

1 **Probabilistic inferential decision-making under time pressure in rhesus**
2 **macaques (*Macaca mulatta*)**

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24 Author Footnotes

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47 **Abstract**

48 Decisions often involve the consideration of multiple cues, each of which may inform
49 selection on the basis of learned probabilities. Our ability to use probabilistic inference
50 for decisions is bounded by uncertainty and constraints such as time pressure. Previous
51 work showed that when humans choose between visual objects in a multiple-cue,
52 probabilistic task, they cope with time pressure by discounting the least informative
53 cues, an example of satisficing or “good enough” decision-making. We tested two
54 rhesus macaques (*Macaca mulatta*) on a similar task to assess their capacity for
55 probabilistic inference and satisficing in comparison with humans. On each trial, a
56 monkey viewed two compound stimuli consisting of four cue dimensions. Each
57 dimension (e.g., color) had two possible states (e.g., red or blue) with different
58 probabilistic weights. Selecting the stimulus with highest total weight yielded higher
59 odds of receiving reward. Both monkeys learned the assigned weights at high accuracy.
60 Under time pressure, both monkeys were less accurate as a result of decreased use of
61 cue information. One monkey adopted the same satisficing strategy used by humans,
62 ignoring the least informative cue dimension. Both monkeys, however, exhibited a
63 strategy not reported for humans, a “group-the-best” strategy in which the top two cues
64 were used similarly despite their different assigned weights. The results validate
65 macaques as an animal model of probabilistic decision-making, establishing their
66 capacity to discriminate between objects using at least four visual dimensions
67 simultaneously. The time pressure data suggest caution, however, in using macaques
68 as models of human satisficing.

69 **Keywords** Rhesus macaque, decisions, probabilistic inference, satisficing

70 **Introduction**

71 Everyday decision-making may require the use of multiple, simultaneous cues with
72 different diagnostic values. A person or animal choosing between pieces of fruit, for
73 example, may assess their ripeness, symmetry, and abrasions; that is, the dimensions
74 of color, shape, and texture. Probabilistically, color may be a better indicator of
75 palatability than shape, which may in turn be more important than texture. In the human
76 cognitive literature, learning the statistical properties of such cues is termed *probabilistic*
77 *inference* (for reviews, see Fiser et al., 2010, and Ma, 2012).

78 The ability to make decisions based on probabilistic inference of multiple,
79 simultaneous cues, such as in our fruit example, has been studied extensively in
80 humans (e.g. Gluck & Bower, 1988; Kemler Nelson 1984; Knowlton et al., 1994; Medin
81 et al., 1987). Much of that work focused on categorization, and recent studies extended
82 the approach to macaques. Presented with stimuli consisting of multiple visual cues,
83 some of which are strong indicators of category (“criterial cues”), it was shown that
84 macaques infer and use the criterial cues to varying degrees depending on task design
85 and cue dimensionality (Couchman et al., 2010; Smith et al., 2010; see also review by
86 Smith et al., 2012). Sigala et al. (2002), similarly, trained macaques on a categorization
87 task that required probabilistic inference of two out of four cue dimensions. Macaques
88 can also infer the probabilities of visual cues that signify various forms of reinforcement
89 (negative vs. positive: Amemori & Graybiel, 2012; risky vs. ambiguous: Hayden et al.,
90 2010; flavor and amount: Raghuraman & Padoa-Schioppa, 2014) or cues that are
91 revealed sequentially (Kira et al., 2015; Yang & Shadlen, 2007). Furthermore, by using
92 opt out and bail out options as a measure of confidence, it has been demonstrated that

93 animals and humans have a probabilistic interpretation of their solutions to such tasks
94 (Kiani & Shadlen, 2009; for a review of both humans and animals, see Kepecs &
95 Mainen, 2014). The present study extends all this work to examine, in a highly
96 quantified task framework, the extent to which macaques apply probabilistic inference in
97 the naturalistic situation of deciding between two objects that each consist of several
98 visual features, all of which have varying levels of learned importance.

99 Decisions based on multiple, simultaneous cues may need to be made under
100 conditions of uncertainty or time pressure. In the example of choosing fruit, a fast
101 decision may be necessary to beat a conspecific to the best piece. Faced with such
102 challenges, humans switch to *satisficing* strategies to reach decisions that are “good
103 enough”; while not necessarily optimal, they are satisfactory and sufficient for the task at
104 hand (Simon, 1955, 1956; Gluck & Bower, 1988). Satisficing includes, for instance, the
105 use of heuristics or “rules of thumb” (Rieskamp & Hoffrage, 2008; Gigerenzer &
106 Gaissmaier, 2011). Human satisficing strategies during probabilistic decision-making
107 were studied recently by Oh and colleagues (Oh et al., 2016) using tasks that involved
108 four simultaneously presented dimensions of visual information. They found that, under
109 time pressure, humans adopt a “drop-the-worst” heuristic by ignoring the least
110 informative cue dimensions. This change in strategy is accompanied by a shift in brain
111 activity from cortical to subcortical networks as indicated by fMRI (Oh-Descher et al.,
112 2017). Another common satisficing strategy is the “take-the-best” heuristic (e.g.
113 Gigerenzer & Goldstein, 1996) in which subjects search through cues from most to least
114 informative and stop when they find the first cue that discriminates between the possible
115 choices (Gigerenzer & Goldstein, 1996; Newell et al., 2003; Karelaia, 2006).

116 The neural basis of probabilistic inference and satisficing could be explored in
117 more detail using rhesus macaques if we had a better understanding of their behavior.
118 Therefore, the goal of the present study was to test two hypotheses: (1) rhesus
119 macaques use probabilistic inference to choose between stimuli that are each defined
120 by jointly presented, statistically informative visual dimensions; and (2) they adopt
121 satisficing strategies when making those decisions under time pressure. We trained
122 macaques on the same decision-making task tested on humans (Oh et al., 2016) that
123 involved visual stimuli composed of four, probabilistically weighted cue dimensions.
124 Using psychometric and modeling approaches, we analyzed the animals' strategies for
125 performing the task under low and high time pressure. Our results supported both
126 hypotheses, with the caveat that satisficing strategies differ in some ways between
127 rhesus macaques and humans.

128

129 **Methods**

130 *Animals and apparatus*

131 Two female rhesus monkeys (*Macaca mulatta*; Monkey A, 6 kg, and Monkey L, 8 kg)
132 were tested in their cages using touchscreens (Elo 1537L 15" Intellitouch SER/USB)
133 mounted onto the cage using custom built attachments. A tube above the screen
134 delivered 1 cc of water reward for every correct trial. The animals received at least 20
135 cc/kg of water per day. If they did not earn this amount of water during a session, they
136 were provided with the remaining water afterward. They also received supplemental fruit
137 daily. Aside from water control, there were no other modifications to the monkeys'
138 routine husbandry. No invasive procedures were required, animals were pair-housed,

139 and environmental enrichment was provided. Experimental control, including stimulus
140 and reward delivery, was performed using Psychtoolbox in MATLAB
141 (www.mathworks.com). All procedures were approved by the Institutional Animal Care
142 and Use Committee at Duke University (protocol A079-17-03).

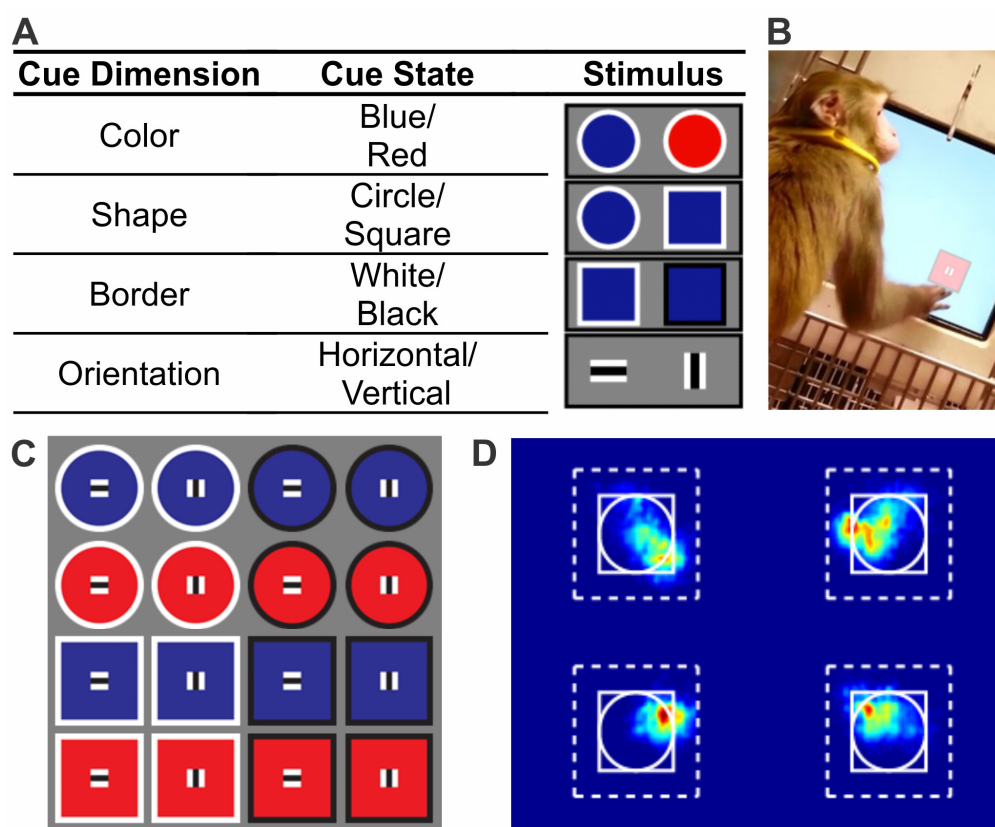
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144 *Task overview*

145 We used the same probabilistic decision-making task as used in Experiments 1 and 2 of
146 Oh et al. (2016) except for slight modifications to facilitate monkey testing (e.g. four
147 possible locations of stimuli instead of two, to discourage spatial habits and maintain
148 attentiveness). Figure 1 illustrates the overall procedure. A monkey viewed stimuli on its
149 in-cage touchscreen. Trials started automatically with a white cross appearing in the
150 center of the gray background for 0.7 seconds. When the cross disappeared, two 2.5 x
151 2.5 cm stimuli appeared in two of four possible quadrants. Each stimulus was
152 constructed of features that varied across four visual dimensions (Figure 1A). The two
153 stimuli remained visible for a maximum duration termed the *response window* (details in
154 next paragraph). Before the response window elapsed, the monkey had to select one of
155 the stimuli by touching it (Figure 1B). If it did not, the trial was aborted. On each trial,
156 two stimuli were drawn without replacement from the 16 possible stimuli (Figure 1C).
157 Distributions of touches to the target locations were distinct (Figure 1D). As soon as a
158 touch was detected, the stimuli disappeared. If the animal earned water reward, it was
159 delivered immediately. After a 2 second inter-trial interval, the central cross re-appeared
160 to start a new trial. Monkeys worked to satiation (~4 hours, several hundred trials/day).

161 In each testing session, a single response window was used that defined the

162 time pressure. For “Low Pressure” (LP) sessions, the response window ranged from
 163 1.75 to 2 seconds. For “High Pressure” (HP) sessions, the response window ranged
 164 from .35 to .50 seconds. We tested hypothesis 1, that macaques use probabilistic
 165 inference to choose between stimuli that are each defined by jointly presented,
 166 statistically informative visual dimensions, by analyzing data from LP sessions. We
 167 tested hypothesis 2, that monkeys make these decisions under time pressure using
 168 satisficing strategies, by comparing data between HP and LP sessions.



169
 170 **Figure 1.** Overview of the task and data collection. (A) The four cue dimensions and the
 171 cue states for each. (B) Monkey A using the in-cage touchscreen setup. (C) All sixteen
 172 possible compound stimuli. (D) Heat map of responses around each of the four possible
 173 stimulus locations during a typical session. Solid lines indicate boundaries of stimulus
 174 display (2.5 x 2.5 cm) while dotted lines show the allowed response area (4.4 x 4.4 cm).

175

176 *Compound visual stimuli and weighting*

177 Each visual stimulus was a compound object consisting of four individual visual
178 features, which we refer to as *cue dimensions*, each of which could take on one of two
179 *cue states* (Figure 1A), as follows. Color dimension: a stimulus could have a blue or red
180 background. Shape dimension: a stimulus could be a circle or a square. Border
181 dimension: a stimulus could be outlined in white or black. Orientation dimension: lines
182 within a stimulus could be horizontal or vertical. Given the combination of these cue
183 dimensions and possible cue states, there were 16 unique compound stimuli (Figure
184 1C). On a given trial in which two different stimuli were presented, there were therefore
185 120 possible unique pairs of compound stimuli.

186 An optimal decision to select one stimulus over another required evaluation of
187 evidence from the four cue dimensions and a comparison between the two different
188 stimuli. Within a cue dimension (e.g. color), each of the two possible cue states (blue or
189 red) had an *assigned weight*. The difference between these assigned weights defined
190 the *net weight* or relative importance for a cue dimension. Table 1 shows all the
191 assigned weights. In experiments with Monkey A, for example, “blue” had an assigned
192 weight of .9 and “red” had an assigned weight of .1, giving the cue dimension “Color” a
193 net weight of .8. At the same time, the cue dimension “Border” had a net weight of .4
194 because the assigned weights for white and black borders were .7 and .3, respectively.
195 For Monkey A, therefore, Color evidence was more informative than Border evidence.
196 Net weights were limited to four values, .2, .4, .6, or .8, but the cue dimensions
197 corresponding to those net weights were reversed between the two monkeys; that is, in
198 order of probabilistic importance, Color > Shape > Border > Orientation for Monkey A

199 but Orientation > Border > Shape > Color for Monkey L. Also, within each dimension,
 200 the relative importance of each cue state was flipped between the monkeys. In the
 201 Color dimension, for instance, blue had a higher weight than red for Monkey A but a
 202 lower weight than red for Monkey L (Table 1; for details, see *Training* section below).
 203

<i>Cue Dimension</i>	<i>Cue States</i>	<i>Assigned weights</i>	
		Monkey A	Monkey L
Color	Blue	0.9	0.4
	Red	0.1	0.6
Shape	Circle	0.8	0.3
	Square	0.2	0.7
Border	White	0.7	0.2
	Black	0.3	0.8
Orientation	Horizontal	0.6	0.1
	Vertical	0.4	0.9

204 **Table 1.** Visual stimulus parameters. Each stimulus had four cue dimensions, each with
 205 two states. Weights were assigned as shown. Between monkeys, the ordering of
 206 importance of the cue dimensions was reversed and, within each dimension, the ordering
 207 of the states was flipped.

208
 209 The assigned weights of each cue state were independent and additive, yielding
 210 a summed, *total weight* for each compound stimulus. For each pair of stimuli in a trial,
 211 the *sum of evidence (SoE)* in favor of one stimulus was the difference between its total
 212 weight and that of the other stimulus. This SoE was used to calculate the probability of
 213 receiving reward after touching a stimulus as follows:

$$214 \quad P(\text{reward} \mid \text{SoE}) = \frac{1}{1+10^{-\text{SoE}}} \quad (1)$$

215 For each pair of stimuli, therefore, selecting the one with the positive SoE
 216 (greater total weight) resulted in higher, above chance probability of reward; it was the
 217 *correct* decision for optimizing reward. Performance was calculated on the basis of

218 making these correct decisions. Trials where the SoE was 0 were ignored when
219 calculating accuracy. Note, monkeys were most likely to receive reward if they selected
220 the stimulus with positive SoE, but because reward was probabilistic, selecting that
221 stimulus might yield no reward, or selecting the other stimulus might be rewarded. This
222 reward contingency encouraged the animals to make their decisions by combining the
223 probabilistic information of the stimuli, rather than on the basis of stimulus-response
224 contingencies. The latter would require memorization of 120 possible pairs of compound
225 stimuli.

226

227 *Training*

228 To counterbalance our experimental design, the two monkeys learned cue dimensions
229 with reversed order of importance and, within each cue dimension, opposite weighting
230 of cue states (Table 1). For example, Color was the most informative dimension for
231 Monkey A (net weight .8) but the least informative for Monkey L (net weight .2). Within
232 the Color dimension, blue was weighted more than red for Monkey A but red was
233 weighted more than blue for Monkey L. The purpose of this manipulation between
234 monkeys was to control for any differences in visual saliency within and across
235 dimensions. Performance therefore benefited from learning the probabilistic weights of
236 the features regardless of whether some features seemed more salient than others.

237 Neither of the monkeys had previous experience with this set of visual cue
238 dimensions. Both monkeys required several weeks of training to learn the task (see
239 *Learning Phase* in Results). Response windows were set to 2 seconds during training,
240 so that monkeys did not experience time pressure until the later, testing sessions.

241 Monkey A was the first one trained. Because this monkey was used to pilot the task and
242 settle on appropriate spatial, temporal, and visual dimension parameters, we do not
243 have a learning curve for it. For the second animal, Monkey L, we used constant
244 parameters and documented the learning curve thoroughly. After a monkey reached
245 asymptotic levels of performance, formal testing sessions commenced, one per day.

246

247 *Subjective weights*

248 A major goal of our analysis was to infer the subjective importance of the various
249 experimental parameters on each monkey's decision-making. The central analytic
250 approach was to perform a logistic regression using variational Bayesian inference
251 (Drugowitsch, 2013; Oh et al., 2016) to calculate *subjective weights*, the inferred values
252 assigned by each monkey to different experimental parameters. Specifically, we
253 analyzed the contribution of the four cue dimension net weights (.2, .4, .6, and .8), as
254 well as the six possible spatial configurations of the stimulus pairs (Up Left–Up Right,
255 Up Left–Down Left, Up Left–Down Right, Up Right–Down Left, Up Right–Down Right,
256 and Down Left–Down Right). Although stimulus location was irrelevant to reward
257 probability, monkeys exhibited varying degrees of preference for certain locations in
258 each location pair, a form of spatial bias likely related to body posture and the arm used.
259 After completing data collection, we calculated the average location preference order
260 across all trials for both monkeys. To keep the direction of location preference
261 consistent between monkeys, the stimulus in the preferred location on a given trial was
262 treated as the positive response in the logistic regression. This was done by first
263 labeling the stimuli in the more and less preferred locations as “stimulus A” and

264 “stimulus B”, respectively. Bayesian logistic regression was then performed to infer the
265 posterior probability of choosing stimulus A, given all of a monkey’s selections on an
266 experimental session. In this way, any spatial biases would be realized positively in the
267 “A” direction for all location pairs and monkeys, independently of cue weight effects.

268 Details of the Bayesian logistic regression are provided in Appendix 1. In brief,
269 the analysis used the cue dimension net weights and target location pairs for each trial,
270 in each session, to fit the monkey’s choice responses. The analysis yielded *subjective*
271 *cue weights* for each of the four cue dimensions and *subjective spatial weights* for each
272 of the six spatial location pairs that best explained the monkey’s responses. As a
273 measure of decision noise and spatial bias, we calculated the *square root of the sum of*
274 *squares* (SRSS) of the subjective cue weights and subjective spatial weights,
275 respectively. To assess strength of the learned cue weight associations, it is useful to
276 compare the SRSS of cue weights to that of an ideal observer. In related human
277 literature, humans tend to match their choice probabilities to the true outcome
278 probabilities (Vulkan, 2000, Oh et al., 2016). We therefore chose to compare monkey
279 performance to an observer that makes decisions based on sampling from the true
280 posterior, i.e. on the observed probability of outcomes. This idealized decision process
281 would yield $SRSS = 1.095$ (the norm of the net weights) and, if nothing else affected
282 performance, an accuracy of approximately 79% (the expected probability of reward).
283 Decisions based on inference of the underlying cue weights rather than reward
284 probability would increase SRSS and accuracy above these levels.

285 To isolate relative differences in subjective cue weighting from overall task
286 knowledge, subjective cue weights were then normalized to their SRSS. Finally, the

287 weights were scaled by the precision of the regression estimates for each session and
288 averaged for each cue to yield the weighted-mean normalized subjective cue weight \bar{w}_{c_i}
289 and its uncertainty $\sigma_{\bar{w}_{c_i}}$ for that cue. Monkeys performing with variable degrees of
290 decision noise but the correct relative valuation of cues would have the same
291 normalized subjective cue weight (represented by a 0.2 : 0.4 : 0.6 : 0.8 ratio). For
292 subjective spatial weights, SRSS measured spatial bias, the *a priori* influence of location
293 before stimuli onset. Decisions made with no spatial bias would yield SRSS = 0.
294 Because the evidence was spatially unbiased, spatially biased behavior would increase
295 SRSS and decrease accuracy.

296

297 *Decision model comparisons*

298 To determine which experimental factors were being utilized for task performance, we
299 searched a model space of 32 decision strategies that accounted for every combination
300 of cue dimension and inclusion or exclusion of spatial location (similar to Oh et al.,
301 2016; Figure 2). Specific models of interest include an “optimal compensatory strategy”
302 of using information from all four cue dimensions to make decisions (Figure 2, models
303 15 and 31), the “drop-the-worst” strategy used by humans under time pressure (Figure
304 2, models 11 and 27; Oh et al., 2016), and the “take-the-best strategy” that searches
305 through cue dimensions in descending order of their assigned weights and stops on the
306 first cue that differentiates the two options (Figure 2, models 16 and 32; Gigerenzer &
307 Goldstein, 1996). The remaining 29 models comprised all possible combinations of cue
308 dimensions crossed (starred models in Figure 2), or not, with the six spatial location
309 pairings. The Bayesian regression described above (Drugowitsch, 2013) was performed

310 for all 32 possible decision strategy models to calculate a lower bound on the marginal
 311 log probability of each model in each session. To characterize decision strategy across
 312 multiple sessions these log model evidences were submitted to a Bayesian model
 313 selection procedure (Stephan et al., 2009). This approach fits a hierarchical model by
 314 treating the decision strategy models as random effects that could vary across sessions
 315 and estimates the *protected exceedance probabilities*, which represent the probability
 316 that each given model is more likely than others, corrected for the possibility that
 317 observed differences are due to chance (Rigoux et al., 2014). The model with the
 318 highest protected exceedance probability was selected as the preferred decision
 319 strategy model for a given monkey and time pressure. Protected exceedance
 320 probabilities were calculated using the `spm_BMS` routine of the SPM12 software suite
 321 (<http://www.fil.ion.ucl.ac.uk/spm/software/spm12/>).

322

Cue Dimension	Strategy Models															
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
	17*	18*	19*	20*	21*	22*	23*	24*	25*	26*	27*	28*	29*	30*	31*	32*
c ₁	●	○	○	○	●	●	●	○	○	○	●	●	●	○	●	○
c ₂	○	●	○	○	●	○	○	●	●	○	●	●	○	●	●	○
c ₃	○	○	●	○	○	●	○	●	○	●	●	○	●	●	●	○
c ₄	○	○	○	●	○	○	●	○	●	●	○	●	●	●	●	○

* = Includes spatial regressors

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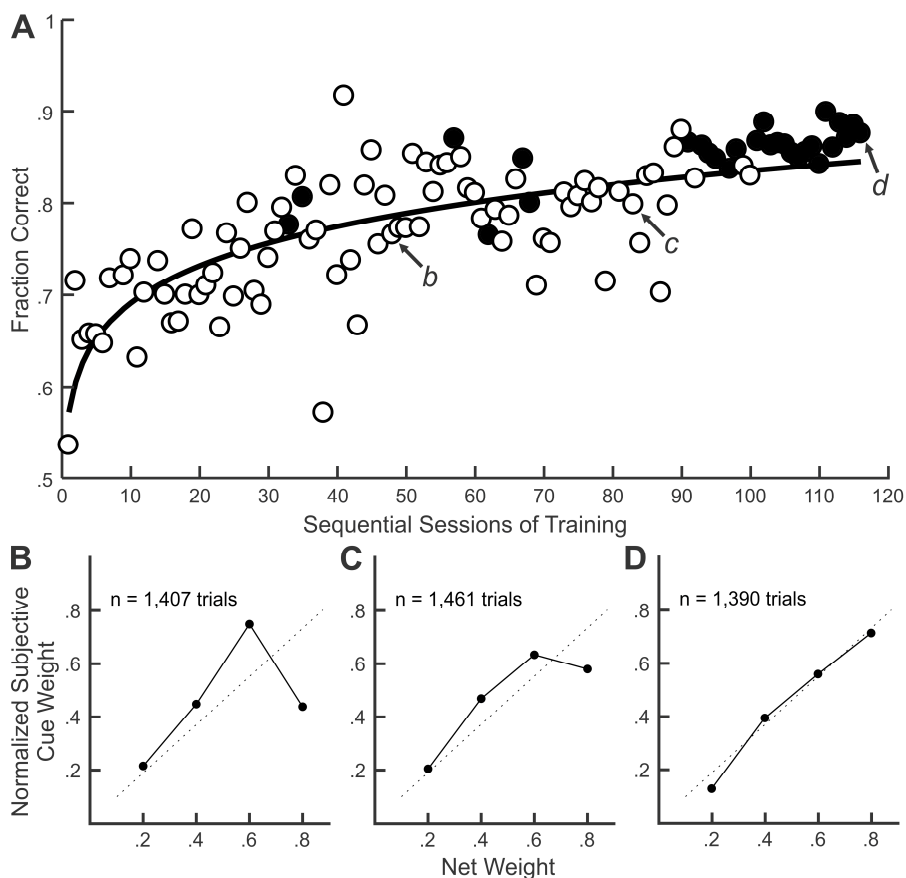
324 **Figure 2.** Complete space of strategy models explored. Filled black circles indicate that
 325 the corresponding cue dimension is included in the regression for the given model. Gray
 326 circles under models 16 and 32 are used to indicate that these models use a “take-the-
 327 best” strategy, where the highest valued cue dimension that differs between both stimuli is
 328 used to make a decision.

329

330 **Results**

331 *Learning phase*

332 Monkeys were initially trained on the low time pressure (LP) version of the task. The
333 learning curve, measured as a fraction of correct responses, is shown for Monkey L in
334 Figure 3A. "Session 1" corresponds to the first day of training. The power law fit shows
335 a rapid increase early in training as the animal began to recognize the probabilistic
336 importance of the different visual stimuli, followed by a more gradual rise toward a
337 steady state plateau. In Figure 3B-D, normalized subjective cue weights are plotted
338 against net weights for three individual sessions (labeled with arrows in Figure 3A).
339 Note that spatial location was included in these regressions but not depicted here. Early
340 in training, this monkey heavily favored the third cue dimension, which had net weight of
341 0.6, even though the fourth dimension was more informative at net weight 0.8 (Figure
342 3B). In time, the monkey appeared to recognize the importance of the fourth cue
343 dimension (Figure 3C), culminating in the correct ordering of cue dimensions during
344 steady state performance (Figure 3D). In the learning curve of Figure 3A, black dots
345 indicate sessions in which the monkey accomplished the correct ordering of cue
346 dimensions. The first occurrence of 3 consecutive days of correct ordering (session 95
347 in Figure 3A) defined the end of the learning phase.



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359 Through the rest of this report, data from the learning phase were excluded. As

360 an additional criterion, we excluded aborted trials as well as each trial that immediately

361 followed a no-response aborted trial (n = 7,679 trials, 12.9% of all trials for Monkey A; n

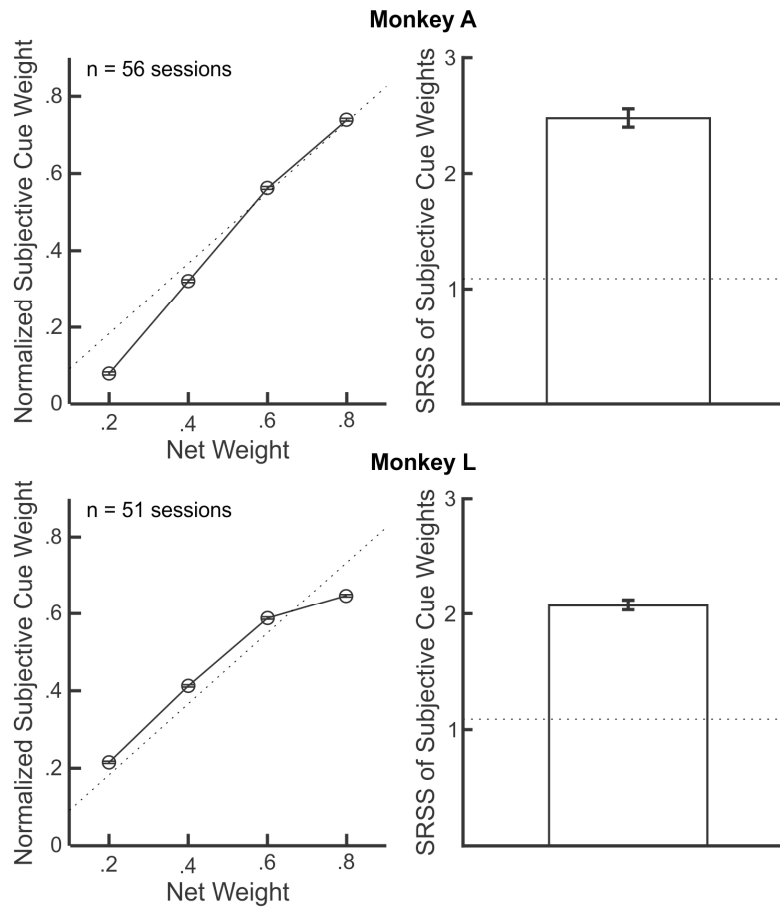
362 = 13,958 trials, 14.5% of all trials for Monkey L), to include only those trials performed at
363 a similar state of alertness or engagement with the task and allow for an accurate
364 measure of response time. Both monkeys were free to roam in their cage and generally
365 performed the task in “bursts” of trials so this criterion typically excluded the first in a
366 string of completed trials. Experimental sessions were excluded if the number of trials
367 performed was too low for the logistic regression to converge. The final dataset
368 consisted of 52,085 trials, with median of 396 (interquartile range 204 to 700) trials per
369 session, from Monkey A and 68,631 trials, with median of 895 (interquartile range 466
370 to 1252) trials per session, from Monkey L.

371

372 *Steady-state behavior at low time pressure*

373 Once trained, the monkeys continued to perform low time pressure (LP) sessions
374 (Monkey A: 56 sessions, 27,773 total trials; Monkey L: 51 sessions, 57,772 total trials).
375 In these LP trials, Monkey A selected the correct stimulus at a rate of 86.0% and
376 Monkey L was correct at 86.5%, with mean response times of 399 ms and 634 ms,
377 respectively. Across these trials, both monkeys accurately discriminated between
378 features in all four visual cue dimensions by inferring the correct order of subjective cue
379 (Figure 4). All subjective cue weights were significantly different in a monotonic rising
380 progression as a function of net weights (statistics are in the *Satisficing* section and
381 numerical data are in Table 2 associated with that section). Recall that the assigned
382 dimension order of importance and within-dimension cue feature weights were
383 counterbalanced between Monkeys A and L, so the ordering was not a salience artifact
384 in monkeys (e.g., if Color happened to be easier to discern than Orientation of the

385 lines). Both monkeys had an average SRSS of subjective cue weights much greater
 386 than 1.095, implying that they used probabilistic inference of cue weights to improve
 387 accuracy above the expected reward rate (see *Methods*).



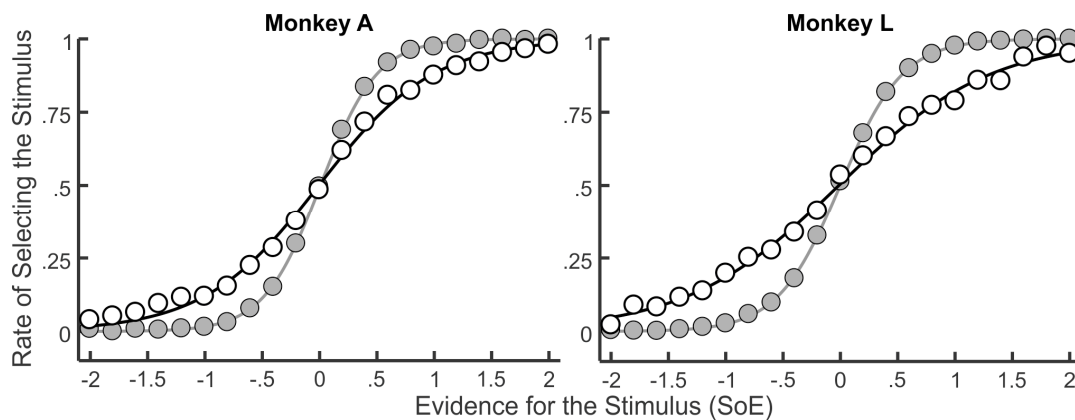
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389 **Figure 4.** Performance for Monkey A (*top*) and Monkey L (*bottom*) at steady state. *Left:*
 390 mean normalized subjective cue weights (\bar{w}_{c_i}) across LP sessions. Error bars, smaller than
 391 the symbols, indicate uncertainty ($\sigma_{\bar{w}_{c_i}}$). *Right:* Mean (and SEM) of the SRSS of subjective
 392 cue weights across LP sessions. The high SRSS levels, much greater than 1.095 (dotted
 393 line), indicates the use of probabilistic inference for high accuracy rather than the matching
 394 of expected reward rates.

395

396 *Performance under high time pressure*

397 Under high time pressure (HP) conditions, mean accuracies across all trials for Monkey
 398 A and L were significantly decreased to 77.23% (Wilcoxon rank sum, Cohen's $d = -.230$,
 399 $Z = 25.56$, $p < .0001$) and 72.57% (Wilcoxon rank sum, Cohen's $d = -.387$, $Z = 35.89$, p
 400 $< .0001$) respectively. The mean response times decreased to 353 ms (t-test, Cohen's d
 401 $= -.354$, $t = 40.78$, $p < .0001$) and 486 ms (t-test, Cohen's $d = -.515$, $t = 50.26$, $p <$
 402 $.0001$) over 48 sessions (24,312 total trials) for Monkey A and 21 sessions (10,533 total
 403 trials) for Monkey L.



404

405 **Figure 5.** Performance as quantified by the psychometric curves for selecting a stimulus
 406 as a function of evidence for it (sum of evidence, SoE), across all LP (gray) and HP (white)
 407 trials. The shallower the slope at SoE = 0, the less sensitive the performance was to SoE.

408

409 The degradation of performance in HP trials coincided with a decreased ability of
 410 the monkeys to utilize and discriminate between the cue features. Figure 5 shows the
 411 psychometric functions between the proportion of trials a stimulus was selected
 412 (ordinate) vs. its SoE (abscissa). The greater the SoE of a stimulus (recall eq. 1), the
 413 more likely it was to be selected. The slope at the inflection point is a measure of the
 414 perceptual sensitivity to SoE as a factor in performance. In HP sessions (Figure 5, white
 415 circles), the psychometric slopes clearly decreased relative to LP sessions (Figure 5,

416 gray circles), for both monkeys. That is, under time pressure, performance was still
417 driven by SoE, but with less sensitivity to it.

418 Multiple hypotheses could account for these effects of time pressure on
419 performance. One possibility is that the monkeys occasionally made cue-independent
420 decisions in HP trials due to lapses in attention (Wichmann & Hill, 2001). This predicts,
421 however, that the psychometric curves would not asymptote to zero or one, and yet they
422 do (Figure 5). Hence this “lapse” hypothesis was ruled out. Three other hypotheses and
423 their predictions are as follows:

- 424 1. Satisficing Limitations in cognitive capacity under time pressure could cause
425 subjects to change how they evaluate the cue dimensions. The least informative
426 cue dimension could be ignored, for example, as found by Oh et al. (2016). Such
427 satisficing strategies would predict changes in the strengths or ordering of the
428 normalized subjective cue weights.
- 429 2. Decision noise Time pressure may introduce more noise, or randomness, into
430 the decision-making process. This would predict a decrease in the SRSS of
431 subjective cue weights under time pressure, with no effect on the relative
432 strengths or ordering of the normalized subjective cue weights.
- 433 3. Biased priors When evidence is weak due to time pressure, subjects might rely
434 more on *a priori* preferences. Here, we consider priors on stimulus locations, i.e.
435 the animals’ spatial biases. Biases toward these priors under time pressure
436 would predict increases in the SRSS of subjective spatial weights.

437 These three hypotheses are not mutually exclusive. In the following sections, we
438 consider the evidence for each of them.

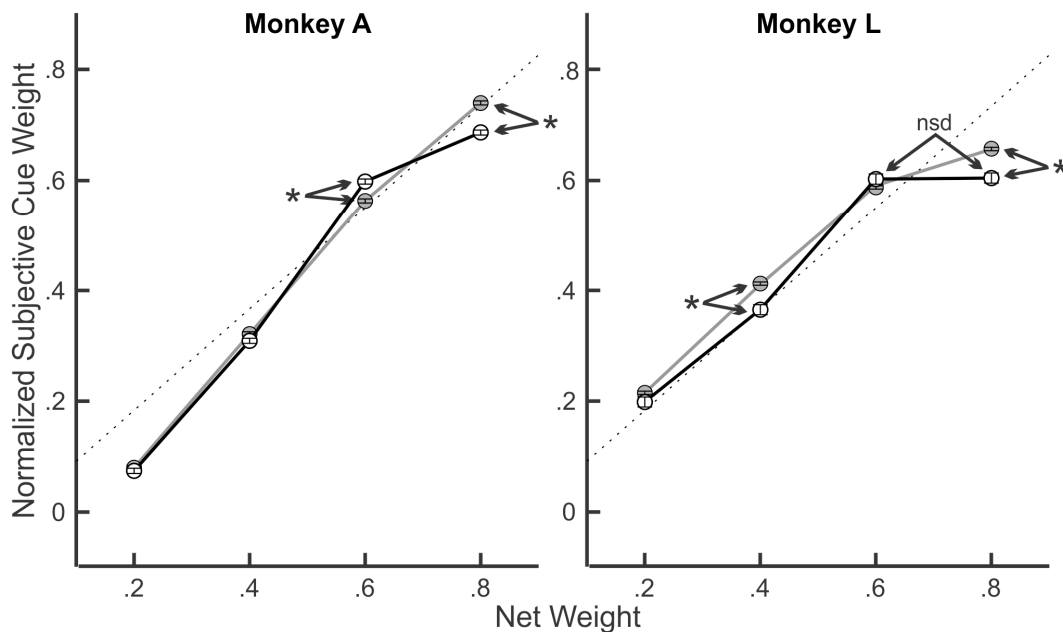
439

440 *Satisficing*

441 As a first step in determining whether the monkeys used satisficing strategies to change
442 their relative weighting of cue dimensions under time pressure, we directly compared
443 the individual subjective cue weights between LP and HP sessions (Figure 6).

444 Specifically, the precision-weighted means of each (normalized) subjective cue weight
445 was compared four times: between the cue dimensions *within* the LP or HP condition
446 (three comparisons), and *between* the LP and HP condition for each cue dimension
447 (one comparison), yielding a corrected criterion level of $p < .0125$. The *null hypothesis* –
448 no effect of time pressure, i.e. HP condition – predicts significant differences for the first
449 three comparisons (clear ordering of the subjective cue weights) but no significant
450 difference for the fourth comparison (no effect of the HP condition on subjective cue
451 weights). In Figure 6, we label each result that deviated from this null hypothesis. *For*
452 *Monkey A*, the first three comparisons (across cue dimensions) were all significant, as
453 expected, in both the LP and HP conditions (t-tests, all $p < 0.0125$). That is, subjective
454 cue weights were ordered systematically as a function of net weights. The fourth
455 comparison (LP vs. HP) was not significant for the lower two dimensions ($p > 0.0125$)
456 but *was* significant for the higher two dimensions. The subjective cue weight dropped in
457 the HP condition for net weight = .8 ($p = 4.00 \times 10^{-8}$) and rose for net weight = .6 ($p =$
458 8.54×10^{-15}), bringing the two subjective weights closer together. *For Monkey L*, all
459 comparisons across cue dimensions were significant in LP sessions ($p < 0.0125$).
460 During HP sessions, however, the subjective cue weights for net weights .6 and .8 were
461 not significantly different from each other ($p = 0.89$), as if the monkey treated them the

462 same. This was due to a significant drop in subjective weighting for net weight .8 in HP
 463 sessions ($p = 1.74 \times 10^{-4}$). A similar drop was found for weight .4 ($p = 4.65 \times 10^{-5}$) but no
 464 HP vs. LP difference was found for weights .2 and .6 ($p > .0125$). The numerical data
 465 from Figure 6 are listed in Table 2. The common finding between the two monkeys,
 466 therefore, was a shift in relative subjective cue weighting for the top cue dimensions,
 467 reducing (or in Monkey L, eliminating) the subjective difference between them. This
 468 “group-the-best” satisficing strategy would serve to reduce the dimensionality of the task
 469 from four sources of probabilistic information to three.



470

471 **Figure 6.** Mean normalized subjective cue weights (\bar{w}_{C_i}) for LP (gray) and HP (white)

472 sessions, for each monkey. Arrows and labels show pairs of values that violated the null

473 hypothesis in that they were significantly different between the LP and HP conditions (*) or

474 not significantly different across dimensions (nsd). Error bars, smaller than the symbols,

475 indicate the uncertainty ($\sigma_{\bar{w}_{C_i}}$). Note, the LP data are the same as in Figure 4, reproduced

476 here for direct comparison with the HP data.

477

	<i>Monkey A</i>				<i>Monkey L</i>			
<i>Net weights</i>	<i>0.2</i>	<i>0.4</i>	<i>0.6</i>	<i>0.8</i>	<i>0.2</i>	<i>0.4</i>	<i>0.6</i>	<i>0.8</i>
LP condition	N = 56				N = 51			
Mean, \bar{w}_{c_i}	0.0797	0.3213	0.5630	0.7395	0.2151	0.4124	0.5877	0.6472
Uncertainty, $\sigma_{\bar{w}_{c_i}}$	0.0040	0.0038	0.0037	0.0037	0.0029	0.0030	0.0030	0.0030
HP condition	N = 48				N = 21			
Mean, \bar{w}_{c_i}	0.0740	0.3087	0.5980	0.6861	0.1984	0.3652	0.6027	0.6045
Uncertainty, $\sigma_{\bar{w}_{c_i}}$	0.0047	0.0046	0.0045	0.0045	0.0090	0.0091	0.0093	0.0092
Cohen's d	-0.0867	-0.1952	+0.5487	-0.8372	-0.2451	-0.6854	+0.2165	-0.6182

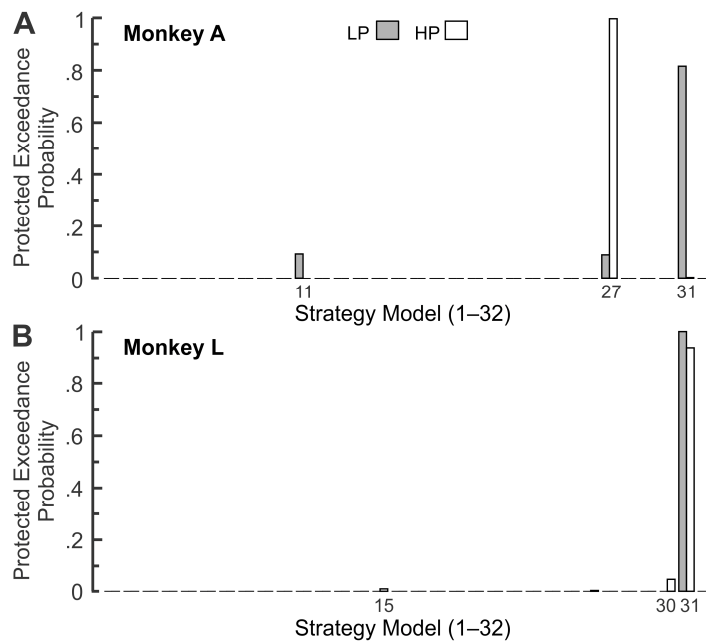
478 **Table 2.** Data shown in Figure 6, plus effect sizes (Cohen's d) for HP-LP difference at each net weight.

479

480 We then examined whether this "group-the-best" effect was present at the level
481 of individual sessions. For each session we calculated the difference in subjective cue
482 weights for the .6 and .8 cue dimensions. Smaller differences would represent closer
483 subjective weights and more of a grouping effect. We found that these differences were
484 significantly smaller in the HP condition for both monkeys (Monkey A: means .153 in HP
485 vs. .228 in LP, Cohen's d = .406, p = .041; Monkey L: means -.0245 in HP vs. .0655 in
486 LP, Cohen's d = .779, p = .00370; t-tests). To compare the effects for both monkeys
487 directly, we performed a two-factor ANOVA on the differences using monkey identity
488 and time pressure condition as factors. Both main effects were significant, due to
489 smaller overall differences for Monkey L ($F = 43.16$, $p = 5.76 \times 10^{-10}$) and smaller overall
490 differences in the HP condition ($F = 10.08$, $p = .00178$). The interaction was not
491 significant, meaning that the test found no difference in HP vs. LP effects between
492 monkeys ($F = .0899$, $p = .765$). In sum, this session-by-session analysis confirmed that
493 both monkeys used a "group-the-best" strategy under high time pressure.

494 When analyzing the same task in humans, Oh et al. (2016) applied Bayesian
495 model selection analyses to infer how strategies changed in HP vs. LP conditions. This

496 approach evaluates strategies that involve using subsets of the visual cues (Figure 2).
 497 Under time pressure, humans consistently resorted to a “drop-the-worst” satisficing
 498 strategy (Oh et al., 2016). We applied the same analysis to the data from our monkeys
 499 across all experimental sessions in the HP and LP conditions. Figure 7 illustrates the
 500 protected exceedance probabilities calculated for each decision model strategy. For
 501 Monkey A (Figure 7A), the maximum marginal likelihood strategy in the LP condition
 502 (gray bars) was model 31, in which all four cue dimensions are used with spatial bias.
 503 Under time pressure (HP condition, white bars), however, Monkey A shifted to model
 504 27, the “drop-the-worst” strategy with spatial bias. Monkey L (Figure 7B) did not exhibit
 505 a significant shift in strategy that could be captured by these models. Its preferred
 506 strategy for LP and HP was model 31. In sum, both animals used a “group-the-best”
 507 satisficing strategy for probabilistic decision-making under time pressure, as described
 508 above, but Monkey A also used a “drop-the-worst” strategy as found for humans.



509

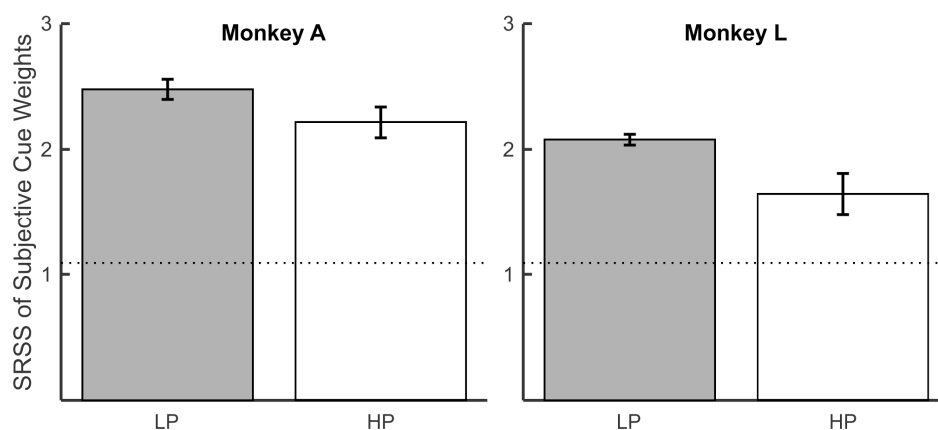
510 **Figure 7.** Protected exceedance probabilities for all 32 strategy models during LP (gray)

511 and HP (white) sessions for (A) Monkey A and (B) Monkey L.

512

513 *Decision noise*

514 To evaluate whether increases in decision noise affected performance in HP sessions,
 515 we calculated the average SRSS of the subjective cue weights for LP and HP sessions
 516 for both monkeys (Figure 8). In this pooled data, the average SRSS decreased
 517 significantly in HP sessions for Monkey L (Figure 8, right; mean SRSS = 1.65 for HP
 518 and 2.08 for LP, Cohen's $d = -.909$, Wilcoxon rank sum, $Z = 2.21$, $p = .027$) but not for
 519 Monkey A (Figure 8, left; mean SRSS = 2.22 for HP and 2.48 for LP, Cohen's $d = -.354$,
 520 Wilcoxon rank sum, $Z = 1.96$, $p = .501$). However, as will be shown in the *Response*
 521 *Time Effects* section, Monkey A did show effects of decision noise when controlling for
 522 response time. To a modest degree, therefore, increased decision noise was a factor in
 523 the monkeys' decision-making under time pressure.



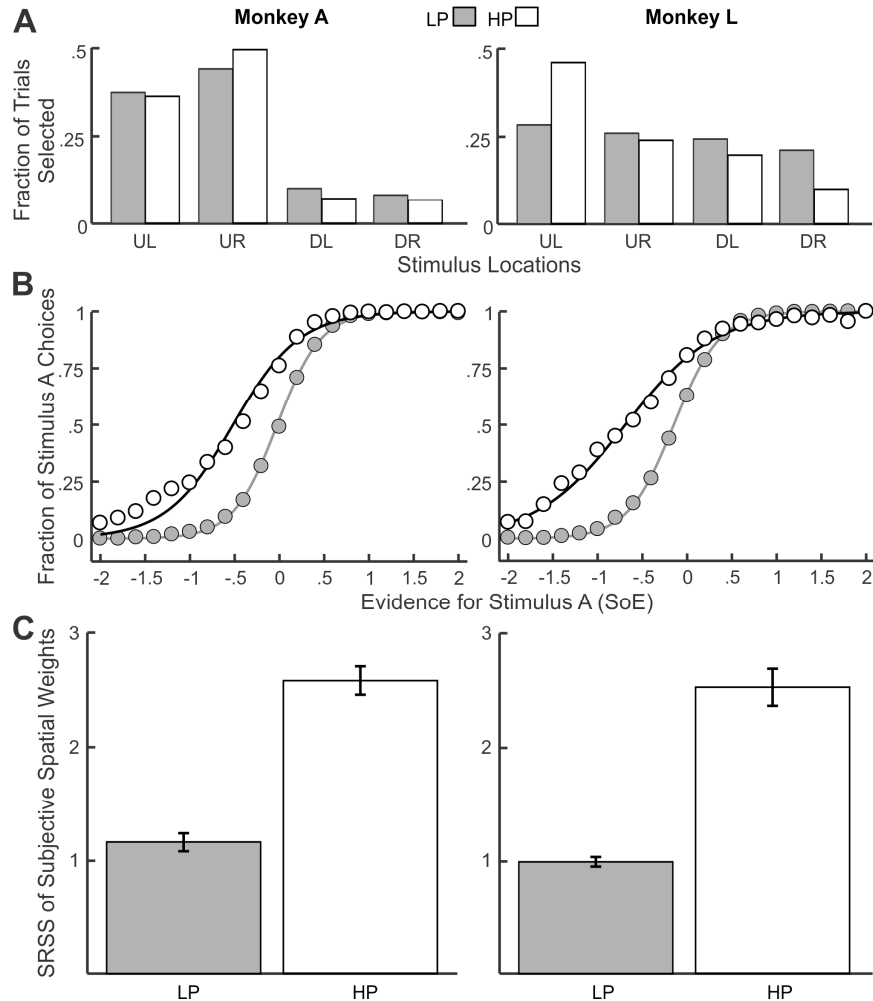
524

525 **Figure 8.** Mean SRSS of subjective cue weights across LP (gray) and HP (white) sessions,
 526 for each monkey. The mean SRSS decreased significantly ($p < .05$) under time pressure
 527 for Monkey L (*right*) but not Monkey A (*left*). Error bars indicate SEM. Dotted line at 1.095
 528 indicates the SRSS of assigned net weights. Note, the LP data are the same as in Figure
 529 4, reproduced here for direct comparison with the HP data.

530

531 *Biased priors*

532 If monkeys were spatially unbiased, we would expect an even distribution of stimulus
533 location selections. However, even in LP sessions, both monkeys showed consistent
534 spatial preferences (Figure 9A, gray). They were biased toward selecting stimuli in the
535 upper two quadrants of the screen and to the right for Monkey A or the left for Monkey
536 L. This is counterproductive because stimulus locations are irrelevant to the probability
537 of receiving reward. The reasons for these biases are unknown but may relate to
538 individual handedness or postures while using the touchscreen. In HP sessions (Figure
539 9A, white), the innate spatial biases were accentuated. The resulting reduction in
540 performance was evident upon recalculating the psychometric functions of Figure 5 with
541 respect to selection of the stimulus in each pair that was at the more-preferred location
542 (termed "Stimulus A"; Figure 9B). Not only did the psychometric slope decrease under
543 HP, the inflection point exhibited a negative shift, indicating elevated decisions to
544 preferentially located Stimulus A even when cue dimension evidence (SoE) was against
545 it (<0). The contribution of prior biases to performance under time pressure is
546 summarized by the SRSS of subjective spatial weights (Figure 9C), which increased
547 significantly in HP sessions for both monkeys (Monkey A: means 2.59 in HP and 1.16 in
548 LP, Cohen's $d = 1.355$, $Z = 5.77$, $p = 7.75 \times 10^{-9}$; Monkey L: means 2.53 in HP and
549 0.988 in LP, Cohen's $d = 1.798$, $Z = 4.15$, $p = 3.32 \times 10^{-5}$; Wilcoxon rank sum tests).
550 Hence, one way that the monkeys compensated under high time pressure was by
551 exaggerating their biased priors for stimulus location.



552

553 **Figure 9.** Spatial effects during LP (gray) and HP (white) sessions, for each monkey. (A)

554 Overall fraction of trials in which a stimulus at each location was selected in LP and HP

555 trials. UL, Up Left; UR, Up Right; DL, Down Left; DR, Down Right. (B) Psychometric curves

556 for LP and HP trials for Stimulus A, the stimulus within each pair that was in the more-

557 preferred location. (C) SRSS of subjective spatial weights in LP and HP trials.

558

559 *Response time effects*

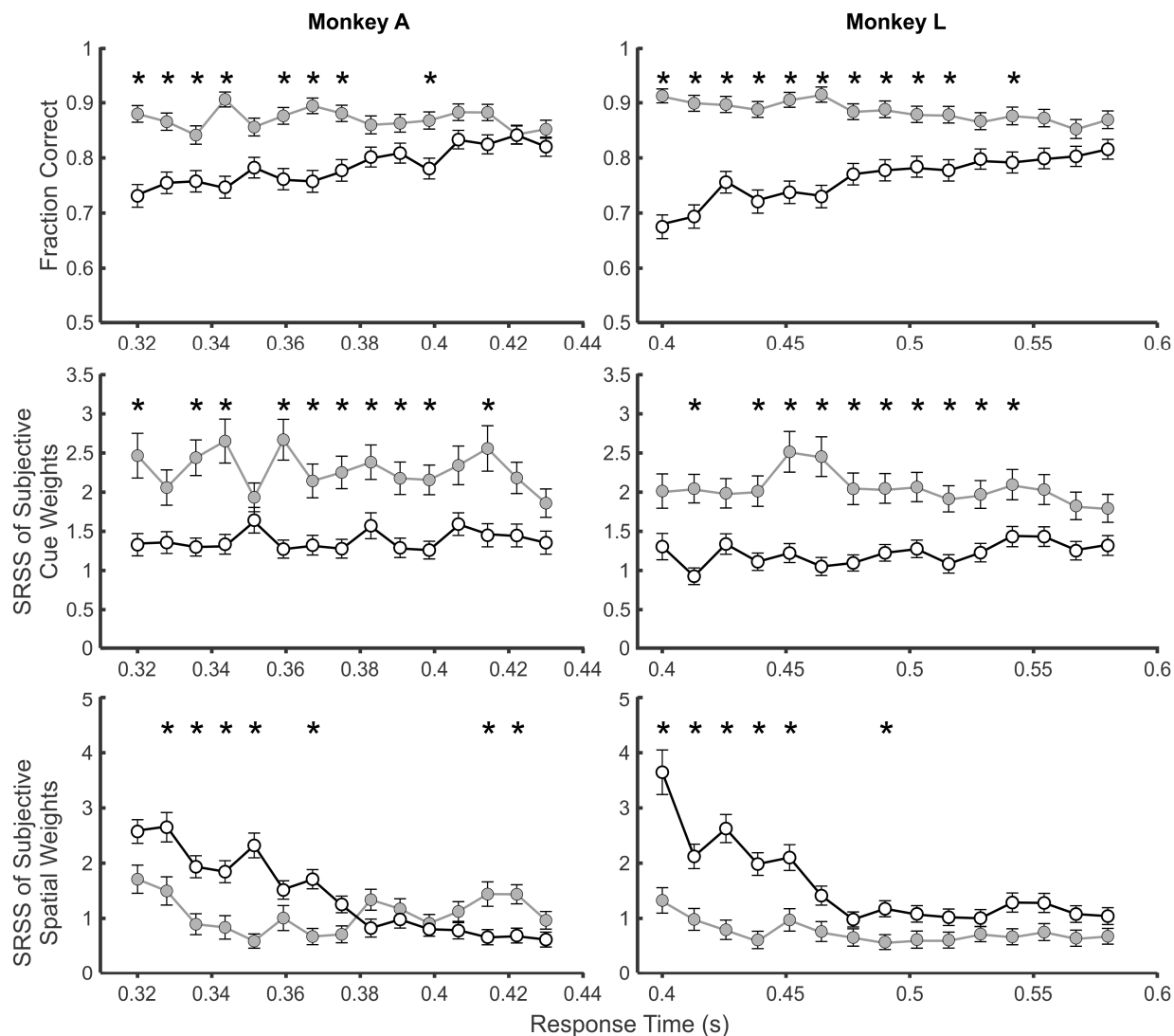
560 One consequence of time pressure is shortened durations for viewing the stimuli.

561 Having less time to see the stimuli could, by itself, worsen performance metrics such as

562 accuracy, decision noise, and spatial bias. Viewing duration had an upper bound of the

563 response window, but on any particular trial it was truncated by the monkey's response
564 time (latency between onset of the stimuli and touching the screen). Therefore, we
565 compared data from LP and HP trials matched by response times, and thus viewing
566 times, to see whether the effects of time pressure on accuracy, decision noise, and
567 spatial bias were still present (Figure 10). For a list of all the numerical data from Figure
568 10, see Table 3 (in Appendix 2). Specifically, we compared performance accuracy
569 (Figure 10, top), SRSS of subjective cue weights (Figure 10, middle), and SRSS of
570 subjective spatial weights (Figure 10, bottom) in LP vs. HP trials within equal-sized
571 response time bins (bootstrapping, 10,000 resamples with replacement, using $p < .0033$
572 criterion to correct for the 15 LP-HP comparisons in each plot). The number of trials in
573 each bin was set to the mean number of trials in LP and HP sessions for each monkey
574 (Monkey A: 496 trials/bin for LP and 506 trials/bin for HP; Monkey L: 1132 trials/bin for
575 LP and 502 trials/bin for HP). At many of the response time bins analyzed, both
576 monkeys had lower accuracy, lower SRSS of subjective cue weights, and higher SRSS
577 of subjective spatial weights in HP compared to LP trials (Figure 10). Hence the effects
578 found in HP trials were *not* just the equivalent of a data analysis that excluded slow
579 trials. Furthermore, the effects of time pressure were not due to limited sensory
580 exposure in HP trials, but were consistent with changes in behavioral and cognitive
581 strategies that allowed monkeys to adapt to the context of high time pressure during the
582 session. Note that when the results are broken down by response time, the variability in
583 SRSS of subjective cue weights for Monkey A explains the negative result in this
584 animal's pooled data (Figure 8, left). The finer-grained analysis of Figure 10, middle,
585 demonstrates that at nearly all response times, decision noise increased (i.e., SRSS of

586 subjective cue weights decreased) similarly in HP trials for both monkeys.



587

588 **Figure 10.** Response time effects for LP (gray) and HP (white) trials. Response time bins

589 (x-axis) are of equal size within a condition, centered at equal intervals. As a function of

590 response time for Monkey A (*left*) and L (*right*), the graphs plot accuracy (*top row*), SRSS

591 of subjective cue weights (*middle row*), and SRSS of subjective spatial weights (*bottom*

592 *row*). Error bars are standard deviations. *, significant difference, $p < .0033$.

593

594 **Discussion**

595 Two rhesus macaques were trained to perform discrimination decisions accurately by
596 evaluating compound visual stimuli and probabilistic feedback under different levels of
597 time pressure. A variational Bayesian regression was used to assess the monkeys'
598 subjective weighting of each dimension of the compound stimuli as compared to the
599 objective weight assignment. For low time pressure sessions (response window of 1.75
600 s to 2 s), both monkeys performed the task accurately by correctly ranking the relative
601 importance each cue dimension. This supported our first hypothesis, that rhesus
602 macaques use probabilistic inference to choose between stimuli that are each defined
603 by jointly presented, statistically informative visual dimensions. Importantly, the visual
604 cues combined to form discrete objects much the same way that co-localized features
605 define objects of interest in a monkey's environment (e.g. a piece of food or a face).
606 This contrasts with prior work that used probabilistic cues to study categorization of
607 single objects (e.g. Couchman et al., 2010; Sigala et al., 2002; Smith et al., 2010),
608 reinforcement context (Amemori & Graybiel, 2012; Hayden et al., 2010; Raghuraman &
609 Padoa-Schioppa, 2014), or the gradual accumulation of evidence (Kira et al., 2015;
610 Yang & Shadlen, 2007). Our data contribute to a quantitative understanding of how
611 macaques use probabilistic inference to compare and choose between the types of
612 visually complex objects they naturally encounter.

613 Under high time pressure (response window less than or equal to 500 ms), the
614 animals still performed the task, but at lower accuracy. Several factors accounted for
615 this change in performance under time pressure. First, decision noise increased, as
616 indicated by a drop in the SRSS of subjective cue weights. Behaviorally, this translates

617 to a higher degree of randomness in choices under pressure. Second, spatial biases
618 increased, as indicated by a rise in the SRSS of subjective spatial weights. Even though
619 spatial biases were always counterproductive (stimulus location was not a factor in
620 correct decision-making), both monkeys exhibited a baseline level of bias even during
621 low time pressure sessions. Under high time pressure, the same biases were present,
622 but accentuated. Third, satisficing strategies emerged. Monkey A showed evidence of a
623 “drop-the-worst” satisficing strategy under high time pressure as found in humans (Oh
624 et al., 2016): the least important cue dimension was ignored in favor of more informative
625 dimensions. Also found in this monkey, and even more so in Monkey L, was evidence
626 for a “group-the-best” strategy, in that the subjective weights of the top two cue
627 dimensions converged toward each other. Finally, all these effects were categorical,
628 influenced by the context of performing decisions in low- vs. high-pressure sessions.
629 They were not simply artefacts of making responses more quickly as demonstrated by
630 response time analyses. The results therefore supported our second hypothesis, that
631 rhesus macaques adopt satisficing strategies when making probabilistic decisions under
632 time pressure, but showed, as well, that satisficing is only one of several factors
633 influencing the behavior.

634 A limitation of our approach was that our visual cue dimensions were selected to
635 be readily distinguishable but not to be of equal salience. It is possible that some cues,
636 e.g. Orientation or Border, were less visually salient to the macaques than others, e.g.
637 Color or Shape. These differences might have influenced performance. We mitigated
638 this potential confound, however, by counterbalancing all of the visual stimulation
639 between the two monkeys. It appears that this worked well, since nearly all results were

640 similar between the monkeys, indicating that they learned and used the probabilistic
641 information in the cues despite any differences in salience. Specifically, even if some
642 cues were less salient than others, both monkeys still sorted out the rankings of each
643 cue dimension in both the LP condition (Figure 5, 7, 8, 9, & 10, gray data) and HP
644 condition (Figure 5, 8, 9, & 10, white data). The only major difference between the
645 monkeys was the use of a “drop-the-worst” satisficing strategy in Monkey A but not in
646 Monkey L (Figure 7). It is possible that this difference was facilitated for Monkey A by
647 assignment of the lowest probabilistic information to a cue (Orientation) that may have
648 been less salient than the others. We did not attempt to equalize salience between the
649 visual dimensions out of concern that we might influence the monkeys’ judgments about
650 the cues through repeated, preliminary testing to titrate salience levels, which might
651 have required more exposure to some cues than others. Another concern was how
652 often (or whether) we would need to interrupt data collection on the task in order to re-
653 test and potentially re-calibrate salience levels. We therefore do not know,
654 quantitatively, the extent to which visual salience contributed to the difference in
655 decision strategies observed in HP conditions. It is not unusual for two monkeys in a
656 study to have different levels of performance and apparently different strategies in a
657 highly demanding task for reasons that are not definitively resolved (e.g. Couchman et
658 al., 2010 and Shields et al., 2005). We do see it as advisable in follow-up work,
659 however, to equalize salience across cue dimensions or to vary salience systematically
660 as a trade-off with probabilistic information to understand how the two factors interact in
661 macaque decision-making.

662 In the human literature, probabilistic inference has been studied with nuanced

663 categorization paradigms, such as the weather-prediction task, that include
664 manipulation of task statistics (Gluck & Bower, 1988; Knowlton et al., 1994). Studies on
665 humans using the present task showed that they infer the probabilistic values of the
666 different visual cues (Oh et al., 2016) and that prefrontal, parietal, and subcortical brain
667 regions encode the inferential operations (Oh-Descher et al., 2017). Comparatively, our
668 macaques exploited stimulus probabilities as humans did, but more slowly, requiring
669 multiple sessions of training to learn the cue-probability associations (Figure 3). After
670 they learned the associations, we did not manipulate task statistics because the goal
671 was to achieve stable, not malleable, probabilistic decision-making in order to isolate
672 the influence of time pressure. Paradigms more akin to classical probabilistic
673 categorization, such as a weather-prediction task modified for macaques (Yang &
674 Shadlen, 2007), were used previously to focus on probabilistic reasoning itself, its
675 flexibility, and its neural correlates (see also Kira et al., 2015). Yang and Shadlen (2007,
676 p. 1079) concluded that their results "... demonstrated a crude capacity for probabilistic
677 inference in monkeys." Our main purpose was to build on this previous conclusion,
678 using a more naturalistic task in which macaques simply chose between visual stimuli,
679 as a way of studying the animals' satisficing strategies. Given that we did not
680 manipulate task statistics, the specific type of probabilistic inference we documented
681 might be more precisely termed "probabilistic preference," in that it was used to select
682 the preferred stimulus (in terms of likelihood of reward). This alternative term, however,
683 is already in use for other purposes in the literature (e.g. Vitelli et al., 2018). All of these
684 considerations should be kept in mind when comparing the present work to prior studies
685 of probabilistic reasoning in macaques and humans.

686

687 *Decision noise and spatial bias*

688 One of the non-satisficing factors that influenced behavior under time pressure, decision
689 noise, is well known to affect the selection of visual stimuli in macaques (reviewed in
690 Gold & Shadlen, 2007) although it had not been evaluated previously in the conditions
691 of our study, namely, probabilistic decision-making across multiple visual dimensions.
692 Time pressure caused approximately a doubling of decision noise for both monkeys
693 (halving of SRSS of subjective cue weights) across many response times (Figure 10,
694 middle). For one monkey, a significant, smaller effect was evident even in its overall
695 pooled data (Figure 8, right). The other non-satisficing factor that was modulated by
696 time pressure, spatial bias, manifested as an increased reliance on favored spatial
697 locations. The specifics of this spatial bias may be partially explained by the in-cage
698 experimental setup. The stimulus locations for each monkey's biases roughly
699 correspond to both the handedness and height of each monkey. Decisions may have
700 been made based on the effort required to make the appropriate reach, with further
701 reaches judged as less valuable (see Morel et al., 2017). Indeed, our behavioral results
702 provide evidence that the monkeys applied a subjective value to the spatial location of
703 onscreen stimuli that became more important to them under time constraints. Moreover,
704 the time pressures used in this study may approach the physiological limit for a
705 macaque to process the visual information and physically reach toward the stimulus. At
706 high speeds, the use of *a priori* biases becomes especially important when executing a
707 quick reach (Wolpert & Landy, 2012). Further studies may address this by either
708 continuing to use touch responses but including variations of the spatial presentation of

709 stimuli, or using eye movements to report decisions.

710

711 *Satisficing*

712 The “drop-the-worst” strategy observed in Monkey A is consistent with satisficing
713 exhibited in the same task in humans (Oh et al., 2016). By selectively discounting less
714 valuable information, the cognitive load for decisions is lowered. Additionally, both
715 monkeys showed a “group-the-best” strategy, reducing or eliminating the difference in
716 subjective weights attributed to the top two stimulus dimensions under time pressure.
717 Similar to a “take-the-best” strategy, the end result is to save time by focusing on the
718 dimensions of information that are most valuable. Unlike a “take-the-best” strategy,
719 however, this “group-the-best” strategy serves to categorize the two best dimensions
720 together, evaluate this new category together with the lower two dimensions, and thus
721 effect a form of dimensionality reduction. Grouping of the two best dimensions was
722 manifested as a steady behavior exhibited across trials as the sessions unfolded.
723 Human subjects are known to improve on “take-the-best” strategies by exploiting
724 confirming evidence within trials (Newell et al., 2003; Karelaia, 2006). In our task this
725 would be revealed as selection based on a stimulus’s top two cue dimensions (strategy
726 5/21, without/with spatial regressors, in Figure 2), but we found no evidence for such a
727 strategy in our monkeys (Figure 7).

728 The differences in type and degree of satisficing strategies between Monkeys A
729 and L may suggest that satisficing in macaques may be more idiosyncratic than in
730 humans, but such a conclusion has two caveats. First, our sample size ($n = 2$ monkeys)
731 was much smaller than that tested in studies of human satisficing, e.g. Oh et al. (2016;

732 46 humans). Second, humans also exhibit considerable inter-subject variability in their
733 satisficing behavior. On an individual basis, approximately 32% of participants studied
734 by Oh et al. (2016) showed the “drop-the-worst” strategy under time pressure while 26%
735 of individuals continued to use the full cue integration strategy and thus failed to
736 satisfice at all (author Oh-Descher, personal observation). It is possible, of course, that
737 the latter group may have learned to satisfice in the task if given more than one session
738 to perform it. Individual use of a “group-the-best” strategy was not examined in humans
739 (Oh et al., 2016). Satisficing is therefore variable in both species, and comparisons
740 between them need to consider the strengths and limitations inherent to the study
741 designs used for each species (e.g. few subjects in macaque studies and few testing
742 sessions per subject in human studies).

743

744 *Potential neural mechanisms*

745 Studies of the neural basis of probabilistic inference and uncertain decision-making in
746 humans have used fMRI to identify several areas of interest (Knowlton et al., 1996;
747 Poldrack et al., 2001; Behrens et al., 2007; Gold & Shadlen, 2007; Shohamy et al.,
748 2008; Oh-Descher et al., 2017). However, these data are limited by both the temporal
749 and spatial resolution of the blood-oxygen-level dependent (BOLD) signal. Animal
750 models and invasive techniques allow for a finer-grained analysis of the underlying
751 neural mechanisms. Research into neural correlates of decision-making in macaques is
752 extensive and has revealed that the subjective value of decisions can be tracked at the
753 single neuron level in the lateral intraparietal area (LIP; Platt & Glimcher, 1999; Roitman
754 & Shadlen, 2002; Rorie et al., 2010) and prefrontal cortex (Kim & Shadlen, 1999).

755 Furthermore, LIP neurons are able track the accumulation of evidence across
756 sequentially presented visual cues (Yang & Shadlen, 2007; Kira et al., 2015). The
757 present work demonstrates the feasibility of extending this research to neural studies of
758 probabilistic visual discrimination under low and high time pressure. An important
759 caveat, however, is that not all macaques react to high time pressure with the human
760 “drop-the-worst” strategy. If the aim is to test that form of satisficing, monkeys should be
761 pre-screened to find those that exhibit it. Comparing neural activity between satisficing
762 strategies would be informative too, and macaques appear to provide the opportunity to
763 compare at least the “drop-the-worst” and “group-the-best” strategies, sometimes in the
764 same subject (such as Monkey A in our study).

765

766 *Conclusion*

767 The present work explored the psychophysics of making decisions between objects
768 based on probabilistic visual cues in rhesus macaques. We found similarities between
769 macaque behavior and previously reported human behavior, in that both species can
770 perform probabilistic discrimination between visual stimuli and can satisfice under time
771 pressure, in some cases even using the same strategy (“drop-the-worst”). We found
772 differences as well, likely reflecting a mix of real inter-species differences and necessary
773 task design and sample size differences. Future work that compares macaques and
774 humans with even more closely-matched experiments, complemented by computational
775 models that probe and compare the underlying algorithms used by each species, would
776 help to address unresolved issues. Overall, our results provide support for using
777 macaques to study the neural basis of probabilistic decision-making and satisficing

778 under time pressure.

779

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913 **Appendix 1**

914 Regressors for the effect of cue dimension net weights were coded into a $T \times 4$ matrix,
 915 X_C , with columns for each dimension (1 through 4; color, shape, orientation, and border)
 916 and rows for each trial (up to T total trials per session). If $w_{A_{i,j}}$ and $w_{B_{i,j}}$ are the assigned
 917 weights of the cue state on trial i in cue dimension j for stimuli A and B , respectively,
 918 then the elements of X_C are defined as follows: $X_{C_{i,j}} = 1$ if $w_{A_{i,j}} > w_{B_{i,j}}$, $X_{C_{i,j}} = -1$ if
 919 $w_{A_{i,j}} < w_{B_{i,j}}$, and $X_{C_{i,j}} = 0$ if $w_{A_{i,j}} = w_{B_{i,j}}$. The effect of spatial location was entered into
 920 the regression by assigning each of the six location pairs a unique row vector in a $T \times 6$
 921 matrix X_S . The row vectors contained five zeros and a single entry of '1' in a column
 922 unique to the stimulus location pair. This coding scheme allows location pairs to be
 923 treated as discrete categorical variables, while returning continuous numerical
 924 coefficients indicating the degree of spatial bias through regression.

925 Logistic regression was performed for each experimental session, fitting cue
 926 states and spatial locations in matrix $X = [X_C, X_S]$ to a $T \times 1$ response vector. Each
 927 response was 1 if stimulus A was selected or -1 if stimulus B was selected. The
 928 regression returned model parameters by fitting the following hierarchical model
 929 (Drugowitsch, 2013):

$$930 \quad P(\text{select } A \mid X, \mathbf{w}_{out}) = \frac{1}{1 + e^{-(X\mathbf{w}_{out})}} \quad (2)$$

$$931 \quad P(\mathbf{w}_{out} \mid \alpha) = \mathcal{N}(\mathbf{w}_{out} \mid 0, \alpha^{-1}I) \quad (3)$$

$$932 \quad P(\alpha) = \text{Gamma}(\alpha \mid a_0, b_0) \quad (4)$$

933 where I is the 10×10 identity matrix. The regression returned estimated coefficients in
 934 10×1 vectors \mathbf{w}_{out} , and precisions in V_n^{-1} . The elements of \mathbf{w}_{out} and V_n^{-1} each
 935 correspond to cue and spatial dimensions in the columns of X_C and X_S . The values of

936 the hyper parameters a_0 and b_0 were set in accordance with an empirical Bayesian
 937 approach. First, w_{out} was calculated for each session using relatively uninformative
 938 hyperparameters ($a_0 = 0.01, b_0 = 0.0001$). Then all regressions were run again with a_0
 939 = 1 and the value of b_0 estimated as the variance of w_{out} across all sessions individually
 940 for each monkey ($b_0 = 0.729$ for Monkey A and $b_0 = 0.382$ for Monkey L). This strategy
 941 selected an exponential conjugate prior on α with the appropriate mean.

942 To calculate subjective weights, each w_{out} was converted to exponential base 10
 943 in vector w_n^* , (for experimental session n) to remain consistent with the base used on
 944 each trial to calculate reward probability:

$$945 \quad w_n^* = \log_{10} e^{w_{out}} \quad (5)$$

946 Subjective weights were then divided into sets corresponding to the four cue
 947 dimensions (*subjective cue weights* $w_{n,C}^*$) and six spatial location pairs (*subjective*
 948 *spatial weights* $w_{n,S}^*$). For each experimental session, the *square root of the sum of*
 949 *squares* (SRSS) of subjective cue weights and subjective spatial weights were
 950 calculated, respectively, as follows:

$$951 \quad SRSS_{n,C} = |w_{n,C}^*| = \sqrt{\sum_{i=1}^4 w_{n,C_i}^{*2}} \quad (6)$$

$$952 \quad SRSS_{n,S} = |w_{n,S}^*| = \sqrt{\sum_{j=1}^6 w_{n,S_j}^{*2}} \quad (7)$$

953 To compare relative changes in subjective cue weights between HP and LP
 954 conditions, the weights in each session n and cue dimension i were normalized by the
 955 mean SRSS across all sessions both conditions as follows:

$$956 \quad \hat{w}_{n,C_i} = \frac{w_{n,C_i}^*}{\frac{1}{N} \sum_n SRSS_{n,C}} \quad (8)$$

957 where N is the number of experimental sessions in the given condition. This
 958 normalization controls for the absolute magnitude of the subjective weights in order to
 959 isolate the relative importance between the weights. Finally, to account for variability in
 960 precision (V_{n,C_i}^{-1}), the weighted mean of each normalized subjective cue weight, \bar{w}_{C_i} and
 961 its corresponding uncertainty $\sigma_{\bar{w}_{C_i}}$ were calculated as follows:

$$962 \quad \bar{w}_{C_i} = \frac{\sum_n V_{n,C_i}^{-1} \hat{w}_{n,C_i}}{\sum_n V_{n,C_i}^{-1}} \quad (9)$$

$$963 \quad \sigma_{\bar{w}_{C_i}} = \sqrt{\frac{1}{\sum_n V_{n,C_i}^{-1}}} \quad (10)$$

964 Because all the regressors were binary, \bar{w}_{C_i} provides a measure of the relative
 965 subjective importance of each cue dimension and spatial location pair.

966

967 Appendix 2

Monkey A					Monkey L				
LP		HP		Cohen's d	LP		HP		Cohen's d
mean	s.d.	mean	s.d.		mean	s.d.	mean	s.d.	
<i>Fraction Correct</i>									
0.880	0.015	0.731	0.021	-8.204	0.912	0.013	0.676	0.022	-14.626
0.865	0.016	0.755	0.020	-6.189	0.899	0.014	0.693	0.022	-12.245
0.841	0.017	0.759	0.020	-4.478	0.896	0.014	0.756	0.012	-8.616
0.906	0.014	0.748	0.020	-9.295	0.888	0.015	0.722	0.021	-9.803
0.856	0.016	0.782	0.019	-4.203	0.905	0.014	0.738	0.021	-10.406
0.878	0.015	0.762	0.020	-6.517	0.914	0.013	0.730	0.021	-11.694
0.895	0.014	0.758	0.020	-7.944	0.884	0.015	0.772	0.019	-6.860
0.881	0.015	0.775	0.019	-6.115	0.887	0.015	0.779	0.019	-6.725
0.860	0.016	0.802	0.018	-3.340	0.878	0.015	0.785	0.019	-5.622
0.863	0.016	0.810	0.018	-3.139	0.878	0.015	0.778	0.019	-5.972
0.868	0.016	0.778	0.019	-5.129	0.866	0.016	0.799	0.019	-3.984
0.883	0.015	0.832	0.017	-3.181	0.876	0.015	0.791	0.019	-5.111
0.883	0.015	0.826	0.018	-3.464	0.872	0.016	0.800	0.019	-4.380
0.843	0.017	0.840	0.017	-0.143	0.853	0.017	0.803	0.018	-2.888
0.852	0.016	0.817	0.018	-2.003	0.869	0.016	0.815	0.018	-3.254
<i>SRSS of Subjective Cue Weights</i>									
2.463	0.282	1.334	0.142	-5.066	2.007	0.223	1.299	0.169	-3.404
2.057	0.224	1.361	0.147	-3.684	2.041	0.182	0.916	0.105	-6.922
2.440	0.226	1.304	0.118	-6.328	1.976	0.181	1.345	0.134	-3.758
2.652	0.287	1.336	0.129	-5.930	2.006	0.194	1.102	0.109	-5.246
1.932	0.185	1.643	0.173	-1.618	2.511	0.260	1.208	0.121	-5.755
2.672	0.261	1.278	0.118	-6.915	2.453	0.255	1.041	0.117	-6.371
2.144	0.216	1.324	0.133	-4.586	2.040	0.201	1.102	0.104	-5.309
2.249	0.207	1.280	0.121	-5.728	2.044	0.189	1.230	0.107	-4.856
2.385	0.220	1.577	0.168	-4.143	2.062	0.191	1.275	0.115	-4.598
2.178	0.204	1.291	0.126	-5.245	1.910	0.172	1.083	0.117	-5.265
2.159	0.188	1.265	0.115	-5.755	1.963	0.181	1.229	0.119	-4.468
2.339	0.246	1.596	0.142	-3.704	2.092	0.191	1.432	0.128	-3.785
2.562	0.295	1.461	0.142	-4.772	2.029	0.190	1.429	0.126	-3.466
2.187	0.202	1.453	0.149	-4.142	1.818	0.176	1.255	0.117	-3.516
1.857	0.179	1.364	0.148	-2.997	1.788	0.181	1.316	0.126	-2.848
<i>SRSS of Subjective Spatial Weights</i>									
1.707	0.248	2.583	0.211	3.801	1.311	0.225	3.636	0.404	7.983
1.498	0.249	2.654	0.277	4.389	0.972	0.194	2.101	0.219	5.581
0.893	0.189	1.942	0.201	5.368	0.783	0.170	2.633	0.256	9.222
0.837	0.213	1.858	0.199	4.957	0.598	0.160	1.977	0.201	7.945
0.587	0.131	2.328	0.229	9.298	0.962	0.200	2.100	0.235	5.374
1.012	0.228	1.524	0.172	2.533	0.749	0.177	1.397	0.170	3.711
0.671	0.148	1.720	0.178	6.405	0.650	0.154	0.985	0.136	2.253
0.709	0.151	1.254	0.153	3.589	0.560	0.140	1.159	0.144	4.252
1.341	0.190	0.825	0.165	-2.900	0.602	0.160	1.088	0.152	3.079
1.171	0.179	0.983	0.158	-1.111	0.598	0.147	1.006	0.149	2.765
0.911	0.159	0.809	0.129	-0.709	0.707	0.145	1.000	0.153	1.991
1.122	0.179	0.778	0.147	-2.107	0.660	0.145	1.272	0.172	3.975
1.439	0.222	0.648	0.134	-4.319	0.748	0.151	1.271	0.171	3.316
1.439	0.179	0.691	0.141	-4.730	0.635	0.148	1.087	0.152	3.027
0.964	0.156	0.623	0.138	-2.324	0.673	0.143	1.025	0.152	2.416

968 **Table 3.** Data from Figure 10. For each monkey and measure (e.g. Fraction Correct),
969 entries are means, standard deviations (s.d.), and effect sizes (Cohen's d). Rows in each
970 section correspond to response time bins along the abscissas of the respective panels of
971 Figure 10, from shorter (upper rows) to longer (lower rows) response times.