

Uncertainty is Maintained and Used in Working Memory

Aspen H. Yoo^{1,2,3}, Luigi Acerbi^{1,2,4}, Wei ji Ma^{1,2}

Department of Psychology, New York University, NY, USA¹

Center for Neural Science, New York University, NY, USA²

Department of Psychology, University of California, Berkeley, CA, USA³

Department of Computer Science, University of Helsinki, Helsinki, Finland⁴

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1 Abstract

2 What are the contents of working memory? In both behavioral and neural computational models, the working mem-
3 ory representation of a stimulus is typically described by a single number, namely a point estimate of that stimulus.
4 Here, we asked if people also maintain the uncertainty associated with a memory, and if people use this uncertainty
5 in subsequent decisions. We collected data in a two-condition orientation change detection task; while both condi-
6 tions measured whether people used memory uncertainty, only one required maintaining it. For each condition, we
7 compared an optimal Bayesian observer model, in which the observer uses an accurate representation of uncertainty
8 in their decision, to one in which the observer does not. We find that this “Use Uncertainty” model fits better for all
9 participants in both conditions. In the first condition, this result suggests that people use uncertainty optimally in a
10 working memory task when that uncertainty information is available at the time of decision, confirming earlier results.
11 Critically, the results of the second condition suggest that this uncertainty information was maintained in working
12 memory. We test model variants and find that our conclusions do not depend on our assumptions about the observer’s
13 encoding process, inference process, or decision rule. Our results provide evidence that people have uncertainty that
14 reflects their memory precision at an item-specific level, maintain this information over a working memory delay, and
15 use it implicitly in a way consistent with an optimal observer. These results challenge existing computational models
16 of working memory to update their frameworks to represent uncertainty.

17
18 **Keywords:** visual working memory, Bayesian observer, optimal, uncertainty

19 2 Introduction

20 Visual working memory, the process involved in actively maintaining visual information over a short period, is essen-
21 tial for numerous everyday behaviors as “simple” as integrating visual information across saccades and as “complex”
22 as reading comprehension, problem solving, and decision making (Baddeley & Hitch, 1974; Baddeley, 2003; Fukuda,
23 Vogel, Mayr, & Awh, 2010; Conway, Kane, & Engle, 2003; Just & Carpenter, 1992). As important as it is, visual
24 working memory is also a notoriously limited process, resulting in an imperfect and incomplete picture of the world it
25 aims to represent.

26 Both behavioral (e.g., Zhang & Luck, 2008; Bays & Husain, 2008; van den Berg, Shin, Chou, George, & Ma,
27 2012; Fougnie, Suchow, & Alvarez, 2012) and neural (e.g., Ermentrout, 1998; Wang, 2001; Compte, 2006) models of
28 visual working memory typically represent people’s memory as a single number, a noisy estimate of the value of the
29 stimulus. For example, someone may remember a 34° oriented line as 37°. It is, however, important in many visual
30 working memory decisions to represent more than just a point estimate of the remembered stimulus, but the uncertainty
31 as well. Uncertainty is technically defined as the width of a belief distribution over a stimulus, but intuitively represents
32 how unsure an observer is about the stimulus. This is different from memory precision, which is how precisely an
33 observer actually remembers the stimulus. An ideal observer’s uncertainty will reflect the precision with which they
34 remembered an item, such that they are less uncertain for more precise memories. In a variety of domains, taking
35 uncertainty into account would increase performance and thus should be used. For example, high uncertainty over the
36 memory of the location of a coffee cup may result in someone looking at it before reaching for it. High uncertainty
37 over whether a friend changed their appearance may result in someone being less likely to comment on it.

38 Does uncertainty get taken into account in working memory-based decisions? An intuitive first place to look
39 is the literature on working memory confidence, since confidence can be thought of as a readout of uncertainty.
40 Experimenters have probed memory confidence by asking people to provide a rating (Rademaker, Tredway, & Tong,
41 2012; Vandembroucke et al., 2014; Samaha & Postle, 2017), choose the best remembered item (Fougnie et al., 2012;
42 Suchow, Fougnie, & Alvarez, 2017), or make a memory-based bet (Yoo, Klyszejko, Curtis, & Ma, 2018; Honig,
43 Ma, & Fougnie, 2020). These studies have demonstrated that people have higher working memory confidence on
44 trials that are remembered more accurately (but see Sahar, Sidi, & Makovski, 2020; Bona, Cattaneo, Vecchi, Soto,
45 & Silvanto, 2013; Bona & Silvanto, 2014; Vlassova, Donkin, & Pearson, 2014; Maniscalco & Lau, 2015; Adam &
46 Vogel, 2017; Samaha, Barrett, Sheldon, LaRocque, & Postle, 2016 for conflicting results), and a computational model
47 in which memory judgements and confidence ratings are derived from the same underlying memory precision can
48 quantitatively account for these joint data (van den Berg, Yoo, & Ma, 2017).

49 All these studies ask the participant to consciously access the quality of their memory. However, in naturalistic
50 settings, people are typically not directly interrogated about their uncertainty, but use it implicitly in other decisions.
51 For example, looking before reaching for one’s coffee cup or commenting on a friend’s appearance are decisions that
52 presumably use uncertainty without conscious report. In this study, we take inspiration from perceptual decision-
53 making studies, which have demonstrated that people implicitly incorporate uncertainty in a variety of decisions (e.g.,
54 van Beers, Sittig, & Gon, 1999; Ernst & Banks, 2002; Alais & Burr, 2004; Körding & Wolpert, 2004; Knill & Pouget,

55 2004; Ma, Navalpakkam, Beck, van den Berg, & Pouget, 2011; Jazayeri & Shadlen, 2010; Stocker & Simoncelli,
56 2006).

57 There is already some evidence that people use uncertainty implicitly in working memory-based decisions. Kesh-
58 vari and colleagues had humans complete a four-item orientation change detection task (Keshvari, van den Berg, &
59 Ma, 2012); Devkar and colleagues had humans and monkeys complete a three-item orientation change localization
60 task (Devkar, Wright, & Ma, 2017). Stimuli in both studies were ellipses, which were independently assigned to
61 be longer and narrower, providing “high-reliability” orientation information, or shorter and wider, providing “low-
62 reliability” orientation information. The reliability of ellipses affected the precision with which they were encoded,
63 and thus should have affected the memory uncertainty associated with each item. To maximize performance in both
64 tasks, participants’ uncertainty would need to reflect this variability in item-specific precision. Both studies found that
65 a computational model that assumes participants use item-specific uncertainty accounted better for people’s choices
66 than alternative models.

67 Crucially, while these two studies provide evidence that people can implicitly use uncertainty, some experimental
68 design choices do not allow us to conclude that people are actually maintaining uncertainty per se. First, participants
69 in the study by Devkar and colleagues received trial-to-trial feedback on the correctness of their response. It is thus
70 possible that participants simply learned a stimulus-response mapping (Maloney & Mamassian, 2009) rather than per-
71 forming Bayesian inference or other forms of probabilistic computation (i.e., still using uncertainty in their decision;
72 Ma, 2010). Second, precision in both studies was experimentally manipulated through ellipse reliability, which was
73 held constant through a working memory delay. Thus, participants could have used this ellipse reliability as a proxy for
74 uncertainty, rather than maintaining this exact information over the working memory delay (Barthelme & Mamassian,
75 2010).

76 Thus, the goal of this study was to investigate whether and how uncertainty is maintained over a working memory
77 delay and used implicitly in a working memory task. To reach this goal, we collected data in a two-condition orienta-
78 tion change detection task and developed computational models to test different hypotheses about uncertainty. In the
79 first condition, we established that people use uncertainty if a proxy to it is provided to them, replicating the results
80 from Keshvari and others (2012). In the second condition, we asked if people still use uncertainty if this proxy is not
81 provided at the time of decision. In other words, we asked if uncertainty is being maintained in working memory.

82 **3 Experimental Methods**

83 **3.1 Participants**

84 Thirteen participants (11 female; mean age $M = 21.1$ years, $SD = 2.5$) completed both conditions. All participants had
85 normal or corrected-to-normal vision. Participants were naive to the study’s hypotheses and were paid \$12/hour and
86 a \$24 completion bonus. We obtained informed, written consent from all participants. The study was in accordance
87 with the Declaration of Helsinki and was approved by the Institutional Review Board of New York University (IRB-
88 FY2019-2490). Seven other participants were excluded because they did not meet performance criteria (explained in

89 the Cross-session procedure section).

90 **3.2 Stimuli**

91 Stimuli were four, light-grey, oriented ellipses on a medium-grey background. Each ellipse could be long or short,
92 to provide respectively higher or lower reliability information regarding the orientation of the ellipses. All ellipses
93 had an area of 1.19 degrees of visual angle (dva). The high-reliability ellipse had an ellipse eccentricity of 0.9, such
94 that the major axis and minor axes were 1.02 and 0.37 dva, respectively. The low-reliability ellipse eccentricity was
95 determined separately for each participant to equate performance (details in Procedure).

96 On every trial, a stimulus display consisted of four ellipses. The probability of each ellipse being high reliability
97 was 0.5, independent of the reliability of the other ellipses. The location of the first ellipse was drawn from a uniform
98 distribution between polar angles 0° and 90° . Each ellipse after that was placed such that all ellipses were 90° apart
99 on an imaginary annulus that was 7 dva away from fixation. Afterward, the x- and y- location of the ellipses were
100 independently jittered -0.3 to 0.3 dva. In one condition, there were additionally oriented line stimuli, which were set
101 to have approximately the same area as the ellipses. Stimuli were displayed on a 23 inch LED monitor with a refresh
102 rate of 60 Hz and a resolution of 1920 x 1080 pixels.

103 **3.3 Procedure**

104 **3.3.1 Trial Procedure**

105 **Ellipse condition.** A trial began with a fixation cross presented for 1000 ms. Four ellipses were presented for 100 ms,
106 followed by a 1000 ms delay, then by another four ellipses for 100 ms. On half of the trials, all ellipses in the second
107 stimulus presentation were identical to the ellipses in the first stimulus presentation. On the other half of the trials, one
108 ellipse changed in orientation. This change was drawn from a uniform distribution, so change of any magnitude had
109 equal probability. Each ellipse had an equal probability of containing the change. “Change” and “no change” trials
110 were randomly interleaved throughout the experiment. The participant indicated with a keyboard button press whether
111 they believed there was an orientation change between the two displays.

112 **Line condition.** In the Line condition, the stimuli in the second presentation were oriented lines rather than
113 ellipses. The task was otherwise identical. An example of a trial in the Ellipse and Line conditions is illustrated in
114 Figure 1.

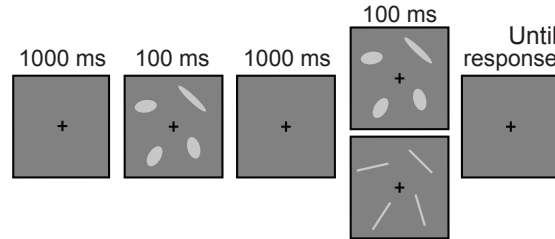


Figure 1: **Trial sequence.** Participants fixated on a cross, saw four ellipses (here showing one high-reliability ellipse and three low-reliability ellipses), maintained them over a delay, saw four stimuli again, and reported whether they believed there was an orientation change or not. In the Ellipse condition, ellipses in the second presentation were of the same reliability as in the first. In the Line condition, lines replaced ellipses in the second stimulus presentation, to avoid providing cues to the precision with which the first items were maintained.

115 3.3.2 Cross-Session Procedure

116 Participants completed both conditions over six one-hour sessions. They began their first session with a Practice
117 block, designed to ease the participants into the task. They then completed 2000 trials of each condition, preceded
118 by a Threshold block to set the “short” ellipse reliability for each condition. Participants completed all of one con-
119 dition before completing the other, and the order was counterbalanced across participants. Participants were verbally
120 informed that each trial had a 0.5 probability of a change occurring, that a change (if present) would occur in exactly
121 one ellipse, and the change could be “of any magnitude; big changes are as possible as small changes.” Participants
122 were also verbally informed that some ellipses would be more elongated than others, that this may affect performance,
123 and that half of the experiment would involve the stimuli changing from ellipses to lines. They were informed that
124 their task did not change; the goal was always to indicate whether there was a change in orientation.

125 The Practice block consisted of 256 trials and was designed to ease naive participants into the speed of the task.
126 The stimulus presentation time decreased throughout the course of the Practice block, from 333 ms to 100 ms, in 33
127 ms increments every 32 trials. Unlike the actual task, the ellipse eccentricities (i.e., reliabilities) of all ellipses within
128 each trial were the same, but changed across trials. The stimuli in the second stimulus presentation corresponded to
129 the condition that the participant completed first. For example, the stimuli in the second presentation were lines if the
130 participant completed the Line condition first.

131 The Threshold block consisted of 400 trials and was used to set the ellipse eccentricity of the low-reliability ellipse
132 in each condition. Like the Practice block, the ellipse eccentricities of all ellipses on each trial were the same, but
133 changed on a trial-to-trial basis. The second stimulus presentation set were either ellipses or lines, corresponding to
134 which condition the threshold was being set for. A cumulative normal psychometric function was fit to the accuracy as
135 a function of ellipse eccentricity, and the low-reliability ellipse eccentricity was set as the value that corresponded to a
136 predicted 65% accuracy. If the ceiling performance of the participant was estimated to be less than 75%, the Threshold
137 block was repeated. If the psychometric function could not estimate an ellipse reliability for which performance would

138 hit 65% after the second try, the participant was excluded from the experiment. Seven participants were excluded based
139 on these criteria.

140 4 Experimental Results

141 The goal of our study was to investigate whether people maintained and used uncertainty implicitly in a working
142 memory-based decision. To do this, we conducted a two-condition orientation change detection task. People could use
143 memory uncertainty to maximize performance in both conditions, but only the Line condition required maintenance of
144 that uncertainty. We conducted five repeated-measures ANOVAs to test whether condition (Ellipse, Line), the number
145 of high-reliability ellipses displayed (N_{high} : 0, 1, 2, 3, 4), or their interaction significantly affected the following values:
146 proportion report change, false alarm rate, hit rate (for all items), hit rate (when the changed item was a low-reliability
147 ellipse), and hit rate (when the changed item was a high-reliability ellipse). These values are visualized in Figure 2,
148 and the statistics are reported in Table 1.

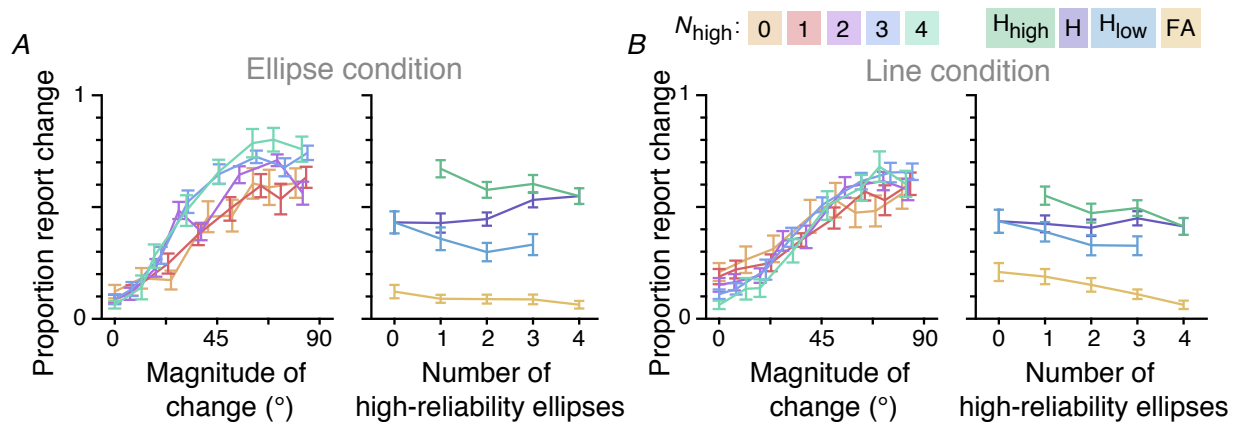


Figure 2: **Behavioral data.** Illustration of behavioral data for (A) Ellipse condition and (B) Line condition. For each condition, the left plots illustrates proportion report change as a function of magnitude of change. Data are binned by quantile, and different colored lines illustrate data from trials with different numbers of high-reliability ellipses presented on the first display. The right plots illustrate the proportion report change as a function of number of high-reliability ellipses, conditioned on whether there was no actual change (false alarm (FA): gold), a change in a low-reliability ellipse (H_{low} : blue), a change in a high-reliability ellipse (H_{high} : green), or a change in any ellipse (hit (H): purple). The color legend is displayed above the plots. Note that the aggregated hits are a weighted combination of the reliability-conditioned hits. The “Z” shape formed by the hit lines are an instance of Simpson’s paradox.

Dependent Variable	Factor	Statistics	p	ε	η^2
Proportion Report Change	N_{high}	$F(1.38, 16.50) = 3.37$	0.07	0.34	0.03
	Condition	$F(1, 12) = 1.33$	0.27	–	0.01
	$N_{\text{high}} \times \text{Condition}$	$F(2.12, 25.38) = 6.32$	0.005	0.52	0.04
False Alarm Rate	N_{high}	$F(1.93, 23.17) = 18.21$	2.07×10^{-5}	0.48	0.14
	Condition	$F(1, 12) = 6.50$	0.03	–	0.08
	$N_{\text{high}} \times \text{Condition}$	$F(1.95, 23.36) = 4.94$	0.02	0.49	0.05
Hit Rate (all)	N_{high}	$F(1.36, 16.30) = 5.29$	0.03	0.34	0.04
	Condition	$F(1, 12) = 2.47$	0.14	–	0.03
	$N_{\text{high}} \times \text{Condition}$	$F(2.04, 24.48) = 5.33$	0.01	0.51	0.03
Hit Rate (low-reliability)	N_{high}	$F(1.76, 21.07) = 23.26$	8.43×10^{-6}	0.59	0.08
	Condition	$F(1, 12) = 0.29$	0.60	–	0.005
	$N_{\text{high}} \times \text{Condition}$	$F(2.01, 24.15) = 0.37$	0.69	0.67	0.002
Hit Rate (high-reliability)	N_{high}	$F(1.98, 23.79) = 35.44$	7.72×10^{-08}	0.66	0.13
	Condition	$F(1, 12) = 14.66$	0.002	–	0.17
	$N_{\text{high}} \times \text{Condition}$	$F(2.15, 25.80) = 0.75$	0.49	0.72	0.003

Table 1: **Results of two-way repeated-measures ANOVA.** Independent variables are N_{high} (0,1,2,3,4) and condition (Ellipse, Line), and dependent variables are displayed as the first column. Statistics of significant effects are bolded. For all ANOVAs, we report the Greenhouse-Geisser corrected results and ε (sphericity correction) when appropriate.

149 There was a statistically significant interaction between N_{high} and condition on proportion report change. In only
150 the Ellipse condition, the proportion report change was modulated by the number of high-reliability ellipses (left plot
151 of Fig. 2 A, B). There were significantly more false alarms in the Line condition ($M = 0.14$, $SEM = 0.03$) than in
152 the Ellipse condition ($M = 0.09$, $SEM = 0.02$; purple lines in right plots of Fig. 2 A, B). Perhaps people mistook the
153 change in stimulus as a change in orientation. Both reliability-conditioned hit rates (blue and green lines in right plots
154 of Fig. 2 A, B) decreased with increasing N_{high} . Additionally, participants had significantly lower high-reliability hits
155 in the Line condition and the Ellipse condition.

156 There is an interesting reverse in the qualitative trend when looking at all hit rates across all trials: hit rate increases
157 as a function of N_{high} . This Simpson's paradox is a result of weighted averaging and the performance difference
158 between the reliability-conditioned hit rates. As the number of high-reliability ellipses in a display increases, so does
159 the probability of a change occurring in a high-reliability ellipse. Thus, the total hit rates for higher N_{high} s contain more
160 high-reliability hits than low-reliability hits, driving this value upward. Similarly, the trials to compute hit rates for
161 lower N_{high} s predominantly contain changes in low-reliability ellipses, thus driving the average downward. There was
162 also a significant interaction between condition and N_{high} because this increase was greater in the Ellipse condition.
163 This unsurprisingly reflects the results of proportion report change, for they are related values.

164 These statistics show that differences between factors and conditions exist, but are dissatisfying because they do not
165 offer explanations of what these differences mean. In this paper, we take an approach to understand underlying working
166 memory processes through computational modeling. Computational modeling plays a crucial role in the interpretation
167 of data and the understanding of the underlying working memory and decision-making processes (Levenstein et al.,
168 2020; Edwards, 1954). It allows us to make explicit assumptions and precise quantitative predictions, which provide
169 committal, falsifiable explanations of the processes involved.

170 **5 Modeling Methods**

171 To test whether people are maintaining and using uncertainty when making their change detection decision, we use
172 Bayesian observer models. Bayesian models provide a normative, flexible, and interpretable framework to study the
173 working memory process. These models are particularly useful in cases where the observer is trying to make a decision
174 without full knowledge of task-relevant information. In working memory, people do not have full knowledge because
175 information is not remembered perfectly. While Bayesian decision theory describes how an observer should behave
176 in order to maximize performance, different components of the model can be easily substituted with incorrect beliefs
177 or suboptimal use of information, and thus provides a good template for building models with “imperfectly optimal
178 observers” (Maloney & Zhang, 2010) or “model mismatch” (Orhan & Jacobs, 2014; Beck, Ma, Pitkow, Latham, &
179 Pouget, 2012; Acerbi, Ma, & Vijayakumar, 2014).

180 We model the observer’s decision process as consisting of an encoding stage and decision stage. The encoding
181 stage describes the task statistics and our assumptions about how memories are generated. In the decision stage,
182 the observer calculates a decision variable based on their belief of the encoding stage and decides whether to report
183 Change or No change based on some decision rule. We compared two models: one in which uncertainty is maintained
184 and used and another that is not, named the “Use Uncertainty” and the “Ignore Uncertainty” model, respectively. This
185 section describes how these models were defined, fit, and compared.

186 **5.1 Encoding Stage**

187 In this section, we define the statistical structure of the experiment and define our assumptions about how memories
188 are generated in an observer. On every trial, there is a 0.5 probability of there being a change, $p(C = 1) = 0.5$, where C
189 takes values 0 (no change) and 1 (change). On change trials, exactly one item changes in its orientation, and each item
190 is equally probable to be changed. The orientation change, Δ , is drawn from a uniform distribution, $p(\Delta) = \frac{1}{2\pi}$. (For
191 mathematical convenience, and without loss of generality, we doubled the actual orientation of stimuli in all model
192 specifications such that the values span 0 to 2π rather than 0 to π . We do not double these values when illustrating
193 model fits.)

194 We denote the vector of all orientations of the items presented on the first display by ξ , in which each element is an
195 independent draw from a uniform distribution over orientation space. The vector of orientations at the second display,
196 ϕ , was identical to ξ in no change trials. In change trials, the i th element of ϕ , the location of change, was equivalent

197 to $\xi_i + \Delta$.

198 We model the memory process for each item of each display according to the Variable Precision model (van den
199 Berg et al., 2012; Fougne et al., 2012), by which memories are described as a continuous resource that randomly
200 fluctuates across items and trials. The noisy measurements of each item on each display, $\mathbf{x} = (x_1, \dots, x_N)$ and $\mathbf{y} =$
201 (y_1, \dots, y_N) , are conditionally independent and drawn from a Von Mises distribution centered on the actual orientation
202 presentation,

$$p(\mathbf{x}|\boldsymbol{\xi}; \boldsymbol{\kappa}_x) = \prod_{i=1}^N p(x_i|\xi_i, \kappa_{x,i}) = \prod_{i=1}^N \frac{1}{2\pi I_0(\kappa_{x,i})} e^{\kappa_{x,i} \cos(x_i - \xi_i)}$$

$$p(\mathbf{y}|\boldsymbol{\phi}; \boldsymbol{\kappa}_y) = \prod_{i=1}^N p(y_i|\phi_i, \kappa_{y,i}) = \prod_{i=1}^N \frac{1}{2\pi I_0(\kappa_{y,i})} e^{\kappa_{y,i} \cos(y_i - \phi_i)}.$$

203 The κ s are the concentration parameter of the Von Mises distribution, and are related to the precision with which each
204 item is remembered; a higher κ corresponds to higher precision. The subscript of each κ indicates which item it refers
205 to (e.g., $\kappa_{x,i}$ is concentration parameter for x_i , the i^{th} item the first stimulus presentation). We assume that memory
206 precision varies across items, above and beyond the precision differences due to stimulus reliability. In other words,
207 $\kappa_{x,i}$ and $\kappa_{y,i}$ are themselves random variables, rather than single values. Rather than sampling κ itself, we sample the
208 Fisher information of the Von Mises distribution, J , from a gamma distribution:

$$p(J) = \frac{1}{\Gamma\left(\frac{\bar{J}}{\tau}\right)} \bar{J}^{\frac{\bar{J}}{\tau}-1} e^{-J/\tau},$$

209 where τ is the scale parameter of the gamma distribution and \bar{J} is the mean precision. The relationship between J and
210 κ is the following:

$$J = \kappa \frac{I_1(\kappa)}{I_0(\kappa)},$$

211 where I_0 is a modified Bessel function of the first kind of order 0 and I_1 is a modified Bessel function of the first kind
212 of order 1 (van den Berg et al., 2012; Keshvari et al., 2012). We allow the mean precision to differ across stimulus
213 shape; the precisions of memories corresponding to low-reliability ellipses are drawn from a gamma distribution with
214 mean \bar{J}_{low} and high-reliability ellipses with mean \bar{J}_{high} . Parameter τ is shared across both distributions. Because items
215 in the first display were presented earlier, there are certainly differences in the precision with which items in the first
216 and second display are maintained, independent of ellipse reliability. However, the amount that the first and second
217 displays contribute to the overall measured change are extremely hard to tease apart in the model. Thus, we use one
218 parameter per reliability and recognize that this estimate will be some average of the precisions of the first and second
219 display.

220 When modeling the Line condition, we have an additional parameter, \bar{J}_{line} , which corresponds to the mean precision
221 with which each line on the second display is remembered by the observer. To limit model complexity, the gamma
222 function from which each line's precision is drawn shares the same scale parameter τ as the distributions from which
223 the ellipse precisions are drawn.

224 5.2 Decoding Stage

225 5.2.1 Decision Variable

226 The essence of Bayesian inference is that an observer can compute a posterior over task-relevant latent variables, and
 227 should if they want to maximize performance. In this case, the observer should calculate the probability of the state
 228 of the world (i.e., change or no change) given their observations, $p(C|\mathbf{x}, \mathbf{y})$, which they can compute using Bayes rule.
 229 With a scenario in which there are only two states of the world, it is convenient to combine these into a ratio. Thus,
 230 we assume the observer calculates, for each item, the ratio of the likelihood of there being change and the likelihood
 231 of there being no change:

$$d = \frac{p(C = 1|\mathbf{x}, \mathbf{y})}{p(C = 0|\mathbf{x}, \mathbf{y})} = \frac{p(\mathbf{x}, \mathbf{y}|C = 1)p(C = 1)}{p(\mathbf{x}, \mathbf{y}|C = 0)p(C = 0)}. \quad (1)$$

232 Details of the derivation can be found in Appendix 8.1, but this simplifies to the following expression:

$$d = \frac{p(C = 1)}{p(C = 0)} \frac{1}{N} \sum_{i=1}^N d_i, \quad (2)$$

233 where

$$d_i = \frac{I_0(\kappa_{x,i})I_0(\kappa_{y,i})}{I_0\left(\sqrt{\kappa_{x,i}^2 + \kappa_{y,i}^2 + 2\kappa_{x,i}\kappa_{y,i}\cos(x_i - y_i)}\right)}. \quad (3)$$

234 I_0 is a modified Bessel function of the first kind of order 0, and the κ s are the concentration parameters of the noise
 235 distributions for the item indicated in the subscript. Intuitively, d_i provides a measure of the evidence of change for the
 236 i^{th} item. It increases with the measured amount of change, $x_i - y_i$, weighted by a function of the precisions with which
 237 x_i and y_i are remembered. The d_i s are averaged in the decision variable d , providing the optimal measure of evidence
 238 of change of the entire display.

239 This is the step in which the use of uncertainty comes in. Observers who correctly maintain and use uncertainty
 240 (i.e., observers who act in accordance with the optimal, “Use Uncertainty” model) compute exactly d_i as described.
 241 However, observers acting in accordance with the “Ignore Uncertainty” model do not know or do not consider that
 242 the precision of their memories for all items in both displays varies. Computing the decision rule for the Ignore
 243 Uncertainty observer is the same as replacing all κ s in Eq. 3 with a constant, resulting in the following local decision
 244 variable:

$$d_i = \frac{I_0^2(\kappa_{\text{ass}})}{I_0\left(\kappa_{\text{ass}}\sqrt{2 + 2\cos(x_i - y_i)}\right)}, \quad (4)$$

245 where κ_{ass} is the assumed precision for all items on all displays. The decision variable thus becomes just a function of
 246 $\cos(x_i - y_i)$, because the remainder of the expression is constant.

247 5.2.2 Decision Rule

248 The observer maps this decision variable onto a response by reporting Change whenever the probability of there being
 249 a change is greater than 0.5. An optimal observer would thus respond Change when the ratio of the likelihood of there

250 being a change and the likelihood of there being no change (Eq. 2) is greater than 1 (Figure 3). However, we allow
251 the observer to have some response bias (e.g., due to unequal priors, rewards, or motor costs), and thus implement the
252 following decision rule:

$$\frac{1}{N} \sum_{i=1}^N d_i > k, \quad (5)$$

253 where k is a free parameter. For both models, we implemented global decision noise by adding zero-mean Gaussian
254 noise with standard deviation σ_d to the log of decision variable d (Keshvari et al., 2012; Acerbi et al., 2014; Mueller
255 & Weidemann, 2008). Additionally, participants randomly guess with probability λ , due to factors such as lapses in
256 attention.

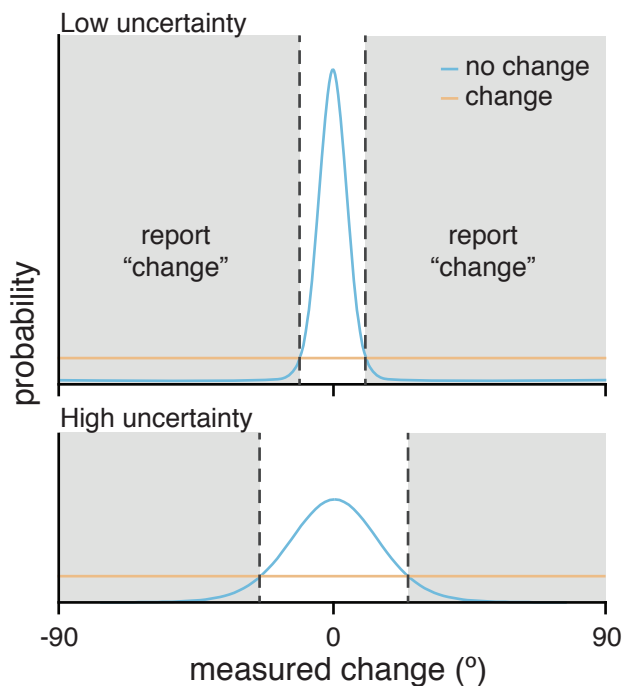


Figure 3: **Model didactics.** This didactic illustrates a simplified one-item version of this task. The probability of the measured change for an item given that the item did (orange) or did not (blue) change orientation, as estimated by the optimal observer. Uncertainty modulates the width of the no change distribution, such that higher uncertainty makes the no change distribution wider (bottom). The optimal observer (with $k = 0$) places their decision boundaries at the intersection of the change and no change distributions (vertical dashed lines), reporting “change” whenever that state of the world is more probable (shaded region) and “no change” otherwise.

257 **5.3 Parameter Estimation and Model Comparison**

258 **5.3.1 Parameters**

259 Both models in both conditions have parameters $\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \tau, k, \lambda$, and σ_d . Parameters \bar{J}_{high} and \bar{J}_{low} correspond to the
260 mean precision of the high- and low-reliability ellipses, respectively. Precision is also affected by the scale parameter
261 of the gamma distribution from which item-wise precision is drawn, τ ; this value is shared across the two ellipse types
262 and the line when applicable. Parameter k is the observer's response bias; λ is the probability on each trial that the
263 observer lapses and responds randomly; σ_d is the standard deviation of the Gaussian from which decision noise is
264 simulated.

265 When fitting data from the Line condition, there is an additional parameter \bar{J}_{line} , corresponding to the mean preci-
266 sion with which the line stimulus is represented. The Ignore Uncertainty model has one additional parameter: J_{ass} , the
267 assumed precision of all stimuli in both displays.

268 **5.3.2 Parameter Estimation**

269 The likelihood of the parameter combination θ for a given participant and model is the probability of the data given
270 the parameter combination. We used the log likelihood, which we denote LL:

$$\begin{aligned} \text{LL}(\theta) &= \log p(\theta | \text{data, model}) \\ &= \log \prod_t^{N_{\text{trials}}} p(r_t | \theta) \\ &= \sum_t^{N_{\text{trials}}} \log p(r_t | \theta), \end{aligned}$$

271 where r_t is the participant's response on the t^{th} trial. For each participant, we used maximum-likelihood estimation
272 to find which parameter combination best describes participant's data. Computing the LL analytically is intractable,
273 so we used Inverse Binomial Sampling (van Opheusden, Acerbi, & Ma, 2020), a method which efficiently computes
274 an unbiased estimate of the LL. This calculation is stochastic, so we additionally used an optimization algorithm that
275 can account for stochasticity and expensive LL evaluations (BADS; Acerbi & Ma, 2017). BADS explicitly incorpo-
276 rates uncertainty in the estimated LL and converges in fewer function evaluations than other stochastic optimization
277 methods (e.g., CMA-ES, genetic algorithms), making it an ideal optimization method when likelihood calculations are
278 computationally expensive and stochastic. We used 20 different starting positions, using Latin hypercube sampling, to
279 reduce the probability of finding a local minimum. We took the parameter combination corresponding to the minimum
280 negative log-likelihood of our runs as the ML parameter estimate. The estimated LL at the candidate optimum was
281 reevaluated using 1000 samples in IBS, in order to reduce the standard deviation of estimation noise to less than 1. We
282 denote the maximum log-likelihood by LL^* .

283 5.3.3 Model Comparison

We compared models using corrected Akaike Information Criterion (AICc; Hurvich & Tsai, 1987) and the Bayesian Information Criterion (BIC; Schwarz, 1978). BIC penalizes for additional parameters harsher than AICc.

$$\text{AICc} = -2\text{LL}^* + 2N_{\text{pars}} + \frac{2N_{\text{pars}}(N_{\text{pars}} + 1)}{N_{\text{trials}} - N_{\text{pars}} - 1}$$

$$\text{BIC} = -2\text{LL}^* + 2N_{\text{pars}} \log N_{\text{trials}}$$

284 5.4 Modeling Results

285 We compared the fits of the Use Uncertainty and Ignore Uncertainty models to each of the conditions separately. The
286 Use Uncertainty model provides a good qualitative fit to the data in both conditions (top row of Figure 4A), while the
287 Ignore Uncertainty model is unable to capture the data (bottom row of Figure 4A). This result is reflected quantitatively
288 (Figure 4B). For both conditions, all of the 13 participants were better fit by the Use Uncertainty model than the Ignore
289 Uncertainty model (median [95% bootstrapped confidence interval (CI)] ΔAICc across subjects – Ellipse: 208 [109,
290 368], Line: 108 [58, 370]. ΔBIC – Ellipse: 221 [122, 381], Line: 122, [71, 383]). The summed ΔAICc and ΔBIC are
291 consistent and are available in Appendix 8.4. Parameter estimates for the Use Uncertainty model in the Ellipse and
292 Line condition can be found in the Appendix (Tables 4 and 5, respectively).

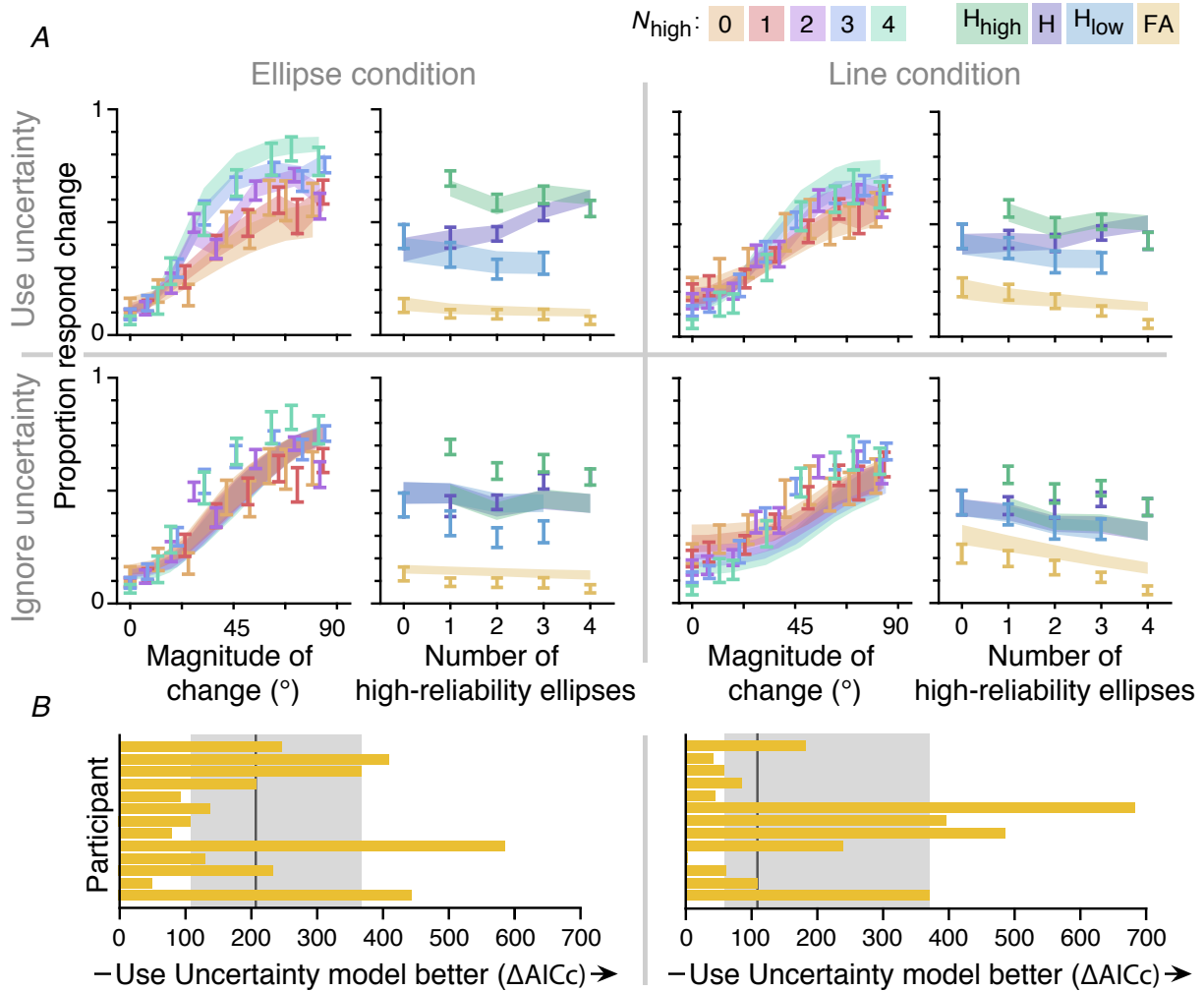


Figure 4: **Model fits.** *A.* $M \pm SEM$ data (error bars) and model fits (fills) for the Use (top) and Ignore (bottom) Uncertainty models and the Ellipse (left) and Line (right) conditions. For each model and condition, the left graph illustrates the proportion report change as a function of amount of change. Data and models are binned by quantiles, and color indicates the number of high-reliability ellipses. The right graph illustrates the proportion hits for high-reliability items (green), hits for low-reliability items (blue), total hits (purple), and false alarms (gold) as a function of number of high-reliability items. *B.* Model comparison for the Ellipse (left) and Line (right) conditions. Each bar indicates the individual-subject $\Delta AICc$ between the Use and Ignore Uncertainty models, where a positive value indicates that the Use Uncertainty model is favored. The vertical grey line indicates the median across participants, and the shaded region illustrates the 95% bootstrapped confidence interval of the median. Only $\Delta AICc$ s are illustrated because the two model comparison metrics gave similar results.

293 **6 Model Variants**

294 While the Use Uncertainty model provides a good fit to the data, the two models we have considered thus far contain
295 assumptions that could be modified. In this section, we factorially compare different formulations of the encoding,
296 inference, and decision stage of the model (van den Berg, Awh, & Ma, 2014; Acerbi, Wolpert, & Vijayakumar, 2012;
297 Keshvari et al., 2012). A factorial model comparison is an effective way of testing which assumptions we made were
298 critical for accounting for human behavior, and thus which are reasonable to make conclusions about. In this section,
299 we demonstrate that our general conclusions about the use of uncertainty do not depend on the specific assumptions
300 we made when defining our model. We only discuss the results of the Line condition here, since it is the only condition
301 that investigates the maintenance of uncertainty in working memory. However, we did the same analysis to the Ellipse
302 condition data and found consistent results (Appendix 8.3).

303 **6.1 Encoding**

304 In both the Use and Ignore Uncertainty models, we assumed that observers' encoding noise followed that of a Variable
305 Precision model (van den Berg et al., 2012; Fougny et al., 2012). Here, we also consider that observers' memory pre-
306 cision varies only based on stimulus type, and does not fluctuate on an item-to-item basis. With this "Fixed Precision"
307 assumption of encoding noise, the κ for each item is determined only by its stimulus type; high-reliability ellipses
308 would be encoded with parameter κ_{high} , low-reliability ellipses with κ_{low} , and lines with κ_{line} .

309 **6.2 Inference**

310 Observers calculate the decision variable according to some inference process, which we allow to be independent of
311 the true generative process. The potential model mismatch (Orhan & Jacobs, 2014; Beck et al., 2012; Acerbi et al.,
312 2014) between the true and believed generative process could be due to a result of wrong beliefs about the generative
313 process or computation limitations that prevent accurate representation of the generative model. We consider that
314 observers may use partial knowledge of uncertainty, rather than fully Using or Ignoring uncertainty.

315 We consider that the observer may have one of four inference models, listed below in decreasing order of how
316 many factors the observer takes into account in their uncertainty:

- 317 1. Variable precision (V): the observer believes that mean memory precision varies with the exact stimulus shape
318 (low-reliability ellipse, high-reliability ellipse, line) and that there is additional noise for each item at each
319 presentation. This inference model is optimal when the true generative process is Variable precision.
- 320 2. Fixed precision (F): the observer believes that memory precision varies with the exact stimulus shape (low-
321 reliability ellipse, high-reliability ellipse, line), but does not consider that there is additional noise for each item
322 at each presentation. This inference model is suboptimal when the true generative process is Variable precision,
323 but optimal when the true generative process is Fixed precision.

324 3. Limited (L): the observer believes that memory precision varies across shapes (ellipse vs. line). This observer
325 does not consider differences in precision between high- and low-reliability ellipses or additional noise for each
326 item at each presentation. This observer is suboptimal.

327 4. Same precision (S): the observer believes that memory precision is the same throughout the condition, and does
328 not vary with stimulus shape or anything else. This is the “Ignore Uncertainty” observer and is suboptimal.

329 Note that the Variable and Same precision inference schemes here are identical to that of Keshvari and others’ (2012),
330 and the Fixed precision here is equivalent to their “Equal” precision inference scheme.

331 **6.3 Decision Rule**

332 The Use and Ignore Uncertainty models use the optimal decision rule (Eq. 5). Note that participants may have
333 incorrect assumptions about the noise in their memory, but still be acting in accordance with Bayesian decision theory
334 (i.e., still using the correct decision rule), resulting in “imperfectly optimal observers” (Maloney & Zhang, 2010).
335 Alternatively, participants could be calculating the optimal decision variable, but be using a suboptimal decision rule.
336 Here, we consider observers who use the max rule, responding Change whenever the maximum evidence of change is
337 greater than some criterion, k ,

$$\max_i d_i > k, \quad (6)$$

338 rather than averaging d_i s. These observers are not Bayes-optimal, but are still using probabilistic computation (i.e., still
339 using their uncertainty) in the calculation of d_i . In fact, in many cases these decision rules do not result in substantially
340 different behavior (Ma, Shen, Dziugaite, & van den Berg, 2015). For example, if all d_i s are similar, then a max and an
341 average will result in similar values. If the maximum d_i is substantially larger than the others, both decision rules can
342 result in similar behavior by adjusting k .

343 **6.4 Parameters**

344 There are two possible encoding schemes ((V)ariable, (F)ixed), four possible inference schemes ((V)ariable, (F)ixed,
345 (L)imited, (S)ame), and two possible decision rules ((O)ptimal, (M)ax). Factorially combining each of these char-
346 acteristics would yield 16 different models. We choose not to consider the models in which the generative model is
347 “F” but the observer assumes “V” under the assumption that people tend not to assume the (perceptual) world is more
348 complicated than it actually is; thus, we test a total of 14 models. We denote each model by the letters corresponding to
349 their encoding scheme, inference scheme, and decision rule (e.g., VVO is the model with Variable precision encoding,
350 an observer assumes Variable precision, and an Optimal decision rule). The VVO model is the Use Uncertainty model;
351 the VSO model is the Ignore Uncertainty model.

352 *Encoding parameters.* Like before, observers with Variable precision encoding have parameters \bar{J}_{high} , \bar{J}_{low} , \bar{J}_{line} ,
353 and τ . Observers with Fixed precision encoding have parameters J_{high} , J_{low} , and J_{line} .

354 *Inference parameters.* For the observer who correctly infers their encoding process (i.e., VVO, VVM, FFO, or
 355 FFM), there are no additional parameters. If the observer has Variable precision encoding but does not take into account
 356 individual-item variations (i.e., VFO or VFM), then the assumed precision is $J_{\text{high}} = \bar{J}_{\text{high}}$, $J_{\text{low}} = \bar{J}_{\text{low}}$, and $J_{\text{line}} = \bar{J}_{\text{line}}$
 357 for high-reliability ellipses, low-reliability ellipses, and lines, respectively. Limited inference observers (i.e., VLO,
 358 VLM, FLO, FLM) have two additional parameters: $J_{\text{ass},e}$ and $J_{\text{ass},l}$, corresponding to the assumed precision of the
 359 ellipses and lines, respectively. Same inference observers, who do not take any memory variations into account (i.e.,
 360 VSO, VSM, FSO, FSM), have one additional parameter J_{ass} , corresponding to the assumed precision of all items.

361 *Decision parameters.* Observers using both the optimal or max decision rule have parameter k , corresponding to
 362 the decision criterion. If any item has a decision variable greater than k , then they will respond Change.

363 Each model and their corresponding parameters is listed in Table 2. Note that the Same inference observer who
 364 uses the max rule (i.e., VSM, FSM) has one less parameter than their Optimal decision rule counterpart (i.e., VSO,
 365 FSO) because making a decision depends only on the item with the largest measured change.

Encoding	Inference	Decision Rule	
		(O)ptimal	(M)ax
(V)ariable	(V)ariable	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}})$	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}})$
	(F)ixed	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}})$	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}})$
	(L)imited	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \bar{J}_{\text{ass},e}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}}, \bar{J}_{\text{ass},l})$	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \bar{J}_{\text{ass},e}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}}, \bar{J}_{\text{ass},l})$
	(S)ame	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \bar{J}_{\text{ass}}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}})$	$\bar{J}_{\text{high}}, \bar{J}_{\text{low}}, \tau, k, \lambda, \sigma_d(\bar{J}_{\text{line}})$
(F)ixed	(F)ixed	$J_{\text{high}}, J_{\text{low}}, k, \lambda, \sigma_d(J_{\text{line}})$	$J_{\text{high}}, J_{\text{low}}, k, \lambda, \sigma_d(J_{\text{line}})$
	(L)imited	$J_{\text{high}}, J_{\text{low}}, J_{\text{ass},e}, k, \lambda, \sigma_d(J_{\text{line}}, J_{\text{ass},l})$	$J_{\text{high}}, J_{\text{low}}, J_{\text{ass},e}, k, \lambda, \sigma_d(J_{\text{line}}, J_{\text{ass},l})$
	(S)ame	$J_{\text{high}}, J_{\text{low}}, J_{\text{ass}}, k, \lambda, \sigma_d(J_{\text{line}})$	$J_{\text{high}}, J_{\text{low}}, k, \lambda, \sigma_d(J_{\text{line}})$

Table 2: **Model parameters.** Model parameters for Line condition. Parameters unnecessary for fitting the Ellipse condition are displayed in parentheses. The top colored cell corresponds to parameters of the Use Uncertainty (VVO) model. The bottom colored cell corresponds to the parameters of the Ignore Uncertainty (VSO) model.

366 6.5 Model Comparison Results

367 As previously described, we estimated parameters for each participant and compared models using AICc and BIC. In
 368 this section, we only discuss the results of the Line condition using median AICc and BIC differences between the
 369 VVO (Use Uncertainty) and other models. However, we report the results of the Ellipse condition in the Appendix
 370 8.3.

371 The factorial model comparison results corroborate our earlier result. Models in which observers correctly used
 372 their memory uncertainty (i.e., VVO, VVM, FFO, FFM) were indistinguishable from one another according to ΔAICc
 373 and ΔBIC (Table 3, bar graphs in Figure 5). These four models, however, fit substantially better than the remaining
 374 10 models in which the observer does not fully know or use their memory uncertainty in their decisions, indicated

375 by the 95% CI of the median ΔAICc and ΔBIC being greater than 0. These results imply that the specific encoding,
 376 inference, and decision rule do not matter as much the match between the encoding and inference scheme. In other
 377 words, the models that are able to capture the data are those in which observers' uncertainty reflects that of the true
 378 encoding process.

379 In the Appendix, we additionally report the sum of the ΔAICc and ΔBIC and group Bayesian Model Selection
 380 (BMS) for both conditions (Appendix 8.4 and 8.5, respectively). Summing the ΔAICc and ΔBIC explicitly assumes
 381 that participants are all fit by the same model, while group BMS allows for participant heterogeneity and directly infers
 382 the distribution of participants across models. Using these alternative model comparison metrics do not change the
 383 results; behavior was overwhelmingly best explained by a model that assumes that uncertainty is maintained accurately
 384 and used.

Encoding	Inference	Decision Rule			
		(O)ptimal		(M)ax	
		ΔAICc	ΔBIC	ΔAICc	ΔBIC
(V)ariable	(V)ariable	0 [0, 0]	0 [0, 0]	4 [-1, 13]	4 [-1, 13]
	(F)ixed	11 [4, 26]	11 [4, 26]	22 [11, 50]	22 [11, 50]
	(L)imited	97 [43, 256]	123 [69, 283]	255 [30, 366]	282 [56, 392]
	(S)ame	108 [58, 370]	122 [71, 383]	170 [138, 235]	170 [138, 235]
(F)ixed	(F)ixed	3 [3, 19]	-10 [-16, 9]	19 [9, 38]	6 [-4, 25]
	(L)imited	53 [23, 82]	66 [37, 96]	51 [24, 100]	64 [37, 113]
	(S)ame	39 [17, 91]	39 [17, 91]	148 [84, 167]	135 [70, 154]

Table 3: **Median ΔAICc and ΔBIC : Line condition.** The median and 95% bootstrapped confidence interval of the ΔAICc and ΔBIC . A positive value indicates that the VVO model provides a better fit to the data. The cells corresponding to the Use (VVO) and Ignore (VSO) Uncertainty models are colored in blue.

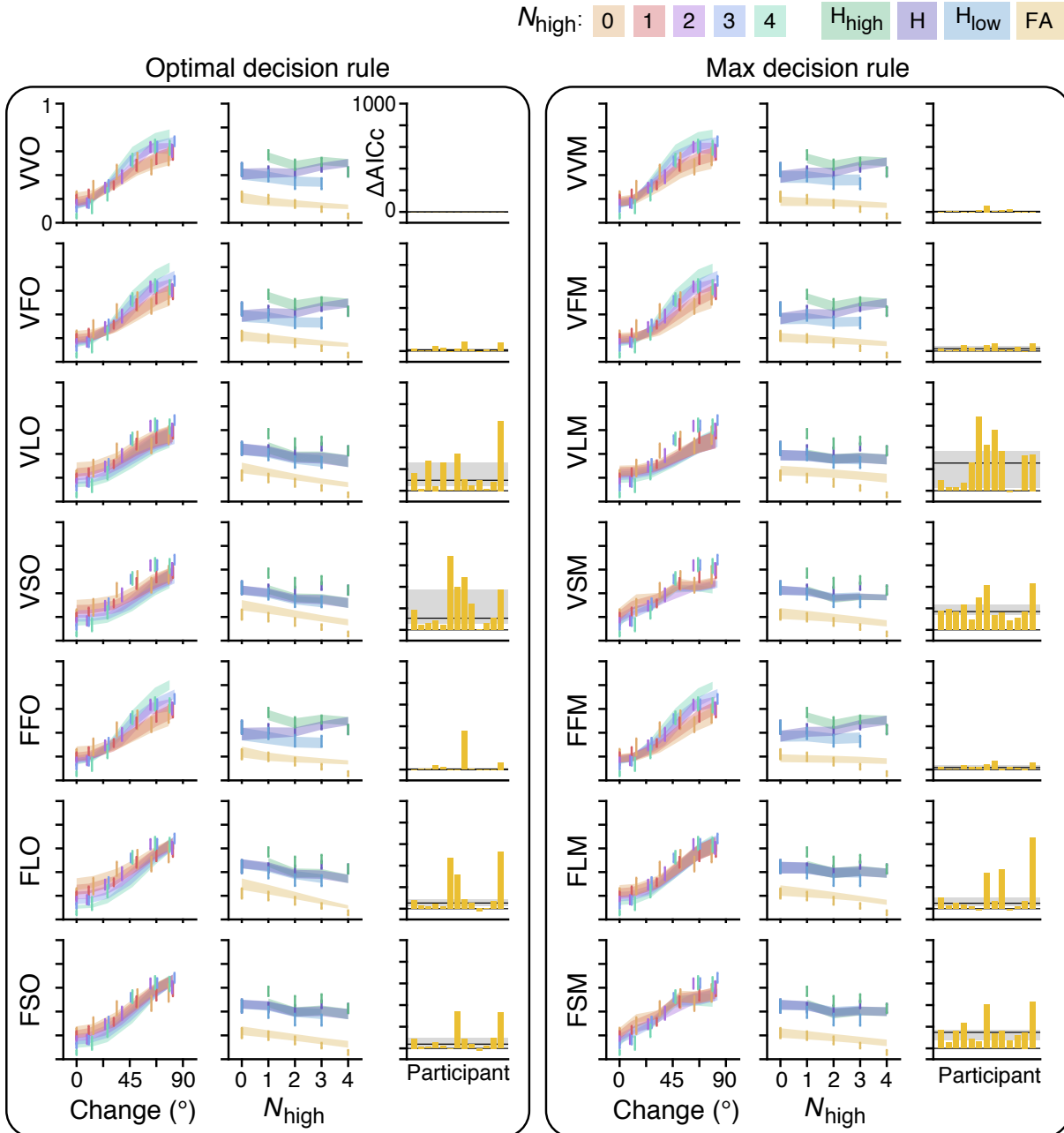


Figure 5: **Factorial model comparison.** Model predictions and performance of all possible combinations of different encoding, inference, and decision rules. $M \pm SEM$ data (error bars) and model fits (fills) for all models, organized into two columns by decision rule. For each model (each row within each column), the left graph illustrates the proportion report change as a function of amount of change. Color indicates the number of high-reliability ellipses (legend at the top of the figure). The middle graph illustrates the proportion hits for high-reliability items (green), hits for low-reliability items (blue), hits averaged across the display (purple), and false alarms (gold) as a function of number of high-reliability items (legend at the top right of the figure). The right graph illustrates the individual-participant $\Delta AICc$, where positive numbers indicate the VVO model is a better fit to the data. The grey horizontal line and shaded region illustrates median and the 95% bootstrapped confidence interval of the median across participants.

385 7 Discussion

386 In this paper, we investigated whether uncertainty is maintained and implicitly used in a working memory-based
387 decision. First, we demonstrated that people use uncertainty implicitly in a working memory task if that uncertainty
388 information was available after the delay (i.e., if uncertainty did not need to be maintained). Second, and more
389 importantly, we showed that people not only use uncertainty, but maintain this information over the working memory
390 delay. Finally, we factorially tested different model encoding schemes, inference schemes, and decision rules and
391 found that people were best described by models in which observers accurately maintain and use uncertainty in their
392 decision.

393 First, we demonstrated that people could use uncertainty implicitly in a working memory task if that uncertainty
394 information was experimentally available. While the change detection task has been an experimental staple in the
395 working memory literature (e.g., Luck & Vogel, 1997; Phillips, 1974; Pashler, 1988), the majority of these tasks
396 feature large, categorical changes in the stimulus. In contrast, our task, which is a direct experimental replication of
397 that of Keshvari and others (2012), featured changes that varied on a trial-to-trial basis. Trial-to-trial fluctuations in
398 stimuli and withholding of feedback allow for a strongest test of probabilistic computation because observers would
399 need to maintain a belief distribution over stimulus values to maximize performance in this task (Ma & Jazayeri,
400 2014). Through formal model comparison, we showed that all participants in the Ellipse condition are better fit by the
401 Use Uncertainty model than the Ignore Uncertainty model. The Use Uncertainty model was identical to the model that
402 was found to describe participant data best in the study by Keshvari et al. (2012). These results are also qualitatively
403 consistent with Devkar and others' (2017) work, despite being slightly different tasks.

404 Second, and more importantly, we showed that people not only use uncertainty, but maintain this information
405 over the working memory delay. Like in the Ellipse condition, we found that all participants in the Line condition
406 were better fit by the Use Uncertainty model than the Ignore Uncertainty model. However, the conclusion of this
407 model comparison is critically different. In the Ellipse condition as well as in previous studies (Keshvari et al., 2012;
408 Devkar et al., 2017), the ellipses were presented after the working memory delay, with the same reliability as before.
409 With these experimental designs, reliability information could be used as a heuristic to inform uncertainty, thus not
410 requiring this information to be maintained in memory. In other words, these previous studies cannot make any
411 conclusions about the contents of working memory, only the decision-making process that follows it. Our result, in
412 contrast, demonstrates that uncertainty was actually *maintained* in working memory, since the information was not
413 available to the participants through a heuristic such as ellipse reliability.

414 These results provide evidence that people can maintain and use uncertainty in an *implicit* decision-making
415 paradigm. This is in agreement with studies that asked participants to make an explicit reports such as confidence
416 ratings (Rademaker et al., 2012; Vandenbroucke et al., 2014; Samaha & Postle, 2017). This is also in agreement with
417 the “choose best” (Fougnie et al., 2012; Suchow et al., 2017) and wager paradigms (Yoo et al., 2018; Honig et al.,
418 2020). These paradigms are explicit in the sense that participants deliberate on a decision that is directly related to their
419 conscious uncertainty in a memory, but implicit in the sense that this uncertainty must be taken into account in another
420 perceptual decision.

421 Finally, we conducted a factorial model comparison to investigate whether our conclusions were due to specific
422 assumptions about model encoding schemes, inference schemes, and decision rules. We found that the most important
423 aspect of a model was that its encoding and inference schemes were matched, providing strong evidence that people
424 accurately maintain and use their uncertainty in working memory-based decisions. Our results are somewhat incon-
425 sistent with research showing strong support for Variable precision encoding over Fixed precision encoding (van den
426 Berg et al., 2014; Keshvari et al., 2012), and consistent with research showing that optimal and max decision rules are
427 difficult to distinguish through model comparison (Ma et al., 2015). Future experiments may attempt to tease apart
428 these two decision rules by manipulating the prior probability of change trials or the behavioral relevance of individual
429 items.

430 Our results suggest that existing computational models of working memory that currently ignore uncertainty should
431 be updated. For example, attractor network models currently maintain a point estimate of a single item feature through
432 the mean of a stereotyped bump in a network of neurons (Ermentrout, 1998; Wang, 2001; Compte, 2006). Thus,
433 there is typically no notion of uncertainty in this framework. Lim and Goldman (2014) demonstrated that altering the
434 network connectivity and dynamics results in “negative-derivative feedback models,” in which networks can vary not
435 only in mean but also in amplitude. Probabilistic population coding (PPC) and neural network models have imple-
436 mented precision through input gain (Ma, Beck, Latham, & Pouget, 2006; Orhan & Ma, 2017). Additional research
437 must investigate whether these negative-derivative feedback models can represent a memory’s precision through the
438 amplitude of the network maintaining it, precision which could be read out from the observer as uncertainty.

439 Additionally, computational models could be used to decode uncertainty from neural activity in working memory
440 tasks. Work in visual perception demonstrates that uncertainty information is represented in primary visual cortex
441 (van Bergen, Ma, Pratte, & Jehee, 2015; van Bergen, 2019; Walker, Cotton, Ma, & Tolias, 2020; Hénaff, Boundy-
442 Singer, Meding, Ziemba, & Goris, 2020). These studies built normative Bayesian models to infer stimulus value from
443 BOLD signal. The likelihood of the stimulus, and thus uncertainty, could be read out from the models. Estimates
444 of trial-specific uncertainty are positively correlated with error, suggesting that primary visual cortex held uncertainty
445 information. Since working memories have been shown to be maintained in the same sensory areas with which they
446 are perceived (e.g. Curtis & D’Esposito, 2003; Postle, 2006; D’Esposito & Postle, 2015; Harrison & Tong, 2009),
447 perhaps visual working memory uncertainty is also stored in visual cortex. To more rigorously test the representation
448 of uncertainty decoded from BOLD data, future studies can correlate decoded uncertainty with behavioral measures of
449 uncertainty such as confidence ratings (Rademaker et al., 2012) or post-decision wagers (Yoo et al., 2018; Honig et al.,
450 2020). Additionally, future studies can try to fit individual-trial data using these methods, which is more compelling
451 evidence in favor of a model than a correlation.

452 Overall, this paper shows that people have uncertainty that reflects their memory noise at an item-specific level
453 and they maintain this information over a working memory delay. This research demonstrates that there is other
454 information, beyond a point estimate, maintained in working memory and used in later decisions.

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