to regions of feature space previously used for distractors, fall in

68   between the modes of the bimodal distribution, or have feature values outside the previous

69   distribution range. We assume that observers' templates reflect what has been relevant on recent

70   trials. If templates contain features of distractors to be ignored, which then become targets on test

71   trials, search should be slower than otherwise (Chetverikov, Campana, & Kristjánsson, 2016;

72   Kristjánsson & Driver, 2008; Lamy, Antebi, Aviani, & Carmel, 2008; Maljkovic & Nakayama,

73   1994; Wang, Kristjánsson, & Nakayama, 2005). Crucially, experiments with varied set size and

74   trial numbers show that learning in this paradigm cannot be explained by the sampling of a few

75   items (Chetverikov, Campana, & Kristjánsson, 2017d, 2017b). It also cannot be explained by

76   simple decision rule learning (e.g., all stimuli that have features in a certain range are

77   distractors), because observers response times, on average, reflect the shape of the distractor

78   distribution rather than just a boundary between a target and distractors (Chetverikov et al., 2016,

79   2017b; Chetverikov, Campana, & Kristjánsson, 2017c; Chetverikov, Hansmann-Roth, Tanrikulu,

80   & Kristjansson, 2019). However, it is not yet clear whether each single set of learning trials can

81   feed observers' templates with the feature probability distribution of distractors, nor is it clear

82   how accurately the information is stored in the templates.

83   Under the *strong* probabilistic template hypothesis, templates would include information

84   about both peaks of a bimodal distribution. That is, observers would develop an accurate internal

85   model for the task and the template would accurately reflect the information about the full

86   probability distribution. Alternatively, templates might include only a single peak (e.g., the

87   attended one), or might reflect only the summary statistics, such as the averages of the whole

88   distribution (Alvarez, 2011). Using a two-target search task we were able to test whether

89   observers encode both peaks of a distribution following a single learning sequence. The

90   predictions of these models (see Simulations) are qualitatively different regarding both the order

91   in which targets are reported in a two-target search, and search times. If observers accurately

92   encode a bimodal distribution, on trials with a target on a peak and target between peaks, targets

93   between the peaks (associated with a lower distractor probability) should be reported before

94   targets on peaks (associated with the highest distractor probability, Figure 1A). In contrast, if

95   only one peak is encoded or if the whole distribution is averaged, targets on peaks would be

96   associated with a lower distractor probability and should be reported no later than targets

97   between the peaks (associated with lower distractor probability in this case). Notably, while all

98   three hypotheses postulate that observers can use probabilistic *inference*, only the first one

99   assumes that the distractor probability distribution is encoded accurately, that is, that the

100   observers use relatively accurate probabilistic *templates*.

101
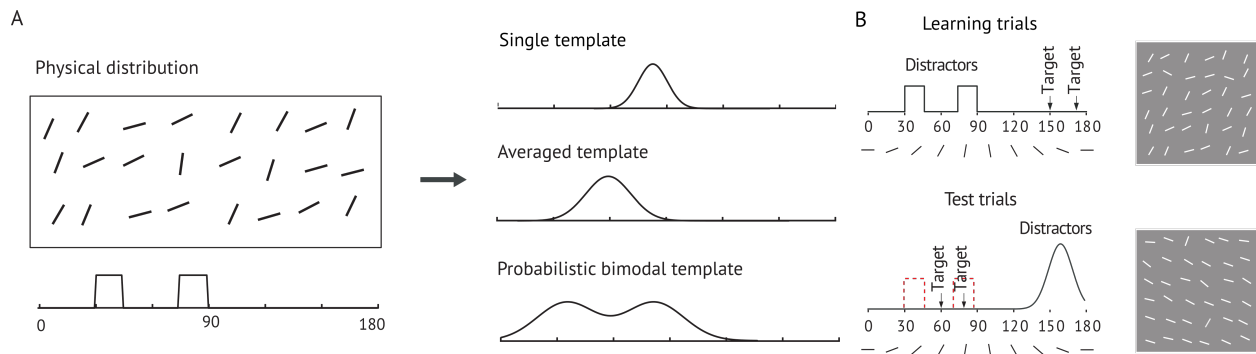
Figure 1. Panel A: The same physical bimodal distribution can be represented in different ways. Panel B:
Example learning and test trials with distractor distributions and targets shown on the left.

104

105   **Experiment**

106   **Ethics Statement.** The study was approved by the ethics committee of St. Petersburg

107   State University (#75, 21.06.2017). All participants signed a consent form before taking part in

108   the study.

109   **Participants.** Fifteen observers (ten female, age $M = 25.67$) at St. Petersburg State

110   University, Russia, participated voluntarily in a single experimental session lasting

111   approximately 30 min. The data from two observers were excluded because their response times

112   on test trials were too slow ($M = 1464$ and $M = 1871$ ms), compared with other observers ($M =$

113   1064 ms). Following our previous studies (Chetverikov et al., 2016, 2017b, 2017c, 2017d), the

114   design of this study utilized within-subject comparisons with a relatively small number of trained

115   observers (each observer was trained for at least 100 trials before the main session) performing a

116   large number of trials. The sample size and the trial numbers were similar to those in previous

117   studies using the same paradigm.

118   **Method.** We used a task similar to our previous studies (Chetverikov et al., 2016,

119   2017b). Stimuli were presented on an Acer V193 display (19" with 1280 × 1024 pixel resolution)

120   using PsychoPy 1.84.2 (Peirce, 2007, 2009). Viewing distance was ~ 60 cm. Observers searched

121   for two oddly oriented lines in a 6×6 grid of 36 lines subtending 16°×16° at the centre of a

122   display. The length of each line was 1.41°. Line positions were jittered by randomly adding a

123   value between ±0.5° to both vertical and horizontal coordinates.

124   Observers were instructed to search for two targets on each trial, with targets being the

125   stimuli that were most different from all the others ("odd-one-out" search (Maljkovic &

126   Nakayama, 1994)). Targets were randomly distributed between the four quadrants of the search

127   display with the constraint that the two targets on a given trial could not appear in the same

128   quadrant. Observers reported the locations of the targets by pressing one of four keys ('f', 'g',

129   'r', 't' on a standard keyboard) corresponding to the quadrants of the search display. They were

130   informed that two targets would be presented on each trial and were encouraged to respond to

131   each target as soon as they found it and not wait until both targets were found.

132   Trials were organized in intertwined prime and test 'streaks'. During prime streaks,

133   distractors were randomly drawn from a bimodal distribution that included two uniform parts

134   with orientations ranging from -30 to -20 and +20 to +30 relative to the overall mean. The

135   distribution mean was the same within streak but chosen randomly between streaks. Target

136   orientations were selected randomly on each trial with the restriction that the distance between

137   target orientation and distractor mean in feature space was 60 degrees at minimum. Prime streak

138   length was set to 6-7 trials (with equal probability) because this streak length is sufficient to learn

139   bimodal distributions with relative accuracy (Chetverikov et al., 2017b).

140   Within test streaks, distractor orientations were randomly drawn from a truncated

141   Gaussian with SD = 10 deg. and range 20 deg. Test streaks had one or two trials (with equal

142   probability). Different *target* types were used on test trials: targets were either located on a peak

143   of the previous bimodal distribution ("Peak", at +/-25 deg. relative to the previous distractor

144   mean), between the peaks ("Between", at 0 deg.) or outside the previous distribution range

145   ("Outside", at +/- 50 deg.). Four types of test streaks were used: 1) with two targets either on two

146   different peaks ("Peak + Peak"); 2) on a peak and in-between the peaks ("Peak + Between"); 3)

147   on a peak and outside the previous distribution range ("Peak + Outside" – where the "outside"

148   target was always 25 deg. away from the target peak, that is, either the two targets were oriented

149   at +25 and +50 deg. or -25 and -50 relative to the previous distractors' mean); 4) between the

150   peaks and outside the range ("Outside + Between"). These four *test types* were presented equally

151   often (40 repetitions by participant) in random order. The distractor mean was chosen to be

152   equidistant from both test targets. The second test trial is not analyzed here as the priming effects

153   from the learning streak are not likely to be significant after the first two-target test search. Two-

154   trial test streaks were added for consistency with previous studies and in order to reduce the

155   potential effects of observers' expectations regarding streak lengths.

156   Observers participated in one session of approximately 1300 trials. Decision time was not

157   limited but participants were encouraged to respond as quickly and accurately as possible.

158   Feedback based on search time and accuracy on previous trials was shown in the upper-left

159   corner of the screen to motivate participants (see Chetverikov et al., 2016, for details on feedback

160   score calculation). The current trial number and the total number of trials were shown beneath

161   the score. If observers made an error, the word "ERROR" appeared in red letters at display centre

162   for 1 second.

163   In addition to this two-target search experiment, we also ran a single-target search study

164   (see Supplementary Experiment). The latter was used as a comparison for the single-target

165   search time analyses to ensure that the introduction of a second target and specific conditions of

166   the main experiment did not affect the pattern of results.

167
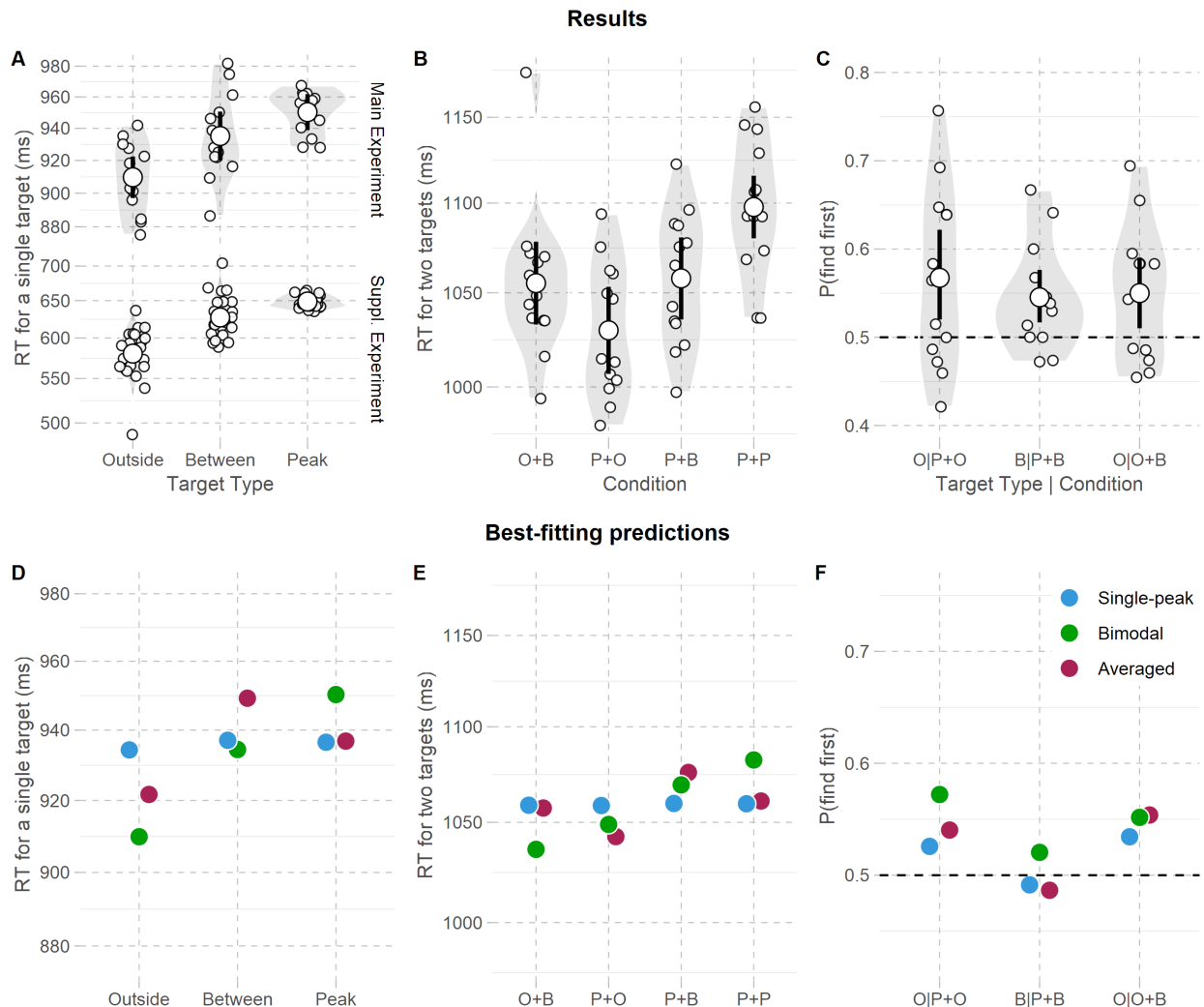
168
169   **Figure 2.** Experimental results and best-fitting predictions of the models (see Simulations). A: Results for
170   different target types from the main Experiment (average search times ignoring the order in which the
171   targets were reported) and the supplementary Experiment where observers searched for only one target on
172   each trial. B: Results for two-target search from the main Experiment. C: Results for the order of target
173   reporting from the main Experiment. D-F: Predictions for single-target search times, search times for two
174   targets, and for the order in which targets would be reported in a two-target search. For A-C large dots
175   show group means, bars show their 95% confidence intervals, smaller dots show individual observers'
176   means, and shaded areas show distributions of individual observers' means. Abbreviations: RT – response
177   times, P - target on a peak, B - target between the peaks, O - target outside the range of previous distractor
178   distribution. The plus sign indicates that two targets of corresponding types are used. For the order of
179   reporting, X|A+B means that target type X was reported first when target types A and B are combined.

180

181   **Results**

182   **Overall performance.** On learning trials, observers found both targets in most cases (M

183   $= 0.72$ [0.67, 0.77]), though the share of trials where only one target was reported was high ($M =$

184   0.27 [0.22, 0.31]; both targets were reported incorrectly on 1% of trials). On test trials, observers

185   reported both targets correctly on $M = 0.91$ [0.89, 0.93] trials (accuracy was comparable to the

186   results of single-target search in the Supplementary Experiment). The delay between the report

187   on the first and the second target was relatively short, but longer on learning than on test trials

188   ($M = 263$ [198, 326] vs. $M = 176$ [130, 233], respectively, $t(12.0) = 4.13$, $p = .001$). Similarly,

189   the first target was reported later on learning than test trials ($M = 973$ [854, 1103] vs. $M = 826$

190   [753, 904], respectively, $t(12.0) = 5.23$, $p < .001$).

191   The learning effects were also comparable to those from the single-target search

192   experiment (see supplement). A linear mixed-effects regression with Helmert contrasts

193   (comparing each trial with the average of the following trials) showed that the first trial was

194   slower, ($B = 0.11$, $SE = 0.01$, $t(52.57) = 9.61$, $p < .001$) and less accurate ($B = -0.04$, $SE = 0.02$,

195   $t(13.12) = -2.62$, $p = .021$) than the later trials. The follow-up trials did not differ from one

196   another.

197   **Test trials.** Replicating previous results, search times differed depending on target type

198   ($F(2, 24) = 8.28$, $p = .003$, $\eta^2_G = .02$, see Figure 2A). Observers search longer for "Peak" targets

199   compared to "Between" targets, which were in turn, found later than "Outside" targets.

200   Crucially, a repeated-measures ANOVA indicated that the time needed to find *both* targets on

201   test trials was affected by the condition ($F(3, 36) = 6.66$, $p = .002$, $\eta^2_G = .02$, Figure 2B).

202   Comparisons between conditions with the same feature difference between the targets showed

203   that performance on "Peak + Peak" trials was slower than on "Outside + Between" trials ($t(12.0)$

204   $= 3.10$, $p = .009$), while "Peak + Between" trials were not different from "Peak + Outside"

205   ($t(12.0) = -1.68$, $p = .118$) trials. Finally, the "Peak + Peak" condition was also slower than the

206   "Peak + Between" condition ($t(12.0) = 2.58$, $p = .024$).

207   We then analyzed which type of target was reported first in each condition using a

208   binomial mixed-effects regression. The results showed that targets on peaks were reported after

209   targets between the peaks ($Z = -2.01$, $p = .044$, Figure 2C) or targets outside the preceding

210   distribution range (Z = -2.43, p = .015), while the latter were reported earlier than targets

211   between the peaks (Z = 2.08, p = .037).

212   In sum, search with two targets on the peaks was the most difficult. A comparison of the

213   "Peak + Between" and "Peak + Outside" conditions showed only a numerical difference in total

214   RT. However, in the "Peak + Between" condition, targets on peaks were reported later than

215   targets between the peaks, whereas in the "Outside + Between" condition targets between the

216   peaks were reported later than the "Outside" targets. This shows again that targets on peaks were

217   the most unexpected for observers, followed by targets between the peaks, followed in turn by

218   "Outside" targets that led to the fastest search times.

219   **Simulations.** We simulated the predictions from three models (Figure 2E-F; the

220   simulation code is available at https://osf.io/rg2h8). For our main model of interest, the

221   "bimodal" model, we assumed that the probabilities of different distractors can be represented by

222   two Gaussian templates (for simplicity, we ignore the fact that the stimuli distributions might be

223   more accurately represented by non-Gaussian templates (Chetverikov, Campana, & Kristjánsson,

224   2017a)) centered on the means of distractor distribution segments. We assumed that observers

225   utilize the knowledge they obtained about distractors and targets optimally. To find a target in a

226   localization search task, an ideal observer , would compare the probability that a given noisy

227   measurement of orientation x at each location L is a target versus the probability that it is a

228   distractor (Ma, Navalpakkam, Beck, van den Berg, & Pouget, 2011; Ma, Shen, Dziugaite, & van

229   den Berg, 2015):

230    $$p(L|x) \propto p(L)\frac{p(x|T)}{p(x|D)} = p(L)\frac{p(x|s_L)p(s_L|T)ds_L}{p(x|s_L)p(s_L|D)ds_L}$$

231   where s_L is a true stimulus value at this location, $p(L)$ is the probability that a target is presented

232   at this location, T and D are the parameters of target and distractor distributions, respectively. In

233   our simulations, we assumed that internal representations of target and distractor distributions are

234   independent and response times are inversely proportional to the amount of evidence $p(L|x)$.

235   Given that all locations in our experiment were equiprobable, that is, $p(L)$ is the same for all

236   locations, response times will, on average, be proportional to the probabilities of the test target θ_T

237   under given distractor template parameters:

238    $$RT \propto p(\theta_T|D)$$

239   The width of the Gaussian templates was estimated by fitting the model to single-target

240   response time data. To increase the robustness of the estimates, we used an approach similar to

241   bootstrap aggregating ("bagging"), often employed in machine learning (Breiman, 1996). For

242   each model we obtained 500 bootstrapped samples grouped by participant (that is, on each

243   iteration, sampling with replacement was done for each subject and then the samples were

244   combined). We then estimated the template widths for each sample by fitting response times as a

245   linear function of the stimuli probability. For a "bimodal" model:

246
$$RT_{1T} = a + b\left(\frac{1}{2}p(\theta_T|\mu_1, \sigma) + \frac{1}{2}p(\theta_T|\mu_2, \sigma)\right)$$

247   where $\mu_1 = 25$ and $\mu_2 = -25$, the means of bimodal distractor distribution peaks, and a and

248   b are the scaling parameters necessary to translate the probabilities into response times. The

249   template widths obtained for each sample were then averaged to get the resulting estimates.

250   Estimated template widths were similar for the experiment reported here (18 deg.) and the

251   supplemental experiment (21 deg.).

252   For the "single-peak" model, we assumed that only one of the two peaks was encoded

253   (with the same approach as with the "bimodal" model). Given that the peak means are

254   equidistant to the overall distractor mean:

255
$$RT_{1T} = a + b\big(p(\theta_T|\mu_1, \sigma)\big)$$

256   The estimated template widths were 27 and 22 deg. for the main and the supplemental

257   experiment.

258   Finally, the "averaged" model was based on the idea that observers might use a single set

259   of summary statistics to represent the stimuli. Accordingly, we assumed that observers use a

260   single Gaussian template centered at the mean of the overall bimodal distribution:

261
$$RT_{1T} = a + b\big(p(\theta_T|0, \sigma)\big)$$

262   The template width was also obtained using ML optimization and bootstrapping. For the

263   main experiment the estimated width was 114 deg., while for the supplemental experiment it was

264   140 deg. (i.e., almost flat template), already suggesting that this model provides a poor fit to the

265   experimental data.

266   We then used the estimated template widths to obtain the predictions of the three models

267   for the search times for different target types (Figure 2D), total search time for two targets in

268   different conditions (Figure 2E), and for the order in which the targets should be reported (Figure

269   2F). For single-target search the equations were the same as when we estimated the template

270   widths, however, we used the data averaged by target type for each subject to reduce the effect of

271   trial-by-trial variability. Two-target search times were assumed to be proportional to a sum of

272   two search times predicted in the same way as for a single target:

273   $$RT_{2T} = a + b\big(p(\theta_{T1}|D) + p(\theta_{T2}|D)\big)$$

274   where D reflects the distractor distribution parameters for a given model, that is, the

275   template mean(s) and its estimated width(s).

276   Finally, we assumed that all other things being equal, the order in which the targets are

277   reported would depend on the ratio of the probabilities of observing the test targets under the

278   given distractors template:

279   $$P(find\ T2\ first) = 0.5 + k\ log\left(\frac{p(\theta_{T1}|D)}{p(\theta_{T2}|D)}\right)$$

280   with k as a scaling constant. The ratio was transformed to logarithm to allow for both

281   positive and negative values.

282   Figures 2D and 2E show that the bimodal model provided more accurate predictions for

283   response times than the other models. For single-target response times, it accurately predicted

284   that targets on peaks would be the hardest to find and targets between the peaks would be harder

285   to find than targets outside the range of previously learned distractors. In contrast, the averaged

286   model (ΔBIC = 5.94; here and later ΔBIC refers to the difference in Bayesian Information

287   Criterion compared to the bimodal model, positive values meaning that the bimodal model has

288   better fit) suggested that the targets in-between the peaks would be hardest to find, while the

289   single-peak model (ΔBIC = 12.47) predicted relatively similar response times for between targets

290   and targets on peaks. For two-target RTs, the bimodal model failed to predict slower search for

291   the "outside + between" condition compared to the "peak + outside" condition. Note, however,

292   that this difference was also not significant in our results. Speculatively, it might be a result of a

293   higher similarity between the targets in the latter than in the former. Nevertheless, the predictions

294   of the bimodal model were still better than of the averaged (ΔBIC = 8.04) or the single-peak

295   model (ΔBIC = 6.59).

296   Crucially, the bimodal, single-peak, and averaged models gave qualitatively different

297   predictions for the order in which the targets would be found. For both the single-peak and

298   averaged model, the probability of first reporting targets between the peaks when combined with

299   targets on peaks was below 0.5 (Figure 2C). As outlined in the introduction, when observers

300   encode only one peak, on 50% of the trials, the "peak" target on test trials should be on this peak

301   while in the other half of the trials it will be on the non-encoded peak. Depending on the width of

302   the template, the average ratio of the probabilities for a target would vary: with very large or very

303   small template widths, it will be close to 0.5 because targets between the peaks and at the non-

304   encoded peaks will be equally probable, and with intermediate template widths it will be below

305   0.5 (note that this conclusion is not limited to the specific equation we used for determining the

306   probability of finding one target before another; in fact, it could be shown that this is the case for

307   any monotonic function describing the transformation of a ratio of probabilities of observing the

308   target under a given Gaussian distractor template into average probability of a given reporting

309   order). For the averaged model the target between the peaks should always be reported later than

310   targets on the peaks. In contrast, for the bimodal model that accurately encodes the probabilities

311   of distractors, the target between the peaks should be reported before the target at the peak.

312   Accordingly, the bimodal model describes the results better than the single-target (ΔBIC =

313   13.11) or the averaged model (ΔBIC = 6.86).

314

315   **Discussion**

316   Can observers develop an accurate internal model for the probabilities of to-be-ignored items in a

317   visual search task? We assessed the content of templates guiding visual search in the orientation

318   domain, by measuring slowing for targets drawn from a preceding distractor orientation

319   distribution. The distribution was bimodal and the searches used to probe the representations

320   involved two simultaneous targets within a trial. Response times were slower when the targets

321   corresponded to the two modes ("peaks") of previous distractor distributions than when one

322   target was from one of the modes and another from between them, while the latter combination

323   of targets resulted in slower search than when one of the targets was outside the previous

324   distractor range. Furthermore, the order in which the targets were reported on a test trial followed

325   the distractor probabilities observed during prime trials. Targets outside the previous distractor

326   range were reported earlier than the ones between the modes, while the latter were reported

327   before the targets at the modes of previous distractor distribution. The search times and the order

328   in which targets are reported allowed us to assess the internal model used by observers.

329   We simulated the predictions of a bimodal, single-template, and averaged template

330   models. The first model accurately reflects the actual distribution of distractor features, while the

331   other two oversimplify it in different ways. We found that the bimodal model predicts the

332   response times pattern for different target types and different conditions far better than the other

333   models. Moreover, only the bimodal model could accurately predict the order in which the

334   targets were reported. Both the single-template and the averaged-template model predicted that

335   the target between the peaks should on average be reported after the targets at the peaks, while

336   the reverse was accurately predicted by the bimodal model. The target between the peaks in the

337   "Peak + Between" condition was on average reported before the target at one of the peaks. This

338   shows that observers simultaneously represent both modes of distractor distributions. Their

339   representations approximate the physical stimuli, and they fill in the gaps in probability space as

340   demonstrated by slower responses when one of the targets was between the peaks compared to

341   when it was outside the previous distractor range, or on the peaks.

342   Notably, all three models can be considered probabilistic in a sense that they do provide

343   observers with a measure of probability that a certain feature belongs to a distractor class. The

344   difference is in the degree of simplification. The bimodal model reflects the probability

345   distribution accurately (with the assumption of Gaussian approximation). The two other models

346   taken into consideration, however, diverge from an accurate representation in different ways: the

347   "averaged" assumes the use of overall summary statistics, while the "single-peak" assumes the

348   encoding of only one part of the distribution (which could be caused, for example, by biased

349   sampling). Furthermore, every heuristic or decision rule can be cast in terms of probabilities

350   (e.g., a delta function that assigns probability of 1 for one part of feature space and 0 for the rest).

351   Here we show that the representations used by observers mirror the probability distribution of the

352   stimuli.

353   Unlike previous studies assessing how distracting information is stored in visual working

354   memory (Arita et al., 2012; Won & Geng, 2018), the distractors in our studies were

355   heterogeneous and were generated randomly based on a bimodal probability distribution.

356   Nevertheless, observers were able to integrate the information about distractors into an

357   approximate bimodal representation. Speculatively, this demonstrates that using homogeneous

358   distractors may be an artificial limitation, perhaps brought on by earlier technical restrictions on

359   experimental stimuli in pre-modern computer era. In the real world, distracting information is

360   rarely homogeneous, so it may not be particularly surprising that humans are able to form

361   accurate templates representing probability distributions.

362   Following seminal accounts of priming of pop-out effects (Maljkovic & Nakayama,

363   1994), we argue that the representations of distractor distributions are kept in visual working

364   memory, rather than long-term memory. Woodman et al (Woodman et al., 2013) have

365   demonstrated that the representation of a single attended target is transferred from VWM to long-

366   term memory in 5 to 7 trials. In contrast, we have previously shown that for simple distractor

367   distributions (such as Gaussian or uniform) one or two trials are enough for observers to develop

368   a probabilistic representation of distractors (Chetverikov et al., 2017b). Representations of more

369   complex distractor distributions take more time (or trials) to develop, but they also progressively

370   change with more repetitions: after one or two trials, bimodal distributions are represented as

371   unimodal, and are only later transformed into bimodal ones. This indicates that more time (trials)

372   is required for sharpening the representation, not for the transfer to long-term memory.

373   A question of how the probabilistic templates for rejection are stored also taps into a

374   more general question, regarding how working memory templates are stored. Recently,

375   Christophel, Iamschinina and colleagues (2018) demonstrated that while attended stimuli in

376 visual working memory are represented both in parietal and frontal cortex in addition to visual

377 cortex, the latter is not involved in representations of unattended stimuli. It is possible that

378 rejection templates similarly do not involve early visual areas. However, unlike simple

379 unattended items, templates for rejection are actively used by observers to guide attention. As

380 such, their representation might require a level of precision only achievable with the recruitment

381 of sensory areas.

382   How specific are distractor templates? Won and Geng (Won & Geng, 2018) suggested

383 that distractor templates might be more broadly tuned than target templates. This would allow

384 easy generalization of suppression to similar distractors, while for targets such generalization

385 might be harmful as it would lead to an increased number of false alarms. However, the exact

386 costs of generalization for both target and distractor templates depend on the environment.

387 Specific templates are necessary when a target is similar to distractors, but generalization is

388 helpful otherwise. This has indeed been observed by Geng, DiQuattro, and Helm (Geng,

389 DiQuattro, & Helm, 2017): when a target is similar to distractors, its template is sharpened and

390 shifted away from distractors. Moreover, in the real environment we rarely know how exactly the

391 target or distractors would look under a given illumination and point of view, making some

392 degree of generalization essential for efficient search. In contrast, a typical visual search study

393 would require a very narrow distribution of target features, making a narrow template useful. Our

394 results suggest that distractor templates are specific enough to account for bimodality in the

395 distractor distribution. It remains to be studied whether targets or distractors templates are more

396 specific when their physical distributions are equally shaped.

397   In contrast to our previous studies (Chetverikov et al., 2016, 2017b, 2017d, 2017c;

398 Hansmann-Roth, Chetverikov, & Kristjánsson, 2019), here, we "probed" the distractor

399 representation only at three different points in the feature space. By using targets with a range of

400 features that covered the full feature space, our previous research showed that observers encode

401 the probability distribution of distractors. Here we extend these findings by showing that

402 observers learn the distribution of distractors following a single learning streak. This

403 demonstrates that the previously obtained results are not an artefact of aggregation over multiple

404 trials but rather a true reflection of the templates' content.

405   Our results agree with previous findings on probabilistic concept learning. Briscoe and

406 Feldman (2011) found that when observers have to form a decision rule based on a multimodal

407 probability distribution, they could do this, although performance became worse with increased

408 mode number. We did not explicitly ask our observers to categorize the stimuli (as distractors

409 and targets), but it is conceivable that they might do so if asked.

410 We should note that one might interpret our results as simply demonstrating that humans

411 are capable of learning a nonlinear classification rule/decision boundary over a disjoint set in

412 feature space, and can use this to guide visual search. But we think that this alternative proposal

413 is unlikely to hold water because for a simple classifier in this task, learning is not necessary.

414 There is enough information on each trial to easily tell the target from distractors. Moreover, to

415 include learning in the algorithm, learning of the target would suffice, as the target distribution is

416 constant within the learning streak. The fact that our observers struggle with this shows that they

417 do more than strictly necessary. Second, and perhaps more importantly, we showed in our

418 previous work that observers learn the correct probabilities of the distractor features *on average*

419 rather than learning a simple decision rule (Chetverikov et al., 2016, 2017b, 2017d, 2017c). A

420 decision rule model cannot explain why the response time curves reflect distractor probability

421 both within and outside the distractor distribution range. By using double-target search we

422 further demonstrate that these results cannot be explained by a combination of different decision

423 rules applied on different test trials.

424 **Conclusions**

425 We found that rejection templates are probabilistic, similarly to items in visual working

426 memory that receive attention (Ma et al., 2014). However, our study also shows that templates

427 for rejection do not need to be simple bell-shaped curves, as it is typically modelled in working

428 memory studies. In contrast, they are dynamically adapted to task requirements, reflecting the

429 probabilistic nature of the input. Whether such flexibility also characterizes templates for

430 attended items remains to be seen. However, our results clearly demonstrate that probabilistic

431 computations start in the brain even before something is perceived, to determine what should be

432 prioritized in perception.

433   **Acknowledgments**

437   **Supplementary materials**

438   The data from the experiments reported in this paper and scripts for simulations and analyses are

439   available at https://osf.io/rg2h8. The data include trial-by-trial on presented stimuli and

440   observers' responses. The analyses scripts in R provide the full pipeline, including the data

441   preprocessing.

442   **Author Contributions**

443   All authors participated equally in conceiving and planning the experiments. AC wrote the

444   experimental scripts, oversaw the data collection, analyzed the results, and wrote the initial

445   version of the manuscript. GC and AK took part in data analyses and interpretation and revised

446   the manuscript.

447

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550

551   **Supplemental experiment**

552   **Method**

553   **Participants.** Fifteen observers (ten female, age $M = 25.47$) at St. Petersburg State

554   University, Russia, took part in a single experimental session lasting approximately 30 min. Two

555   of them were excluded because their response times were very high compared with the other

556   observers (1356 and 1393 ms for excluded observers vs. 761 ms for the remaining sample). One

557   more was excluded because of low accuracy ($M = 0.71$ vs. 0.83 for the remaining sample). The

558   study was approved by the ethics committee of St. Petersburg State University.

559   **Procedure.** We used a task similar to our previous studies (Chetverikov et al., 2016,

560   2017b). Stimuli were presented on an Acer V193 display (19" with 1280×1024 pixel resolution)

561   using PsychoPy 1.84.2 (Peirce, 2007, 2009). Viewing distance was ~ 60 cm. Observers searched

562   for an oddly oriented line in a 6×6 grid of 36 lines subtending 16°×16° at the centre of a display.

563   The length of each line was 1.41°. Line positions were jittered by randomly adding a value

564   between ±0.5° to both vertical and horizontal coordinates. Observers indicated whether the target

565   line was in the upper or the lower half of the screen by pressing the 'i' or 'j' keys on a standard

566   keyboard. Trials were organized in intertwined prime and test 'streaks'. During prime streaks,

567   distractors were randomly drawn from a bimodal distribution that included two uniform parts

568   with orientations ranging from -40 to -20 and +20 to +40 relative to the overall mean. The

569   distribution mean was the same within streak but chosen randomly between streaks. Target

570   orientation was selected randomly on each trial with the restriction that the distance between

571   target orientation and distractor mean in feature space was 60 degrees at minimum. Based on the

572   results of previous studies, prime streak length was set to 6-7 trials because this streak length is

573   sufficient to encode bimodal distributions with relative accuracy (Chetverikov et al., 2017b).

574   Within test streaks, distractor orientations were randomly drawn from a truncated

575   Gaussian with SD = 10 deg. and range 20 deg. Each test streak had two trials and the targets on

576   these trials (*target type*) were either located on the "peaks" of the previous bimodal distribution

577   (within the +/- 25 to 35 deg. range relative to the previous distractors' mean), in-between the

578   peaks (within 0 to +/-5 deg. range) or outside the previous distribution range (within +/- 55 to 90

579   deg. range). Three types of test streaks were used with targets on the first and the second test trial

580   either on two different peaks, on a peak and in-between the peaks, or on a peak and outside the

581   previous distribution range. These three conditions were presented equally often in random

582   order. The order of targets within the test trials for each condition was counterbalanced. The

583   distractor mean was chosen randomly with a distance to the target of no less than 60 deg. (as on

584   prime trials).

585   Observers participated in one session of approximately 1244 trials divided into 288 prime

586   and test streaks. Decision time was not limited but participants were encouraged to respond as

587   quickly and accurately as possible. Feedback based on search time and accuracy on previous

588   trials was presented after each trial was shown in the upper-left corner of the screen to motivate

589   participants. The current trial number and the total number of trials were shown beneath the

590   score. If observers made an error, the word "ERROR" appeared in red letters at display centre for

591   1 second.

592   **Results**

593   **Overall performance.** Participants were slower ($M = 738$ [683, 794] vs. $M = 615$ [589,

594   643], $t(11.0) = 5.67$, $p < .001$, $d = 1.64$) and less accurate ($M = 0.78$ [0.75, 0.82] vs. $M = 0.96$

595   [0.95, 0.97], $t(11.0) = -10.29$, $p < .001$, $d = 2.97$) on learning trials than test trials, due to the fact

596   that learning trials had a broader distribution. Response times decreased while accuracy

597   increased during learning trials: A linear mixed-effects regression indicated that the first trials in

598   each learning sequence were slower, ($B = 0.08$, $SE = 0.02$, $t(11.47) = 4.52$, $p < .001$) and less

599   accurate ($B = -0.04$, $SE = 0.01$, $t(12.52) = -4.50$, $p < .001$) than the later trials.

600   **Test trials.** On test trials, observers' performance depended on both target type and

601   condition. Replicating the results of Chetverikov et al. (2017b), on the first trial in a test

602   sequence observers responded more slowly when the target was at one of the peaks of the

603   preceding distractor distribution than when it was in-between the peaks ($t(11.0) = 3.94$, $p = .002$,

604    $d = 1.14$), while responses for the in-between the peaks targets were slower than when they were

605   outside the range of the previous distribution ($t(11.0) = 3.96$, $p = .002$, $d = 1.14$).