

Investigating Confidence Judgments using Reviews in Human and Monkeys

Frederic M Stoll, Emmanuel Procyk

▶ To cite this version:

Frederic M Stoll, Emmanuel Procyk. Investigating Confidence Judgments using Reviews in Human and Monkeys. 2020. hal-03079519

HAL Id: hal-03079519 https://hal.science/hal-03079519

Preprint submitted on 17 Dec 2020

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers. L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1		
2		
3	Investigating Confidence Judgments using Reviews	
4	in Human and Monkeys	
5		
6	Frederic M. Stoll ^{1,†} and Emmanuel Procyk ¹	
7 8	 ¹ Univ Lyon, Université Lyon 1, Inserm, Stem Cell and Brain Research Institute U1208, 69500 Bron, France [†] Current address: Icahn School of Medicine at Mount Sinai, Department of Neuroscience, New York, NY, USA 	
9		
10 11	Correspondence should be addressed to Frederic M. Stoll (<u>frederic.stoll@mssm.edu</u>) or Emmanuel Procyk (<u>emmanuel.procyk@inserm.fr</u>).	
12		
13	Author Contributions: FMS and EP designed research; FMS performed research and analysed data;	
14	FMS and EP wrote the paper.	
15		
16	Abbreviated title: Confidence judgments in Human and monkeys	
17		
18	Acknowledgements: We thank K. N'Diaye and L. Mallet for helping with the task design and for their	
19	comments on the results. We thank J. Benistant for the help in the acquisition of data from human	
20	subjects. We also thank M. Valdebenito, M. Seon and B. Beneyton for animal care and C. Nay for	
21	administrative support. This work was supported by the Agence National de la Recherche (DECCA ANR-	
22	10-SVSE4-1441), the Fondation pour la Recherche Medicale (FMS and DEQ20160334905) and was	
23	performed within the framework of the Labex CORTEX (ANR-11-LABX-0042) of Universite de Lyon,	
24	National de la Recherche Scientifique	
26		
27	Conflict of Interest: No. Authors report no conflict of interest	
28		
29		
30		
31		
32		
33		
34		
35		
36		
37		

Abstract

38

Confidence judgments are self-assessments of the quality of one's own performance, 39 and are a crucial aspect of metacognitive abilities. The underlying neurobiological mechanisms 40 are poorly understood. One approach to understanding these mechanisms would be to take 41 42 advantage of putative metacognitive abilities in non-human models. However, many 43 discrepancies exist between human and non-human studies on metacognition due to the mode of reporting judgements. We here present an attempt to directly compare human and non-44 human primates' metacognitive abilities using a protocol assessing confidence judgments. After 45 performing a categorization test, subjects could either validate their choice or review the test. 46 We could assess whether subjects detected their errors and how they corrected them according 47 to their confidence, and importantly did so in both human and non-human primates. 14 humans 48 and 2 macaque monkeys were tested. Humans showed a well-adapted use of the review option 49 by reviewing more after incorrect choices or difficult stimuli. Non-human primates did not 50 demonstrate a convincing use of the review or validate opportunity. In both species, reviewing 51 did not improve performance. This study shows that decisions to review under uncertainty are 52 not naturally beneficial to performance and is rather perturbed by biases and alternative low-53 cognitive cost strategies. 54

55

56

Introduction

After a decision, and before receiving any feedback, we may feel more or less confident 57 that it was the correct one. For example, being confident you locked your car you will continue 58 shopping, but if you are unsure, you will probably go back and check. Subjective confidence is 59 one core aspect of metacognitive abilities, which represent higher order mental processes by 60 which we monitor and control our own cognition¹. In Humans, subjective confidence has 61 generally been studied using prospective or retrospective questionnaires, requiring explicit 62 verbal reports (e.g. confidence ratings^{2,3}). Subjects are fairly good at judging their accuracy in 63 both perceptual or mnemonic tasks⁴. Both prospective and retrospective confidence ratings 64 appear to be highly correlated with one's own performance, even if humans appear generally 65 overconfident that their choice was/will be correct. Many theories have been proposed to 66 explain how confidence judgments predict accuracy, but they do not account for the wide range 67 of behavioural observations⁵. Nevertheless, an influential proposition is that people rely on 68 inference to judge their performance, by accessing important features such as familiarity or 69 difficulty with the test^{6,7}. 70

To study confidence in non-human animals, researchers have adopted a broader view 71 than for human studies, and explored a wider range of behaviour that might elicit metacognitive 72 processes. Initial demonstration of animal metacognitive abilities involved "uncertain response" 73 protocols, in which difficult tests could be avoided by the use of an alternative non-directed 74 option. This option can be seen as a "choice to not choose", and in theory it should be elicited 75 by higher uncertainty about the outcome of the main choice^{8,9}. Species including monkeys or 76 dolphins efficiently used this option, although doubts have been raised concerning the 77 involvement of metacognition in making such decisions¹⁰. Other studies attempted to 78 approximate human protocols by assessing confidence judgment using a betting procedure¹¹. In 79 these tasks, monkeys were primarily asked to perform a perceptual test. After each trial they 80 were then required to rate their confidence by 'betting on their success' (validating their choice) 81 or alternatively by using a safe option. Monkeys correctly took the opportunity to bet, by betting 82 more when correct^{11,12}. Finally, a large body of work has focused on information-seeking 83 84 behaviour as a mean of understanding metacognitive abilities in non-human animals^{13,14}. This approach appeared more justified from an ecological point of view, as metacognition might 85 enable animals to search for or verify information to improve their decisions. Such behaviour is 86 thought to reflect higher cognitive processing. This is supported by studies highlighting that an 87 animal will search for information when ignorant or uncertain about what to do¹²⁻¹⁶. Taken 88 together, these studies show that information-seeking is targeted, ordered and optional, 89 suggesting that such a search derives from metacognitive processes. 90

However, although information-seeking protocols have provided meaningful behavioural 91 insight concerning putative non-human metacognitive abilities, they often appear inappropriate 92 from a psychophysical or neurophysiological perspective, and are frequently criticised for poor 93 control over experimental conditions. Notably, it has been suggested that simpler heuristics 94 could be used to solve these tasks, questioning the need to rely on metacognition in such 95 information-seeking paradigms¹⁷. Also, available paradigms did not assess an important feature 96 of metacognition, which goes beyond simply validating or not a response based on uncertainty, 97 to explicitly test the use of this decision to further seek information for improving performance. 98 99 The objective of our current study was to test a new protocol adapted to human and non-human primates and devoted to study information-seeking and metacognition, possibly in the context of 100 neurophysiological studies. 101

- 102
- 103
- 104
- 105

Results

106

We designed a new behavioural task that allowed subjects to freely choose whether or 107 not to review a test before validating their decisions (Figure 1A). In each trial, subjects were first 108 (1) asked to report the angle (right or left) of an oriented grating and then (2) proposed to review 109 110 or validate their choice. If subjects decided to review, they were able to go through the 111 categorization and decision stages again. The aim of this task was to promote review depending on one's own perceived uncertainty, as well as allowing subjects to use their uncertainty to 112 guide further decisions. We first tested 14 human subjects in this new task. Subjects' 113 performances in the categorization were standardized using a staircase procedure prior to the 114 experiment, defining the 3 levels of difficulty used thereafter (see Methods and Figure 1B). 115



116

Figure 1. Confidence Judgment Task and categorization performance. A, The events of an individual trial of the task used for human subjects (top) and monkeys (bottom). Frames represent main successive events during a trial. Subjects had to choose whether the stimulus was oriented to the right or to the left. After the right/left choice (*Choice Stage*), subjects could decide whether to validate or review the stimulus to retry the test (*Decision Stage*). Visual feedback was given only after subjects' decision to validate. In the monkey version of the task (bottom panel), they were required to hold a lever to initiate a trial and stimuli were oriented

bars. Also, choice targets were represented by rightward and leftward oriented bars, randomly 124 positioned. Decision targets were represented by a triangle (review option) or a circle (validate 125 option), also randomly positioned. Additionally, correct trials were rewarded by juice, incorrect 126 were penalized by a timeout. B and C, Individuals and average psychometric curve (binomial 127 GLM using a logistic regression) showing performance across stimuli orientations (absolute 128 value by pooling rightward and leftward stimuli) tested during the staircase procedure in human 129 subjects (B) or across different sessions in both monkeys (C). Three absolute stimuli 130 orientations were chosen from individual psychometric curves to elicit 60, 70 and 85% of correct 131 choices (Hard, Medium and Easy conditions respectively). 132

- 133
- 134

An adapted use of the review option in Humans

As expected, human subjects used the review option depending on categorization 135 difficulty (Figure 2A). They reviewed significantly more often for harder stimuli than easier ones 136 (mixed-effect *qlm*, factor difficulty, F=33.6, p=3.3e-9). Contrary to our predictions, however, we 137 observed no gain in performance after reviews (Figure 2B). In fact, the number of successive 138 139 reviews a subject performed had a significantly detrimental effect on performance, notably after 2 successive reviews (mixed-effect *glm*; factor difficulty, F=61.7, p=4.0e-19; factor nbReview, 140 F=4.24, p=0.016; the interaction did not survive model selection) (post hoc comparison of 141 performance after 0 vs. 2 reviews, Wald test p=0.013; other conditions, p>0.12). Thus subjects 142 took the opportunity to review when it made sense to do so, but gained no benefits on 143 performance. This suggests that the probability to review depended on confidence level but that 144 reviewing could not be leveraged to increase performance. 145

A more detailed analysis revealed that subjects not only reviewed more often for difficult 146 trials than for easy ones, but also that decisions were related to categorization accuracy (Figure 147 **2C**). Reviews were significantly more frequent after an incorrect response on the first choice 148 than after a correct one (mixed-effect *qlm*, interaction feedback x difficulty, F=13.3, p=1.04e-5). 149 The percent of reviews after a correct choice decreased with easier conditions, but 150 concomitantly increased after incorrect choices. The difference incorrect versus correct 151 decreased with increased difficulty. Thus, subjects were able to detect their own errors and 152 reviewed appropriately, and this ability was greater when confronted with simple 153 categorizations. This indicates that uncertainty about one's own performance was higher in the 154 most difficult condition, inducing more decisions to review. 155

Response times can reflect the process by which confidence contribute to the decision to review. Indeed, subjects were significantly slower to choose when they subsequently reviewed than when they subsequently validated (**Figure 2D**, mixed-effect *glm*, factor decision, F=684.9, p=7.4e-143). Subjects were slower when making an incorrect choice compared to a correct one, independently of the subsequent decision (validate or review) and more strongly for difficult

bioRxiv preprint doi: https://doi.org/10.1101/741561; this version posted August 22, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

trials (interaction feedback x difficulty, F=9.37, p=8.6e-5; Wald test, p<0.03 for all 161 incorrect/correct comparisons. No other interactions survived model selection). At decision time 162 (review or confirm), subjects were also slower following incorrect choices compared to correct 163 ones, and slower when reviewing compared to confirming their choice (Figure 2E, mixed-effect 164 *qlm*, factor decision, F=63.4, p=2e-15; factor feedback, F=8.51, p=3.5e-3). Difficulty as well as 165 interactions did not survive in that case. Even though similar effects were observed for both 166 response times, differences appeared substantially greater at the choice stage (right/left target 167 selection) than the decision stage. Such observations revealed that subjects' confidence 168 continuously impacted behaviour at all stages and even before the appearance of decision 169 170 targets.





172

Figure 2. Behavioural performance of humans. A, Average percent of review choices for the three difficulty levels. **B**, Average final performance for no review (validate at the first decision), and after 1 or 2 successive reviews. **C**, Percent of reviews for each difficulty level separated by performance at the 1st choice stage (either correct or incorrect). **D & E**, Median response times at the choice (**A**) and decision (**B**) stages depending on performance (correct or incorrect choice, blue/green and red/orange respectively) and difficulties. Blue/red colours represent validated trials, while green/orange colours reviewed ones. Significant post-hoc comparisons (Wald test with FDR correction) are reported as follow: *p<0.05; **p<0.01; ***p<0.001. In D,
 stars and sharp symbols stand respectively for a significant difference between incorrect/correct
 or validate/review. In E, no symbols were reported given that the best final model did not include
 the factor condition. Instead, FDR-corrected p-values were provided. In A-E, dots represent
 individual subjects' performance.

185

Lack of behavioural adaptation following a review in Humans

The above results mostly show that subjects use the review option in an adapted 187 manner. However, the main goal of metacognitive abilities is not only to estimate how uncertain 188 subjects are in a given situation, but also to promote information seeking to improve 189 performance. To investigate such process, we calculated the categorization sensitivity (type1) 190 and metacognitive sensitivity (type2) for each subject and for the three different conditions (see 191 192 Methods for details). As expected, type1 sensitivities decreased with difficulty (mixed-effect glm, F=87.9, p=5.5e-15) (Figure 3A). However, type2 sensitivities revealed an unexpected result. 193 Even though type2 sensitivities varied significantly with difficulty (mixed-effect glm, F=3.96, 194 p=0.028), subjects showed relatively low metacognitive abilities, with type2 sensitivities close to 195 0 in the most difficult conditions. Also, type1 and type2 sensitivities were significantly correlated 196 (Spearman linear correlation, R=0.401, p=0.011, Figure 3B). This suggests that subjects' 197 metacognitive performance depended partially on sources of variation that affected their 198 categorization performances. This might have been the case if for instance subjects used the 199 review option to discriminate difficult vs. easy trials instead of interring the correctness of their 200 choice independently of the categorization's difficulty. 201



Figure 3. Choice and Decision sensitivities. A, Average sensitivity measures (d') for Type1 (Choice, plain grey) and Type2 (Decision, grey stripes) ROC depending on difficulties. Significant post-hoc comparisons (Wald test with FDR correction) are reported as follow: ***p<0.001 for type1 comparisons; #p<0.05 for type2 comparisons. B, Individual d' for type2 plotted against type1, for each difficulty level (Hard in red, Medium in green, Easy in blue). The dotted line represents the Pearson's linear correlation (±95% CI), independent of difficulty.

209

Even if subjects showed markers of their ability to detect errors, they were relatively 210 unable to correct them (as suggested in Figure 2B). Consistent with the overall low level of 211 metacognitive sensitivity, further analysis revealed unexpected consequences of the review 212 process. First, subjects showed on average a significant bias toward repeating the same 213 right/left choice after a review (i.e. percent of shift across difficulties was below 50%. Wilcoxon 214 sign rank test, z=-2.54, p=0.011) (Figure 4A), and this bias toward confirmation was not 215 modulated between conditions (mixed-effect *qlm*, factor difficulty: F=1.97, p=0.152). Figure 4B 216 presents performance of subjects at different levels of review and depending on performance: in 217 grey the performance for first validated choices (D1, no review); in red, final performance 218 following an incorrect first choice (whatever the number of reviews, one or more), and in blue, 219 the final performance following a correct first choice. Note that in the HARD condition, the final 220 performance was particularly low when subjects initially made a mistake (i.e. red bar for HARD, 221 Wald test p<0.001) (mixed-effect glm, interaction difficulty x Trial type, F=2.74, p=0.03). Similar 222 decreases in performance following incorrect trials compared to correct ones was also observed 223 for MED and EASY conditions, albeit to a lesser extent (post-hoc comparison, p<0.018). 224 Alternatively, no differences were observed between the immediately validated performance 225 (D1) compared to the final performance following a correct choice in the first selection (COR) 226 (Wald test, all conditions at p>0.39). Thus, the review process worsened performance only 227 when the trial started with a mistake. In other word, confusion and/or confirmation biases arose 228 after errors during the successive reviews. 229



Figure 4. Performance changes following a review. A, Average percent of shift in response compared to the previous choice following a review. B, Average performance before (grey, first Choice response) and after reviews (blue and red, final Choice response). Final performance was separated depending on the first choice (correct first choice in blue and incorrect first choice in red). Significant post-hoc comparisons (Wald test with FDR correction) are reported as follow: *p<0.05, **p<0.01, ***p<0.001.

239 Categorization performance in monkeys

Two male rhesus monkeys were tested in a task similar to the one used for human 240 subjects (Figure 1A, bottom panel). Monkeys behaved correctly in the categorization test, by 241 242 showing appropriate psychometric performance. The discrimination thresholds differed between monkeys, with monkey H being more accurate with lower angles than monkey D (Figure 1C). 243 To elicit 60, 70 and 85% of correct responses, monkey H was tested with bar orientations of 1°, 244 2° and 5° relative to the vertical (5°, 10° and 20° for monkey D). Both monkeys had slightly 245 better performance for rightward stimuli compared to leftward (0.15° and 3.8° of performance 246 difference between right and left orientations for monkey H and D respectively). 247

To assess whether reaction and movement times varied between conditions, we used a 248 mixed-effect *qlm* for each individual monkey and measure (choice RT, choice MT, decision RT, 249 decision MT), with a random-effect of sessions on the intercept. All initial models included the 3 250 following factors: feedback, difficulty and decision, as well as all possible interactions. The 251 results for the best models are reported below (see also Methods for model selection 252 procedure). Choice RT were slower when monkeys made an incorrect choice compared to a 253 correct one (mixed-effect glm, factor feedback, monkey D: F=40.1, p=2.9e-10; monkey H: 254 F=14.6, p=1.3e-4; factor difficulty and decision, as well as interactions did not survive model 255 selection). Decision RT also increased following incorrect choices for both monkeys, with an 256 additional interaction with difficulty (mixed-effect *glm*, interaction feedback x difficulty, monkey 257 D: F=4.5, p=0.011; monkey H: F=7.3, p=6.8e-4) (Wald test, all difficulty p<0.04, except for 258 monkey H in the hard condition, p=0.33). In only one monkey (monkey D) choice MTs were 259 260 slower following incorrect compared to correct trials, especially in Hard and Easy conditions (mixed-effect *qlm*, interaction feedback x difficulty, F=3.13, p=0.04) (Wald test, p<0.024, but not 261 in Med condition, p=0.08). Decision MT in monkey D did not depend on feedback or difficulty, 262 but significantly change with the subsequent decision to review or validate, as reported in the 263 next section. Overall, monkeys tended to be slower to plan their choice when incorrect, but this 264 was mostly independent of the difficulty of the categorization. 265

- 266
- 267

A sub-optimal use of the review option in monkeys

After an initial use of the review option during the first sessions, both monkeys stopped doing so for a long period of time (**Figure 5A**). Such behaviour forced us to slightly change the task to familiarize them with the review option. Two main changes were tested: forced review trials were included (i.e. in which the validate option was not available) and correct/incorrect feedback was also adjusted to increase review benefits (i.e. more juice reward when correct and less time penalty when incorrect after a review, these parameters also changed over time) (see

also "Notes on training procedure with monkeys" in *Methods*). Contrary to our predictions, these 274 changes did not elicit voluntary reviews (Figure 5A, arrows 'a'). A final change allowed monkeys 275 only one single review, without requiring the validation of their last choice. This was done at 276 session number 61 and 112 for monkey D and H respectively (arrows 'b' in Figure 5A). This 277 modification was efficient in the sense that both monkeys freely selected the review option again 278 after a few sessions, without resorting to a heavier training approach. Thereafter, their 279 behaviour remained stable. For the purpose of this study, we focused our analysis on sessions 280 where monkeys used the review option in a stable way, from session number 64 and 120 until 281 the end for monkey D and H respectively (n = 22 & 38 sessions for monkey D and H) (Figure 282 **5A**, highlighted in grey). 283

Contrary to what was observed with human subjects, monkeys did not use the review 284 option differently with different levels of difficulty (Figure 5B) (mixed-effect glm, factor difficulty; 285 monkey D: F=2.05, p=0.13; monkey H: F=0.41, p=0.66). Moreover, if monkeys were using the 286 review option based on their own uncertainty, one would expect a greater proportion of reviews 287 following incorrect choices compared to correct ones, as observed in human subjects. This was 288 not the case (Figure 5C). In fact, an opposite effect was observed for monkey H (mixed-effect 289 alm, factor feedback; monkey D: F=1.25, p=0.27; monkey H: F=5.86, p=0.017). However, both 290 monkeys repeated more their choices following correct choices compared to incorrect ones, a 291 situation where they usually shifted (mixed-effect *qlm*, factor feedback; monkey D: F=57.1, 292 p=2.3e-9; monkey H: F=372, p=1.3e-30, Figure 5D). Such observation suggests a potential 293 benefit of the review process. 294

As described in the previous section, we did not observe clear modulations in RT and MT depending on the subsequent decision to review or validate. Only decision MT in monkey D were slower for confirmed choice compared to reviewed ones (mixed-effect *glm*, factor decision, F=19.8, p=8.7e-6). In all other cases, the factor 'decision' did not survive model selections. The absence of RT/MT modulations suggests both monkeys might not have use the review option as an expression of their uncertainty.

301

bioRxiv preprint doi: https://doi.org/10.1101/741561; this version posted August 22, 2019. The copyright holder for this preprint (which was not certified by peer review) is the author/funder, who has granted bioRxiv a license to display the preprint in perpetuity. It is made available under aCC-BY-NC-ND 4.0 International license.

Figure 5. Behavioural performance of monkeys. A. Percent of reviews over sessions for 303 monkey D (left panel) and H (right panel). Grey arrows indicate major changes in task design: 304 (a) forced reviews were introduced; (b) the first session where monkeys were proposed to 305 review only once, without the need to validate the second choice. Grey highlight represents the 306 sessions included in the following analyses. B & C, Percent of reviews depending on conditions 307 (B) and previous performance (C; correct in blue; incorrect in red). D, Percent of shifts 308 depending on previous performance. E, Final performance when monkeys validated 309 immediately (No review) or after 1 review depending on conditions (Hard in red; Medium in 310 green; Easy in blue) and for both monkeys. F, Average sensitivity measures (d') for Type1 311 (Choice, plain) and Type2 (Decision, stripes) ROC depending on difficulties. G, Spatial bias 312 (tendency to choose a particular side rather than a particular target) for Choice (Right or Left) 313 and Decision (Review or Validate) stages for both monkeys. Significant post-hoc comparisons 314

(Wald test with FDR correction) are reported as follow: *p<0.05, **p<0.01, ***p<0.001. Dots in
 B-G represent individual sessions' performance.

The behavioural benefits of the review process in terms of performance were different in 318 the two monkeys (Figure 5E). Specifically, for monkey D reviewing was neither advantageous 319 nor deleterious, the performance being modulated only by the difficulty (mixed-effect *qlm*, 320 monkey D, factor difficulty: F=12.3, p=1.3e-5; no other factor or interaction survived model 321 selection). However, monkey H showed a significant increase in performance on reviewed trials, 322 modulated by the difficulty (mixed-effect *glm*, monkey H, interaction difficulty x nbReview, 323 F=4.77, p=9.3e-3; post-hoc comparison for each difficulty, Wald test p<4.5e-17). The 324 discrepancy between monkeys might be explained by differences in experimental conditions. 325 326 Monkey D was allowed to see the stimulus longer during the review (+400ms, representing a duration gain of 80% on average), whereas monkey H was proposed a slightly simpler stimulus 327 after session number 94 (+3°, representing an ideal performance gain of 16.25% on average). 328 Such differences tends to suggest that reviewing the same stimulus (as in monkey D) did not 329 increase performance at all, even when displayed longer. 330

331

317

Similar to what we found in human subjects, monkeys' type1 sensitivities decreased with difficulty (**Figure 5F**) (mixed-effect *glm*, factor difficulty, monkey D: F=4.05, p=0.022; monkey H: F=18.2, p=1.4e-7; post-hoc comparisons, Wald test, monkey D: Hard vs Easy, p=0.027; other comparisons, p>0.051; monkey H: all comparisons at p<1.4e-5, except Hard vs Med at p=0.31). This was not the case for type2 sensitivities, where low values were observed as well as no modulation (mixed-effect *glm*, factor difficulty, monkey D: F=1.98, p=0.15; monkey H: F=2.58, p=0.08).

339

In order to avoid spatial biases, but also to limit preparatory responses, we randomized both Right/Left targets and Review/Validate levers locations between trials (on the right or left of the screen). Yet we observed that both monkeys developed a strong spatial bias toward one side, especially at the decision stage (**Figure 5G**) (Wilcoxon sign-rank test, choice stage; monkey D: z=4.1, p=4e-5; monkey H: z=2.24, p=0.025; decision stage; monkey D: z=4.1, p=4e-5; monkey H: z=5.37, p=7.7e-8). The use of this low cognitively demanding strategy (spatial) strongly suggests that monkeys poorly discriminated between review or validate options.

Taken together, our findings reveal that monkeys were unable to develop and use the opportunity to review or validate the test in an optimal manner. Despite a long and careful training, no clear evidence supported a metacognitive evaluation at the decision stage in monkeys. It is important to acknowledge the possibility that a heavier training approach might have been able to elicit such behaviour. This was however not the objective as we were tryingto obtain a natural development of a review strategy.

353

354

Discussion

355 In this study, we designed a protocol to assess confidence judgments under uncertainty, 356 but also the resulting behavioural adaptations. Inspired by information-seeking tasks, this novel metacognitive task used reviews as a means to reveal confidence and was intended to test both 357 human and non-human primates. Observations in human subjects performing this task was in 358 accordance with previously reported results, showing that subject might be able to report 359 confidence with the opportunity to review or validate. However, in monkeys, the behavioural 360 study did not reveal expected review vs. validate behaviour. The main issue might be that, in 361 both species, reviewing did not improve performance and rather competed with, or was 362 perturbed, by alternative low-cognitive cost strategies. In this context, the design might have 363 hinder monkeys to use the review option appropriately. 364

365

The behavioural task induced a review process triggered by difficulty and estimated 366 performance. Subjects' uncertainty on choice was reflected in the use of this option. They 367 showed behavioural markers of error detection, even before any feedback was delivered. This 368 confirmed previous observations that human subjects can adequately report retrospectively their 369 confidence in a perceptual choice³, although our protocol reveals subjects' confidence through 370 the measure of review behaviour and does not require explicit report. In this sense, this protocol 371 might be useful from a clinical perspective, especially when trying to understand why obsessive 372 compulsive disorder (OCD) patients showed excessive checking behaviour and impairments in 373 self-performance monitoring^{18,19}. Moreover, from a neurophysiological perspective, studies of 374 performance monitoring generally investigate adaptive processes after subjects receive 375 feedback on performance²⁰⁻²² (but see ²³). Our protocol allows us to study markers of 376 performance monitoring in the absence of external feedback. 377

Metacognitive processes might also serve to promote correction of putative mistakes, in order to improve decisions^{1,17}. Apparently, the current task design did not allow subjects to improve their performance after the review process. Rather, subjects developed a bias toward repeating the same choice even if they mostly reviewed after incorrect choices. Such confirmation bias, often reported in the literature²⁴, might contribute to the absence of improvement. But it might also reveal that subjects used reviews as a form of verification, with the objective of reducing their uncertainty about their first decision. This is in contrast to the use

of review to simply revise their first choice (as it would be the case for changes of mind). In that 385 sense, our task design might well capture the use of metacognitive evaluation for adaptive 386 change in control in order to acquire more information. Nevertheless, given that both underlying 387 reasons might contribute to subjects' use of reviews, further experiments are needed to reveal 388 subject's actual strategies at the trial level, for example by varying and controlling the quantity of 389 information given at any moment. Using appropriate modelling tools and experimental changes, 390 it might be possible to dissociate between subjects' overall bias (i.e. reviewing only for 391 confirmation about an uncertain first choice) and decisions that depend on recently collected 392 information. 393

The absence of improvement following a review might also explain why the signal 394 detection approach indicated poor metacognitive abilities. In the procedure, type2 measures 395 reflect the ability to detect and correct wrong decisions²⁵, and scores of this measure were very 396 low. This should not be taken as the sole measure of metacognition. Subjects could not 397 adequately adapt their behaviour under high uncertainty (i.e. following a review), but had 398 chosen to review in a way that indicates some metacognitive process. This dissociation 399 therefore underlines the difficulty of finding a single measure of metacognition, and the fact that 400 several factors impinge on this ability. One interpretation is that, in the present context, the 401 review process counterintuitively generates interference or doubts that prevent the addition of 402 information across the successive reviews and hence the increase in performance. After the first 403 choice, during review, the perceptive information that is offered again to the subjects appeared 404 not to be integrated and cumulated. Rather, subjects might have based their decisions on purely 405 internal information related to performance (the perception of an initial error) or memory of the 406 first perceived stimulus. In this context reviews are detrimental. A study with OCD patients 407 similarly observed that patients seemed to use mnemonic cues to respond to a discrimination 408 test after numerous reviews and did not use the available perceptual information anymore²⁶. 409 More recently, other experiments report similar detrimental effect of reviews in healthy 410 subjects²⁷⁻²⁹. We argue here that subjects did so especially when uncertainty was maximal (in 411 the more difficult condition), by making a choice depending only on a poor memory of the 412 413 stimulus and a pure guess on the current correct response. If this appears to be true, we might expect changes in neurophysiological markers that are incongruent with the information 414 provided by the stimulus. 415

Finally, the existence of a correlation between perceptual and metacognitive abilities suggests that both rely on the same underlying estimation (i.e. perceptual in this case). The difference in choice response times between reviewed trials and validated ones also support such interpretation. Nevertheless, relationships between perceptual and metacognitive

measures have been often reported in the literature (for example ^{4,30,31} but see ²), and have 420 been considered as an argument toward a metacognitive explanation of human and non-human 421 strategies^{5,7}. In our case, subjects might decide whether to review or validate a choice 422 depending on the speed of their responses, by assuming that a long deliberation might be 423 related to greater uncertainty⁶. Even if not metacognitive in the sense defined by Nelson & 424 Narens¹, this gives rise to a widely accepted proposition that metacognitive abilities are based 425 on an *indirect* access to one's own cognition, by making inferences from observable cognitive 426 processing results^{6,7}. Specifically, ease of processing, retrieval fluency or cue familiarity might 427 be used to report confidence and have been argued to reflect metacognitive processes^{4,5,32}. The 428 present data are in favour of such theories. 429

Taken together, our observations highlight that the task might be appropriate to study metacognition from an information-seeking point of view. Review behaviour allowed us to address two metacognitive mechanisms: the monitoring of decisions and the related adaptation that might occur. However, subjects' behaviour suggests that the review option was mostly for self-confirmation rather than a way to modify a choice. Post-decision adaptation was suboptimal in our subjects, possibly due to task design issues as discussed next.

436

Recent studies have shown the possibility to test some forms of checking behaviours in monkeys^{33,34}. In the present study, we were not able to elicit reviews in monkeys that would be based on their perceived uncertainty. Despite weak evidence of their ability to adequately use the review option, monkeys quickly fell into a non-optimal and cognitively less-demanding strategy to perform the task. Such failure might be explained by different factors as discussed below.

First, the difficulty to elicit reviews in monkeys might depend on the learning procedure 443 we adopted, or a related issue concerning the task design itself. Assessing metacognitive 444 abilities in monkeys requires avoidance of the development of alternative strategies³⁵. In 445 particular, reward-induced biases or external cue associations need to be tightly controlled so 446 as to avoid confounds with the intended effect of metacognitive process. In the literature, many 447 studies were debated due to the possible use of alternative non-metacognitive processes^{8,9,13,35}. 448 We tested whether a protocol with an adaptive review process would be efficient. However, as 449 observed by Son & Kornell¹¹, even simpler protocols by comparison to the one we developed, 450 using high and low-bets following a perceptual response, are tricky to use in monkeys. In their 451 study, authors reported their failure to elicit an efficient use of the decision stage, due to the 452 expression of a bias toward a specific option (selecting only the high-bet option). However, after 453

a long training and many modifications in the task design, they were able to elicit what they
 consider to be an optimal use of bet options^{11,12}.

In our task, the credit assignment problem, i.e. figuring out the link between a specific 456 choice (right or left) and a delayed reward (after the decision stage), was arguably the most 457 challenging element. Credit assignment is a complex issue especially in sequentially structured 458 tasks or in multiple choice situations³⁶. For monkeys, one way to bypass such an issue might be 459 to always validate a choice and not take into account the decision stage. This was our monkeys' 460 first strategy. Importantly, when we introduced the single review option, monkeys soon used the 461 opportunity to review. In this case, the association between choice and feedback was 462 sometimes present (after a review, the feedback was given immediately after the second 463 464 right/left choice), and monkeys changed their strategies accordingly. However, both monkeys also adopted a simpler spatial strategy. Reviewing might have been perceived as effortful, and 465 as similar as cancelling a previous choice. Even if a visual cue indicated trial transitions, adding 466 contextual information to clarify the structure of a trial might have helped (e.g. changing the 467 background colour from one trial to another). 468

Another possible explanation was that monkeys never perceived the benefits associated with the review option, even if analyses revealed an advantage for one individual. Reviewing a choice underlies a greater cost than validating, in terms of physical and cognitive effort at least. Delay and effort are two separate features that both depreciate human and non-human decisions when experienced^{37,38}. Even if the review vs. validate options were equalized in duration, our results might suggest that our monkeys were more sensitive to effort than delay, and so were less willing to review a choice than to wait during the time penalty after an error.

Finally, one might question the ability of monkeys to use their own confidence. The 476 failure to induce reviews in our experiment is certainly not only explained by a natural inability to 477 express metacognition. Nevertheless, this question is hotly debated in the literature^{32,39,40}. 478 Information-seeking protocols appear to be highly relevant to study metacognitive processes in 479 animals as one-trial tests have revealed abilities of self-knowledge based adaptive behaviour in 480 macaques¹⁶. Importantly, macaques showed appropriate patterns of responses in uncertainty 481 test whereas new world monkeys (capuchin) did not⁴¹. Yet, few studies reported the relative 482 volatility of metacognitive responses or even the absence of such response in many individuals 483 and different species tested with or without extensive training^{11,14,42}. Concomitantly, two main 484 criticisms have been proposed against the existence of metacognition in non-human animals. 485 The first is that simple heuristics like reward associations, and not metacognition, guide 486 behaviour in information-seeking or uncertainty response paradigms^{10,17,35,40}. The second 487 questions the relevance of metacognition to address problems to which animals are 488

confronted³⁹. Even if animal research tried to answer these issues⁴³, more investigations and
 new protocols are required to confirm whether and how non-human animals have access to
 metacognition^{32,44}.

492

Few improvements are required to adapt our protocol to the study of metacognitive 493 evaluation and control in animals for behavioural and neurophysiological studies. One possibility 494 to explain the failure to induce reviews in monkeys is that, like in humans, the transfer of 495 information from one trial to the next during the review process was not optimal. Hence the 496 review was not beneficial. If this is the case, adding contextual information to link decisions and 497 outcomes across actions and events might help. Similarly, information transfer might not have 498 been facilitated by using fixed stimuli like oriented gratings. Dynamic stimuli (random dot motion 499 for example) could contribute to enhance the gain of perceptual information after a review, and 500 so might be beneficial. 501

502

503 *Methods*

504

Participants and Apparatus

Humans. Fourteen subjects (7 males and 7 females, aged 20-34 years, mean = 24.15 505 years) participated in this study after giving informed consent. The study was carried out in 506 accordance with the recommendations of the Code de la Santé Publique and performed in a 507 laboratory approved by the "Agence Nationale de Sécurité des Médicaments et des produits de 508 santé (ANSM)". All subjects had normal or corrected-to-normal vision and all were right-handed. 509 Testing was performed on an Apple computer (Apple Inc., USA) using Matlab (MathWorks Inc., 510 USA) and the Psychtoolbox⁴⁵. Subjects were comfortably seated 19.6 inches (50cm) away from 511 a 23-inch screen, on which visual stimuli were displayed. Responses were made by using 512 arrows on a computer keyboard with their right (dominant) hand. Experiments were done in a 513 low-luminosity room. 514

515

Monkeys. Two male rhesus monkeys (*Macaca mulatta*), weighing 8 kg and 12 kg (monkeys D & H respectively) were used in this study. All procedures followed the European Community Council Directive (2010) (Ministère de l'Agriculture et de la Forêt, Commission nationale de l'expérimentation animale) and were approved by the local ethical committee (CELYNE, C2EA #42, project reference: C2EA42-13-02--0402-10). Monkeys were trained to perform the task while seated in a primate chair (Crist Instrument Co., USA) in front of a tangent touch-screen monitor (Microtouch System, Methuen, USA). An open-window in front of the chair

allowed them to use their preferred hand to interact with the screen (monkey D, left-handed; monkey H, right-handed). The position and accuracy of each touch was recorded on a computer, which also controlled the presentation of visual stimuli via the monitor (CORTEX software, NIMH Laboratory of Neuropsychology, Bethesda, MD). During experiments, monkeys were not head-restrained and eye movements were not controlled.

528

529 Behavioural Task

Humans. Subjects were first asked to perform a categorization task, based on the 530 orientation of a stimulus following a staircase procedure to adjust difficulty (Figure 1A, top 531 panel). Each trial started with a 1000ms fixation period during which subjects fixated a central 532 dot. Then, a stimulus, consisting of a low-contrast Gabor patch oriented from vertical reference 533 either on the left or on the right, was presented centrally on a grey background during 200ms. 534 After a 500ms delay, subjects reported the orientation of the stimulus by using the right or left 535 arrow keys of a standard keyboard. After reporting their choice (right or left) and an additional 536 delay of 1000ms, they were asked to either validate or review (re-execute) the test (with either 537 the bottom or the top arrow keys respectively). If subjects decided to validate their choice, a 538 visual feedback was displayed centrally for 800ms, consisting of the word "correct" (shown in 539 green) or "incorrect" (in red), and a new stimulus was presented on the subsequent trial. A 540 review was potentially triggered by a subjective lack of confidence. If subjects decided to review, 541 the same stimulus was presented again and a new choice could be made. Note that following 542 half of the reviews, subjects were presented with a longer stimulus than on its first presentation, 543 544 for a duration of 250ms instead of 200ms. The trial ended only after the subject validated their choice. Correct trials were not rewarded per se, but incorrect trials were penalized by a time 545 penalty of 15 seconds. A 1000ms delay was introduced between trials. 546

547 Subjects were required to perform 420 trials, divided into 6 blocks of 70 trials (note that 1 548 subject performed blocks of 65 trials instead). Between blocks, subjects were able to take rest. 549 At the start of the experiment, instructions were given to explain the nature of the task as 550 described above. Emphasis was placed on the general idea that the review option could help 551 the subject complete the experiment more quickly, i.e. that reviews and consequent 552 improvement of performance would compensate for the time-out after errors.

553

554 **Monkeys**. Monkeys were trained to perform a task similar to the one use with humans, 555 where they were required to perform a categorization test based on the orientation of a bar, and 556 then to either validate or review their choice (**Figure 1A, bottom panel**).

To initiate a trial, monkeys had to touch and hold a lever item, represented by a grey 557 triangle on the bottom of the screen. Once touched, a central dot appeared on the screen for 558 800ms. Then, the central dot turned off and the stimulus appeared on the screen (a grey 559 rightward or leftward oriented bar) for a duration between 400 and 900ms (this duration was 560 fixed during a session but changed across training). After a delay of 200ms, two oriented bars 561 (one oriented 45° to the left, the other 45° to the right relative to the vertical) were used as 562 targets. The relative position of targets was randomized from one trial to another (e.g. the 563 leftward bar might be either positioned on the right part or the left part of the screen, randomly). 564 Monkeys reported their choice by touching one of the targets. This was followed by an 565 additional delay of 200ms. The two decision levers were then displayed, allowing monkeys to 566 567 review or validate their previous choice. The review option was represented by a grey inverted triangle lever, and the validate option by a grey disk. The position of each lever on the screen 568 (bottom right or left) was randomly assigned from one trial to the next. 569

If monkeys touched the validate option they received a feedback corresponding to their 570 performance: correct choices were rewarded by a squirt of apple juice lasting between 300 and 571 1000ms, incorrect choices were penalized by a grey screen lasting between 10000 and 572 15000ms (note that rewards and penalties changed over the course of training, hence the range 573 of values). To equalize review/validate options duration, the duration of a penalty for incorrect 574 validation was set to be equal to two review trials. However, it is important to keep in mind that, 575 by design, review trials are more effortful than validated ones, given the number of touches 576 required. After the feedback delivery, a visual signal was displayed on the screen, consisting of 577 a red circle lasting 800ms, and indicating the change of condition. 578

If monkeys touched the review option, the central dot appeared again on the screen for 579 800ms and the stimulus was displayed. Two particular modifications of the task were used to 580 stimulate the review process. First, the duration of the stimulus was increased by 400ms after 581 each review. In some of monkey H's sessions, the duration of the stimulus was not increased, 582 583 but instead the stimulus became easier (larger angle) after reviews (this was the case for all the sessions analysed thereafter, see Results for details). The following events were the same as 584 585 described above. Second, feedback duration was modified if monkeys reviewed at least once. Correct choices were more rewarded after a review than after no review, with duration of reward 586 between 500 and 1400ms (+91.6% and +77.7% of reward for monkey D and H respectively). 587 Also, incorrect choices were less penalized after reviews, with a time penalty between 1000 and 588 3000ms (-82.6% and -79.4% for monkey D and H respectively). These explicit benefits of the 589 review were introduced to help monkeys during the training procedure (by increasing the review 590

591 utility), but were not intended to be used after the completion of the training (see below for 592 details on training).

593 594

Staircase & Psychometric analysis

595 To maintain different levels of uncertainty during the categorization, three different 596 stimulus orientations were used randomly across trials (i.e. HARD, MED and EASY).

For human subjects, orientations were determined depending on subject's own 597 performance using a classical staircase procedure prior to the experiment. In this procedure 598 (which lasted 240 trials), subjects had to choose whether the stimulus was leftward or rightward 599 oriented, without the possibility to review or validate their choice. Stimulus orientations were 600 defined depending on subjects' performance, with 3 randomly mixed staircase rules⁴⁶ (one-up 601 one-down, one-up two-down and one-up three-down). The use of the 3 parallel staircases 602 procedure (80 trials each) allowed us to assess subjects' performance more accurately. Based 603 on performance during the staircase procedure, we calculated a psychometric curve for each 604 subject, using a binomial generalized linear model (logistic regression). Three absolute stimuli 605 orientations were then extracted and used during the main experiment to induce 70%, 75% and 606 85% of correct responses (HARD, MED and EASY conditions respectively, see Figure 1B for 607 an average psychometric curve and related orientations). 608

Similarly, for monkeys, orientations were not fixed between sessions but varied depending on their performance in preceding sessions (by considering the 5 to 10 last sessions). We computed a psychometric curve from past monkeys' performance using a binomial generalized linear model (logistic regression) (**Figure 1C**). Then, stimuli orientations were selected to elicit 70, 80 or 90% of correct responses on average. Such procedure allowed us to maintain uncertainty in categorization trials across sessions independently of other learning-related processes.

- 616
- 617

Notes on training procedures with monkeys

We first trained monkeys on the categorization task alone, which lasted several months. 618 During this period, performance feedback was given immediately after their choices. Once 619 performance in the categorization task was stable and sufficiently accurate, monkeys were then 620 introduced to the decision stage, allowing to review or validate choices. This was done without 621 any particular shaping. That is, we did not imposed any familiarisation with one of the two 622 decision stage options prior to this stage, initially to avoid as much as possible biases toward a 623 specific behaviour (review or validate). Over-training monkeys could lead to non-optimal 624 strategies and is particularly problematic when it comes to understand natural behaviour such 625

as monkeys' metacognitive ability¹⁶. However, during the learning phase with the decision 626 stage, we faced a few issues that led us to modify the task design in several steps. Specifically, 627 after experiencing the review option both monkeys stopped using it within a few sessions (see 628 **Figure 5A**). We thus implemented three main changes: 1) a small proportion of forced review 629 trials (10-25%) were introduced (on these trials, only the review target is presented at the first 630 decision stage), 2) penalties and rewards were adjusted throughout the training to increase the 631 utility of the review and 3) monkeys could not review more than one time in a row, without the 632 need to validate after the review (i.e. no second decision stage were proposed, and importantly, 633 feedback was delivered immediately after the second choice). 634

Here, we report behavioural data for 22 and 38 sessions (for monkey D and H respectively). Sessions were selected based on the frequency in choosing the review option. To accurately assess putative metacognitive performances, we excluded sessions before the monkeys selected the review option in a stable manner (see Results for details).

639 640

Behavioural Analysis

Humans. Classical performance measures were calculated for each subject. 641 Specifically, choice response times (i.e. time between the appearance of the right/left targets 642 and the button press) and decision response times (i.e. time between the appearance of the 643 review/validate targets and the button press) were recorded and analysed. Response times 644 exceeding 10 seconds were rejected from further analyses (n=3 and 1 trials for choice and 645 decision times, respectively, across all subjects). To improve the normality of the data 646 647 distribution, we used the log transform of response times as dependent variable in the statistical analyses. Also, we calculated the percentage of review decisions (whatever the number of 648 successive reviews), depending on conditions or depending on previous performance (correct 649 or incorrect in the first selection). Initial and final performance was computed for each trial. 650 Moreover, subjects' strategy following a review was studied by calculating the percent of shift, 651 which is the proportion of reviewed trials after which the initial choice (before review) was 652 changed in the decision that was made after reviews. As very few subjects made more than four 653 successive reviews, these trials were entirely removed from further analyses (n=6/5850 trials). 654 For similar reasons, we restricted our analyses of the performance against the number of review 655 (Figure 2B) as well as type1/type2 performance (Figure 3) to a maximum of two successive 656 reviews (n=5731/5844 included trials, 2% of trials were rejected). 657

As mentioned previously, the stimulus was displayed for an extra 50ms following half of subjects' reviews. This manipulation did not elicit any difference in performance, as assessed using mixed effect models (see Statistical procedure for more details). Specifically, the

performance after 1 review was only modulated by difficulty; the factor Stim Length did not survive model selection. For the performance after 2 successive reviews, we found a significant interaction (mixed effect *glm*, interaction difficulty x Stim Length, F=3.51, p=0.035) but post-hoc comparisons revealed no statistically significant differences between stimulus length levels (Wald test, W<1.48 and p>0.42 for all comparisons). For this reason, all trials were pooled together in further analyses, independently of stimulus length.

667

Monkeys. In addition to the measures used for human subjects, choice reaction times 668 (choice RT; i.e. time between the appearance of oriented targets and the release of the lever) 669 and choice movement times (choice MT; i.e. time of arm movements from lever release to the 670 671 touch on selected target) were computed on each trial. Decision reaction times (decision RT; i.e. time between the appearance of the decision levers and the release of the target) and 672 movement times (decision MT; time between the target release and the touch of a decision 673 lever) were also recorded. As for human subject analyses, we used the log transform of the 674 reaction and movement times as dependent variables in statistical analyses. Moreover, a 675 measure of spatial bias was calculated for both stages (choice and decision) by dividing the 676 number of touches made ipsilateral to the hand used by the total number of touches (note that 677 monkey D and H use their left and right hand respectively). 678

679

680

Signal Detection Theory approach

To assess subjects' performance in the categorization test and their metacognitive abilities, we used the signal detection theory approach implemented by MacMillan & Creelman²⁵. For this purpose, we computed the receiver operating characteristic (ROC) curve for both categorization (type1) and metacognitive (type2) performance. In this analysis, all trials are designated a 'trial type' amongst HIT, Correct Rejection (CR), False Alarm (FA) and MISS. In a 2-choice task such as ours, a reference for this classification must be chosen. It is the reference that differentiates type1 and type2 performance.

For type1 we sought to measure categorization performance, and the reference was trials on which the stimulus was oriented to the right. Hence a trial that had a rightward stimulus and a response 'right' was classified as a HIT, whereas a trial that had a leftward stimulus and a response 'left' was classified as CR. It follows that rightward stimulus and response 'left' was Miss, and leftward stimulus and response 'right' was a false alarm. This referencing approach allowed us to complete a ROC analysis despite the two-choice nature of the task.

In the type2 analysis, we sought to measure the metacognitive performance, i.e. whether the subject correctly self-diagnosed their performance in their choice to review or not. Hence the

reference was trials where the response was both correct AND validated. In this case a HIT was 696 a correct and validated choice, whereas a CR was an incorrect then reviewed response. As 697 such, FA was a correct reviewed response, whereas a MISS was an incorrect validated 698 response. 699

Finally, we took into consideration the number of reviews (none, one or two) made within 700 a trial, because this can be considered as a rating scale of certainty - no review meant that 701 subjects were sure, 2 reviews that they were really unsure of their response. Hence, for a given 702 trial, each new choice after a review or 2 reviews was assigned a cumulative probability of HIT 703 and FA, based not only on the outcome of that choice but also of the previous choices within the 704 same trial. We then derived ROC curves from cumulative HIT and FA probabilities before 705 applying a Gaussian z transformation (i.e. zROC). We fitted a linear curve in order to obtain the 706 slope of the zROC. We further defined d'₁ and d'₂, the horizontal and vertical intercept of the 707 zROC curve, respectively: 708

709

7'

710	$d'_1 = -z(pFA)$ at the point where $z(pHIT)=0$
711	$d'_2 = z(pHIT)$ at the point where $z(pFA)=0$

712

From there, we then extracted the sensitivity measures (type1 and type2 d'a) according to the 713 formula [1] defined in Chapter 3 of MacMillan & Creelman's guide²⁵ : 714

- 715
- 716
- 717

 $d'_a = \left(\frac{2}{1+s^2}\right)^{1/2} d'_2$

[1]

where d'_a represents the sensitivity and s the slope of the linear zROC curve. This 718 measure of sensitivity, contrary to the classic d', is able to characterize a ROC curve using a 719 single value of distance from each pair of HIT and FA probabilities. 720

721 722

Statistical procedures

All statistical procedures were performed using Matlab. Behavioural differences between 723 conditions were assessed using mixed-effect generalized linear models (glm). For human 724 subjects, each model included a random-effect on the intercept of the variable that the model 725 was fitting (e.g. performance, percent of review, or the log of response times), to account for 726 baseline differences between subjects (random-effect of subjects). For monkeys, models 727 included a random-effect on the intercept to account for baseline differences between sessions 728 (random-effect of sessions). Across models, the following factors (and levels) were considered: 729

Difficulty (Hard, Medium, Easy), Feedback (Incorrect, Correct), Number of Review (0 to 2), 730 Decision (Review, Validate), Trial Type (Validated choice, Correct choice Reviewed, Incorrect 731 choice Reviewed), and Stimulus Length (post-review increased or not). For every model used, 732 we first performed a model selection by repeatedly testing the effect of dropping the least 733 significant factor (starting with the interactions). The most appropriate models were then 734 selected using Log Likelihood ratio test (with p<0.05). F-tests for each fixed-effects term in the 735 selected models were reported in the Results section. Post-hoc comparisons were performed by 736 computing the estimated marginal means⁴⁷ and using Wald test. P-values were corrected with 737 False Discovery Rate (FDR) to account for multiple comparisons. 738

739

740 Data availability

741

All relevant data and codes are available from the authors upon request.

742

743 **References**

- Nelson, T. O. & Narens, L. Why investigate metacognition? in *Metacognition: Knowing about knowing.* (eds. Metcalfe, J. & Shimamura, A. P.) 1–25 (The MIT Press, 1994).
- Fleming, S. M., Weil, R. S., Nagy, Z., Dolan, R. J. & Rees, G. Relating introspective accuracy to
 individual differences in brain structure. *Science* **329**, 1541–1543 (2010).
- Fleming, S. M. & Dolan, R. J. The neural basis of metacognitive ability. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* 367, 1338–1349 (2012).
- Alter, A. L. & Oppenheimer, D. M. Uniting the tribes of fluency to form a metacognitive nation.
 Personal. Soc. Psychol. Rev. Off. J. Soc. Personal. Soc. Psychol. Inc 13, 219–235 (2009).
- 5. Koriat, A. The self-consistency model of subjective confidence. *Psychol. Rev.* **119**, 80–113 (2012).
- Koriat, A. Monitoring one's own knowledge during study: A cue-utilization approach to judgments of
 learning. *J. Exp. Psychol. Gen.* **126**, 349–370 (1997).
- 755 7. Benjamin, A. S., Bjork, R. A. & Schwartz, B. L. The mismeasure of memory: when retrieval fluency is
 756 misleading as a metamnemonic index. *J. Exp. Psychol. Gen.* **127**, 55–68 (1998).
- 8. Shields, W. E., Smith, J. D. & Washburn, D. A. Uncertain responses by humans and rhesus monkeys
 (Macaca mulatta) in a psychophysical same-different task. *J. Exp. Psychol. Gen.* 126, 147–164
 (1997).
- Smith, J. D., Shields, W. E., Schull, J. & Washburn, D. A. The uncertain response in humans and
 animals. *Cognition* 62, 75–97 (1997).
- The control of the cont
- Son, L. K. & Kornell, N. Metaconfidence judgments in rhesus macaques: Explicit versus implicit
 Mechanisms. in *The missing link in cognition: Origins of self-reflective consciousness* (eds. Terrace,
 H. S. & Metcalfe, J.) 296–320 (Oxford University Press, 2005).
- Kornell, N., Son, L. K. & Terrace, H. S. Transfer of metacognitive skills and hint seeking in monkeys.
 Psychol. Sci. 18, 64–71 (2007).
- 13. Call, J. & Carpenter, M. Do apes and children know what they have seen? *Anim. Cogn.* 3, 207–220 (2001).

- 14. Hampton, R. R., Zivin, A. & Murray, E. A. Rhesus monkeys (Macaca mulatta) discriminate between
 knowing and not knowing and collect information as needed before acting. *Anim. Cogn.* 7, 239–246
 (2004).
- 15. Basile, B. M., Hampton, R. R., Suomi, S. J. & Murray, E. A. An assessment of memory awareness in tufted capuchin monkeys (Cebus apella). *Anim. Cogn.* **12**, 169–180 (2009).
- 16. Rosati, A. G. & Santos, L. R. Spontaneous Metacognition in Rhesus Monkeys. *Psychol. Sci.* 27, 1181–1191 (2016).
- 17. Crystal, J. D. & Foote, A. L. Evaluating information-seeking approaches to metacognition. *Curr. Zool.* 57, 531–542 (2011).
- 18. Aouizerate, B. *et al.* Pathophysiology of obsessive-compulsive disorder: a necessary link between
 phenomenology, neuropsychology, imagery and physiology. *Prog. Neurobiol.* 72, 195–221 (2004).
- Hauser, T. U., Allen, M., NSPN Consortium, Rees, G. & Dolan, R. J. Metacognitive impairments
 extend perceptual decision making weaknesses in compulsivity. *Sci. Rep.* 7, 6614 (2017).
- 20. Gehring, W. J., Goss, B., Coles, M. G. H., Meyer, D. E. & Donchin, E. A Neural System for Error
 Detection and Compensation. *Psychol. Sci.* 4, 385–390 (1993).
- 21. Ullsperger, M. & von Cramon, D. Y. Subprocesses of performance monitoring: a dissociation of error
 processing and response competition revealed by event-related fMRI and ERPs. *NeuroImage* 14,
 1387–1401 (2001).
- Vezoli, J. & Procyk, E. Frontal feedback-related potentials in nonhuman primates: modulation during
 learning and under haloperidol. *J. Neurosci. Off. J. Soc. Neurosci.* 29, 15675–15683 (2009).
- 23. Boldt, A. & Yeung, N. Shared Neural Markers of Decision Confidence and Error Detection. *J. Neurosci.* 35, 3478–3484 (2015).
- 793 24. Nickerson, R. S. Confirmation Bias: A Ubiquitous Phenomenon in Many Guises. *Rev. Gen. Psychol.*794 2, 175–220 (1998).
- Macmillan, N. A. & Creelman, C. D. *Detection theory: A user's guide, 2nd ed.* (Lawrence Erlbaum
 Associates Publishers, 2005).
- 26. van den Hout, M. & Kindt, M. Repeated checking causes memory distrust. *Behav. Res. Ther.* 41, 301–316 (2003).
- Alcolado, G. M. & Radomsky, A. S. Believe in yourself: Manipulating beliefs about memory causes
 checking. *Behav. Res. Ther.* 49, 42–49 (2011).
- 28. Medway, M. & Jones, M. K. Further Evidence That Repeated Checking Leads to Reduced Memory
 Confidence, Vividness and Detail: New Evidence That Repeated Object Exposure Also Results in
 Memory Distrust. *Behav. Change* 30, 159–179 (2013).
- 29. Linkovski, O., Kalanthroff, E., Henik, A. & Anholt, G. E. Stop checking: Repeated checking and its
 effects on response inhibition and doubt. *J. Behav. Ther. Exp. Psychiatry* 53, 84–91 (2016).
- 30. Kunimoto, C., Miller, J. & Pashler, H. Confidence and accuracy of near-threshold discrimination
 responses. *Conscious. Cogn.* **10**, 294–340 (2001).
- 31. Kao, Y.-C., Davis, E. S. & Gabrieli, J. D. E. Neural correlates of actual and predicted memory
 formation. *Nat. Neurosci.* 8, 1776–1783 (2005).
- 32. Kornell, N. Where is the 'meta' in animal metacognition? *J. Comp. Psychol. Wash. DC 1983* 128,
 143–149 (2014).
- 33. Stoll, F. M., Fontanier, V. & Procyk, E. Specific frontal neural dynamics contribute to decisions to
 check. *Nat. Commun.* 7, 11990 (2016).
- Bosc, M. *et al.* Checking behavior in rhesus monkeys is related to anxiety and frontal activity. *Sci. Rep.* 7, 45267 (2017).
- 35. Ferrigno, S., Kornell, N. & Cantlon, J. F. A metacognitive illusion in monkeys. *Proc. Biol. Sci.* 284, (2017).
- 36. Walton, M. E., Behrens, T. E. J., Noonan, M. P. & Rushworth, M. F. S. Giving credit where credit is
 due: orbitofrontal cortex and valuation in an uncertain world. *Ann. N. Y. Acad. Sci.* 1239, 14–24
 (2011).

- 37. Walton, M. E., Kennerley, S. W., Bannerman, D. M., Phillips, P. E. M. & Rushworth, M. F. S.
 Weighing up the benefits of work: behavioral and neural analyses of effort-related decision making. *Neural Netw. Off. J. Int. Neural Netw. Soc.* **19**, 1302–1314 (2006).
- 38. Stevens, J. R. & Stephens, D. W. The adaptive nature of impulsivity. in *Impulsivity: The behavioral and neurological science of discounting*. (eds. Madden, G. J. & Bickel, W. K.) 361–387 (American
 Psychological Association, 2010).
- 39. Perner, J. MiniMeta: in search of minimal criteria for metacognition. in *Foundations of Metacognition* (eds. Beran, M. J., Brandl, J., Perner, J. & Proust, J.) 94–116 (Oxford University Press, 2012).
- 40. Le Pelley, M. E. Metacognitive monkeys or associative animals? Simple reinforcement learning
 explains uncertainty in nonhuman animals. *J. Exp. Psychol. Learn. Mem. Cogn.* 38, 686–708 (2012).
- 41. Smith, T. R., Smith, J. D. & Beran, M. J. Not knowing what one knows: A Meaningful failure of metacognition in capuchin monkeys. *Anim. Behav. Cogn.* **5**, 55–67 (2018).
- 42. Suda-King, C. Do orangutans (Pongo pygmaeus) know when they do not remember? *Anim. Cogn.*11, 21–42 (2008).
- 43. Smith, J. D., Couchman, J. J. & Beran, M. J. The highs and lows of theoretical interpretation in animal-metacognition research. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **367**, 1297–1309 (2012).
- 44. Smith, J. D. *et al.* I scan, therefore I decline: The time course of difficulty monitoring in humans (homo sapiens) and macaques (macaca mulatta). *J. Comp. Psychol. Wash. DC 1983* **132**, 152–165 (2018).
- 45. Brainard, D. H. The Psychophysics Toolbox. Spat. Vis. 10, 433–436 (1997).
- 46. Leek, M. R. Adaptive procedures in psychophysical research. *Percept. Psychophys.* 63, 1279–1292
 (2001).
- 47. Hartman, J. emmeans. *https://www.github.com/jackatta/estimated-marginal-means* (2019).
- 843