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Comment from the Handling Editor

Thank you for the thorough revision of your paper. The paper is now acceptable for publication.

Relative numerical middle in rhesus monkeys

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23 **Abstract**

24 Animals show vast numerical competence in tasks that require both ordinal and cardinal numerical
25 representations, but few studies have addressed whether animals can identify the numerical middle
26 in a sequence. Two rhesus monkeys (*Macaca mulatta*) learned to select the middle dot in a
27 horizontal sequence of three dots on a touchscreen. When subsequently presented with longer
28 sequences composed of 5, 7 or 9 items, monkeys transferred the middle rule. Accuracy decreased as
29 the length of the sequence increased. In a second test, we presented monkeys with asymmetrical
30 sequences composed by nine items, where the numerical and spatial middle were distinct and both
31 monkeys selected the numerical middle over the spatial middle. Our results demonstrate that rhesus
32 macaques can extract an abstract numerical rule to bisect a discrete set of items.

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35 **Key words:** Number bisection, middle, rhesus monkeys, comparative cognition, center, abstract
36 concepts.

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40 **1. Introduction**

41 Animals have an intuitive number sense which support the capacity to distinguish which of
42 two sets of objects is numerically greater [1,2], to perform simple summations and subtractions [3–
43 6], to identify a specific ordinal position in a sequence [7–9], and to compare proportions [10,11].
44 While humans and animals share the Approximate Number System, ANS, a fundamental difference
45 between humans and animals is that only humans are capable of precise calculations afforded by the
46 acquisition of a counting system and symbol for number. The ANS has two behavioral signatures:
47 the magnitude and distance effects [12,13]. The magnitude effect refers to the fact that when
48 distance is held constant it is easier to process smaller than larger values, it is easier to discriminate
49 2vs.3 than 88vs.89 dots. The distance effect refers to the observation that as the disparity (distance)
50 increases between two numerical sets, accuracy increases (2vs.8 is easier than 2vs.3). Despite the
51 abundance of scientific evidence documenting the existence and attributes of the ANS there are few
52 studies that address whether animals have a "middle" concept [14]. Here we ask whether rhesus
53 monkeys can abstract a numerical rule to identify the central item in a series of discrete items.

54 Empirical investigation of the "middleness" concept dates back to 1934, when Yerkes trained
55 chimpanzees to identify the middle container in a sequence of three containers for food reward.
56 When the chimpanzees were then presented with longer sequences, comprising five, seven or nine
57 containers, they were unable to select the middle item [15]. The failure in generalize to longer
58 sequences could be due to the task design which made it difficult to open each container.
59 Subsequent tests with containers that were easier to open showed that chimpanzees could
60 successfully identify the middle item in a 5-item sequence [16]. A single female chimpanzee even
61 learned to pinpoint the middle item in sequences containing up to 17 items [17,18]. This single
62 chimpanzee also succeeded when the spacing between the items were unequal across the sequence
63 [18]. Whether the chimpanzee used a middle strategy or instead learned to identify a specific
64 ordinal position was unclear [19]. To differentiate these ideas it is necessary to test transfer to
65 sequences of different lengths.

66 In a recent study, rhesus monkeys learned to select the middle item in horizontal sequences
67 of three items [14]. They transferred the middle rule to longer sequences which were new in color
68 and shape. Crucially, monkeys were also able to select the middle item when presented with
69 sequences of seven items, suggesting that they did not rely on an absolute numerical strategy, which
70 would have resulted in selecting the second item on either side. The monkey could however have
71 used a spatial or numerical strategy to bisect the sequences.

72 Here, we investigated whether rhesus monkeys can flexibly use the abstract numerical
73 concept of middle to navigate novel and expanded sequences, in a high-controlled computerized
74 setting. The main goal of this study was to disentangle if monkeys relied on numerical or spatial
75 information when identifying the middle item.

76

77 **2. Methods**

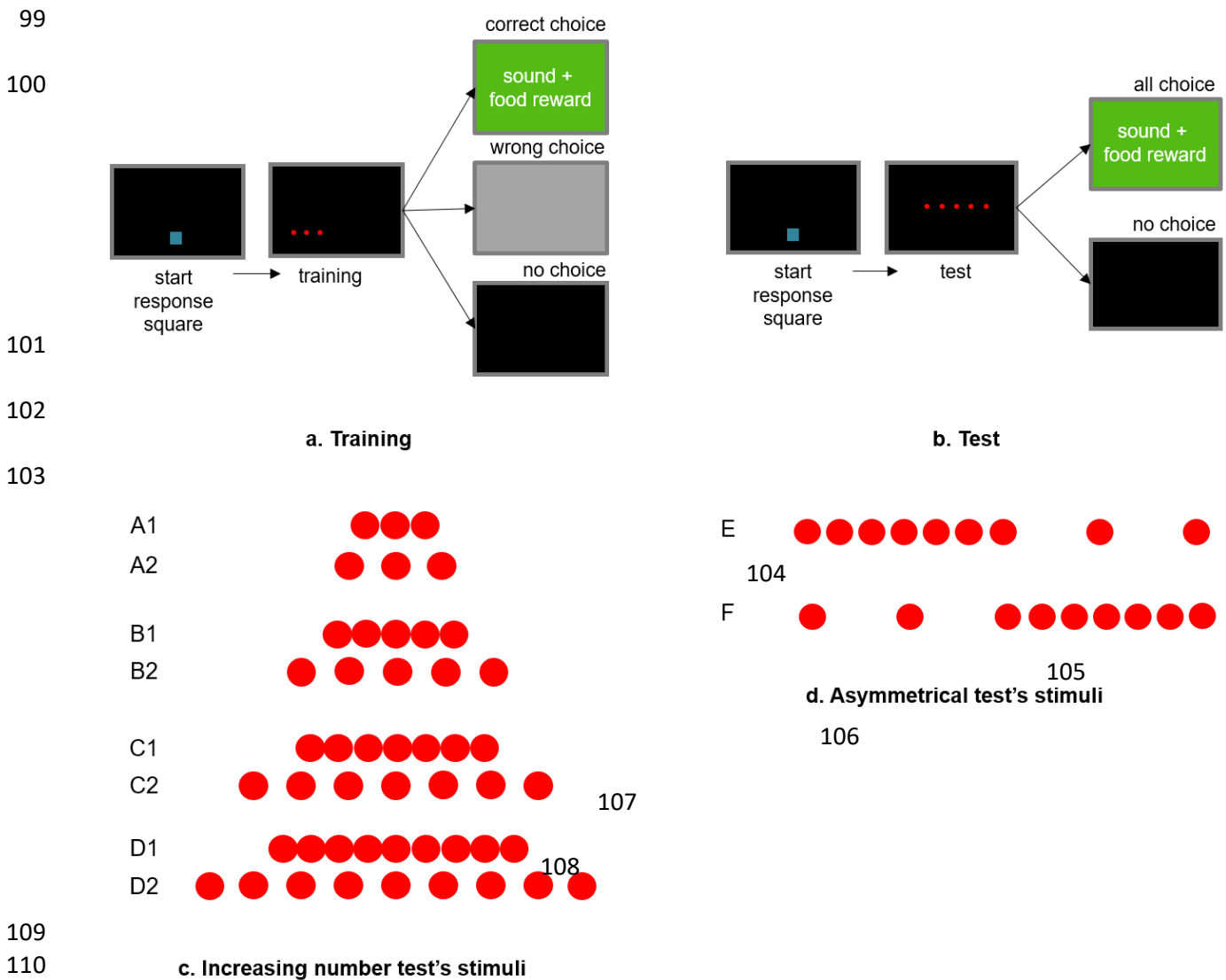
78 *Subjects:* The subjects were two socially housed male rhesus macaques (*Macaca mulatta*),
79 named Arrow (5-year-old) and Tolman (6-year-old). Monkeys were separated for in cage testing.

80 *Apparatus:* This consisted of a 15-inch touch-sensitive computer monitor (Elo TouchSystems,
81 Menlo Park, CA) connected with a food pellet reward delivery system (Med Associates, St. Albans,
82 VT). The monitor was fixed to the front of the macaque's home cage and the pellet reward was
83 connected with a food container behind the monitor. A program written in PsychoPy³⁴⁰ presented
84 the stimuli, controlled the reward delivery and collected data.

85 We first trained monkeys to select the middle dot in an array of three identical dots. To
86 prevent monkeys from learning to touch a specific location on the screen, we presented the three-
87 dot array on 32 different absolute positions on the screen, balanced for left/right, up/down and we
88 used two inter-dot distances (0.75cm and 2cm). On each training trial, monkeys earned a positive
89 reward by touching the middle dot (**Figure 1a**). We then tested the monkeys with two transfer
90 experiments; **Figure 1b** schematically represents the experimental procedure. In the Number
91 Transfer Test we explored whether monkeys' performances showed a magnitude effect, which is a

92 characteristic signature of the ANS. Specifically we tested monkeys with sequences of 3, 5, 7 or 9
 93 identical dots (**Figure 1c**). If middle identification relies on numerical cues, responses would
 94 become less accurate as the number of dots increases. In the Asymmetrical Test we attempted to
 95 disentangle whether monkeys used a numerical or spatial strategy by presenting spatially
 96 asymmetric sequences where the spatial middle and numerical middle were not the same item.
 97 Monkeys were presented with 9-item sequences in non-differentially rewarded trials (**Figure 1d**).

98 **Figure 1**



112 **Figure 1. Schematic illustration of the experimental procedure and stimuli. a.** Training trials. A
 113 start response square then a three-dot stimulus appeared. A food reward, a green screen and a
 114 positive sound occurred after the selection of the middle dot. A grey screen appeared after the
 115 choice of either lateral dot; the screen illuminated black after 5 sec. with no choice. **b.** Testing trials.
 116 A start response square then a stimulus appeared. The selection of all dots, lateral or middle, elicited
 117 a positive reward. The screen illuminated black after no choice within 5 sec. **c.** Stimuli used in the

118 Number Transfer Test: close 3-dots (A1), far 3-dots (A2), close 5-dots (B1), far 5-dots (B2), close
 119 7-dots (C1), far 7-dots (C2), close 9-dots (D1), and the far 9-dots (D2). **d.** Stimuli used in
 120 asymmetrical test: asymmetrical left condition (E) and asymmetrical right condition (F).
 121 (<https://www.nature.com/articles/s41598-020-74533-8>).
 122

123 3. Results

124 We conducted Bayes factor analyses using the version 0.9.12-4.2 of the Bayes Factor package in R
 125 and using the default parameter values for JASP 0.11.1. We used the classification by Lee and
 126 Wagenmakers (2013) to interpret Bayes factor (BF). We conducted frequentist analyses using the
 127 stats package in R and JASP 0.11.1.

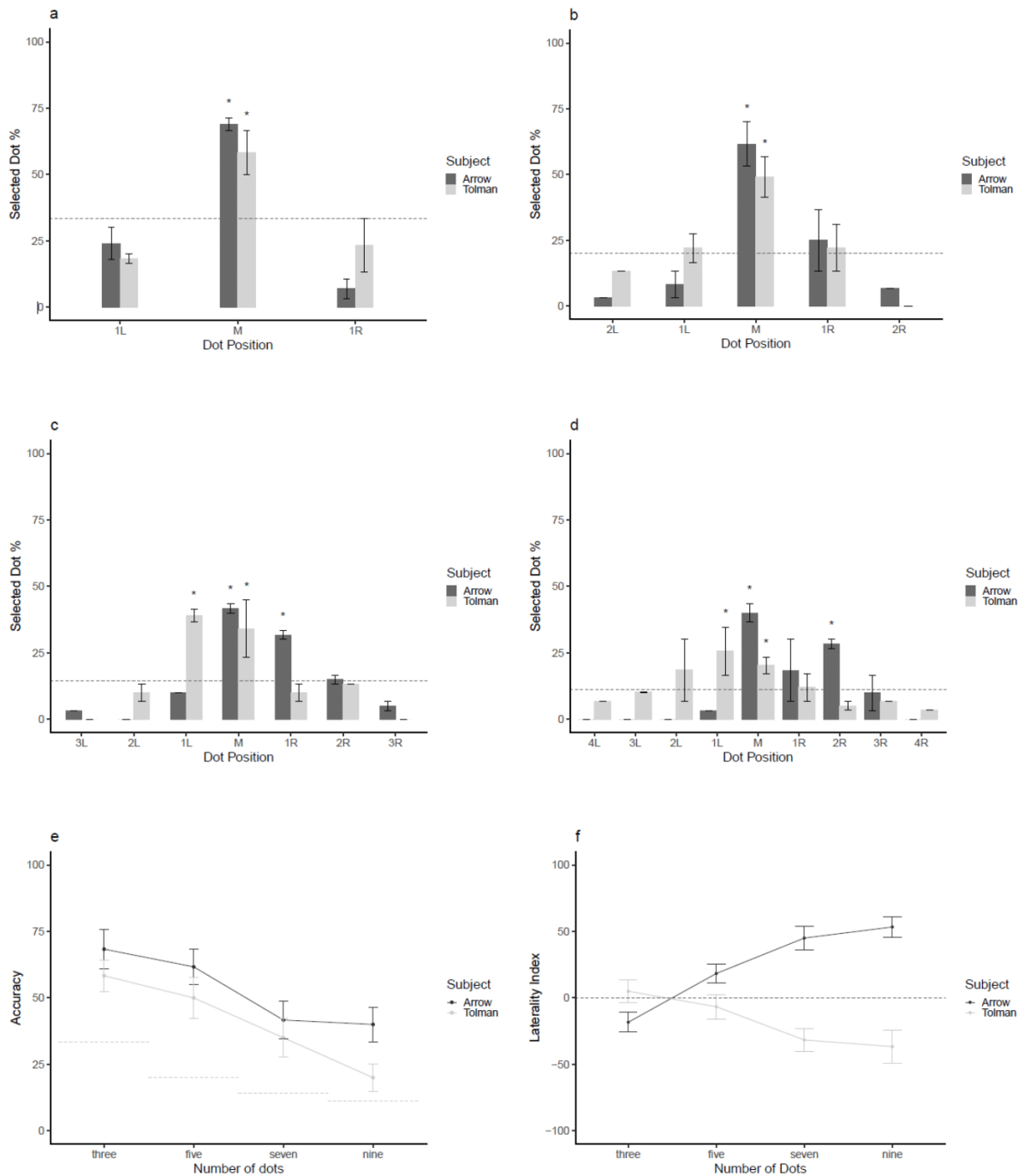
128 Number Transfer Test. Performance did not differ on close and far trials (all $p > .05$ and BF
 129 values rangin from 0.216 to 1.731, see supplementary materials), leading us to merge trial types for
 130 subsequent analyses. Bayes factor analyses revealed that both monkeys transferred the middle
 131 concept from the 3-item sequence to the novel numerical sequences with above chance
 132 expectations, see **Table 1, Figures 2a, 2b, 2c and 2d.**

Monkey	Number of dots	Number of success	Number of trials	p	Cohen's h	BF
Arrow	Three	40	58	<.001	.729	>100
	Five	37	60	<.001	.879	>100
	Seven	25	60	<.001	.628	>100
	Nine	24	60	<.001	.690	>100
Tolman	Three	35	60	<.001	.508	>100
	Five	29	59	<.001	.627	>100
	Seven	20	59	<.001	.468	>100
	Nine	12	59	<.05	.256	2.839

133

134 **Table 1.** Data and results concerning the selection of the middle dot for each sequences
 135 composed of 3, 5, 7 or 9 dots for each monkey, in the Number Transfer Test. Both monkeys
 136 transferred the middle rule to longer sequences.
 137

138 To test whether monkeys' accuracy decreased with magnitude we compared accuracy across
139 trials of different numerical lengths. Bayes Factor analyses revealed strong evidence in favor of a
140 magnitude effect for both monkeys. As shown in **Figure 2e**, accuracy diminished as the number of
141 items increased: Arrow: $\chi^2(3) = 11.817$, $p = 0.008$, $\varepsilon^2 = 0.099$; $BF_{10} = 10.299$; Tolman: $\chi^2(3) = 18.013$,
142 $p < 0.001$, $\varepsilon^2 = 0.151$; $BF_{10} = 192.092$; Kruskal-Wallis rank sum test and Bayesian repeated measure
143 Anova. The Bayes factor indicates that the data are 10.299 (for Arrow) and 192.092 times (for
144 Tolman) more likely under the model that includes numerical magnitude as a predictor, compared to
145 the null model.



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Figure 2. Results of the Number Transfer Test. Monkeys primarily selected the middle dot in all sequences (a. 3-items, b. 5-items, c. 7-items, d. 9-items) e. accuracy diminished as the number of items increased. f. **Laterality index.** Both monkeys showed a side effect in function of numerical

150 magnitude: Arrow showed a right bias while Tolman showed a left bias. In all figures, the central
 151 dot represents the mean, the black bars represents the standard errors, the dashed line indicates
 152 chance level.

153
 154

155 We next investigated whether monkeys showed a laterality effect and whether any such
 156 effect interacted with magnitude. We calculated a laterality index as the percentage of right-sided
 157 choices on the overall number of wrong choices. A laterality index of 100 would indicate that all
 158 wrong choices were to the right of the middle whereas a laterality index of -100 would indicate that
 159 all wrong choices were to the left. A laterality index of 0 would indicate that incorrect choices were
 160 equally likely on the left and right. **Figure 2f** shows that both monkeys exhibited a laterality bias
 161 that increased with the sequence length. Arrow was more likely to make rightward errors
 162 ($\chi^2(3)=37.169$, $p<0.001$, $\varepsilon^2=0.312$; $BF_{10}>100$), whereas Tolman was more likely to make leftward
 163 errors ($\chi^2(3) =13.047$, $p=0.004$, $\varepsilon^2=0.11$; $BF_{10}=8.568$) as the number of dots increased.

164 Asymmetrical Test. Performance did not differ for leftward and rightward asymmetric arrays
 165 for either monkey as indicated by the null evidence provided by the Bayes Factor (Arrow:
 166 $\chi^2(8)=7.915$, $p=0.442$, $\phi=0.297$; $BF_{10}=0.038$; Tolman: $\chi^2(8)=8.451$, $p=0.395$, $\phi=0.306$;
 167 $BF_{10}=0.313$; Pearson's chi squared test and Bayesian contingency tables; **Figure S2** in the
 168 Supplementary material depicts the distribution of the responses). One-tailed exact binomial tests
 169 was used to establish if the spatial middle and numerical middle items were selected with above
 170 chance expectations on each trial type. Monkeys selected the numerical middle, but not the spatial
 171 middle, with above chance expectation. Bayes factor analysis yielded extreme and strong evidence
 172 in favor of numerical middle identification, respectively for Arrow and Tolman, and null evidence
 173 for spatial identification (Arrow, numerical middle: number of successes=20, number of trials=72,
 174 $p<0.001$, Cohen's $h=0.434$; $BF_{10}>100$; spatial middle: number of successes=1, number of trials=72,
 175 $p=0.999$, Cohen's $h=-0.440$; $BF_{10}=0.015$; Tolman, numerical middle: number of successes=17,
 176 number of trials=72, $p<0.001$, Cohen's $h=0.339$; $BF_{10}=13.63$; spatial middle number of
 177 successes=6, number of trials=72, $p=0.817$, Cohen's $h=-0.090$; $BF_{10}=0.036$; Exact binomial test and

178 Bayesian binomial test). Both monkeys showed a strong evidence for the selection of the numerical
179 middle over the spatial middle item on each trial type (Arrow, numerical middle: Mean=27.778,
180 SE=4.648; spatial middle: Mean=1.388, SE=1.388; $W=21$, $p=0.017$, $r=1$; $BF_{10}=28.505$; Tolman,
181 numerical middle: Mean=23.612, SE=1.388; spatial middle: Mean=8.333, SE=3.044; $W=21$,
182 $p=0.017$, $r=1$; $BF_{10}=25.623$; Paired Wilcoxon test and Bayesian Wilcoxon signed-rank test).

183

184

185 **4. Discussion**

186 A plethora of experimental research demonstrates animal numerical competence [3–5].
187 Here, we investigated whether rhesus monkeys spontaneously extract a numerical “middle” concept
188 when they are trained to identify the numerical and spatial middle of a sequence of 3 discrete items.
189 Monkeys preferentially chose the middle item in novel sequences of 3, 5, 7, and 9 items. Monkeys
190 further showed a magnitude effect, with accuracy that decreased as the number of items increased.
191 Although number and space were confounded in our first transfer test to novel numerical values, we
192 dissociated the two with an asymmetric transfer test. We presented monkeys with asymmetrical
193 sequences where the numerical middle item was either on the left or on the right side with respect to
194 the spatial center. Monkeys preferentially chose the numerical middle and ignored the spatial
195 center, providing strong support that they spontaneously encoded the numerical middle concept.

196 In prior research using a manual line bisection task, symbolic and nonsymbolic number has
197 been shown to bias bisection even though the numerical exposure was task irrelevant [20,21]. In
198 those studies adults, young school children, and preschool children were instructed to indicate the
199 midpoint of a horizontal line that was flanked by two arrays of dots of unequal values. Non-
200 symbolic numerical displays systematically biased localization of the midpoint, toward the display
201 depicting the larger magnitude, at all ages. Numerical information was thus automatically extracted
202 from visual arrays of dots, even though number was irrelevant. That phenomenon testifies to the
203 close relationship between spatial and numerical representations [21]. In our task, even though

204 monkeys could have exploited spatial cues to learn the training task, they relied on numerical but
205 not spatial cues when faced with a transfer test in which they could have used either. Our findings
206 are consistent with a previous study with chicks in which numerical and spatial information were
207 redundant during training and dissociated at test. In that study, day-old chicks learned to peck the
208 4th container in a series of 10 identical ones. When, at test, they faced a smaller number of
209 containers, five, and a conflict between ordinal and spatial cue, chicks selected only the numerically
210 correct container [22]. Numerical information appears to be very salient for animals and
211 automatically processed even in circumstances in which other cues could drive behavior.

212 Dehaene et al (1993) first demonstrated the SNARC (spatial numerical association of
213 response code) effect providing strong empirical evidence that humans represent numbers on a
214 mental number line, usually oriented from left to right [23]. Subsequent work with pre-linguistic
215 children, infants, newborns and non-human animals suggests that spatial representation of number
216 emerges early in human ontogeny and it is shared by different species [24–27].

217 We found that the numerosity of a sequence affected middle identification biasing errors.
218 One monkey's errors became increasingly right biased and the other monkey's errors became
219 increasingly left-biased with sequence length. This was consistent with the distribution of choices,
220 which was characterized by significant errors to the right of middle for Arrow and to the left of
221 middle for Tolman. This lateral bias was not evident on the Asymmetrical Test, possibly because of
222 the unbalanced displacement of the items in the series. The two monkeys may have anchored to the
223 left and right and scanned the environment from either side. This finding suggests that the mapping
224 of number onto space may be more flexible in monkeys than humans and show strong individual
225 differences. This pattern of results is consistent with recent evidence in adult gorillas, orangutans
226 and birds [28,29]. Despite variability in the individual directionality of the SNA, its presence in
227 most subjects suggests that mapping number onto space may be a widespread cognitive strategy.
228 Idiosyncratic experiences may influence the individual orientation of the spatial numerical
229 association.

230 The present study provides strong evidence that supports our previous finding that monkeys
 231 can identify the middle in a sequences of discrete items and extends the findings in two important
 232 ways [14]. First we show that monkeys transfer a middle rule learned with a small set of discrete
 233 items to a larger set of discrete items. Second we demonstrate that despite having learned the
 234 middle rule with sequences for which spatial and numerical cues were confounded, monkeys
 235 abstracted numerical information only. Middle identification should thus be considered part of the
 236 suite of quantitative abilities supported by the approximate number system.

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References

- 240 1. Brannon EM, Terrace, H. S. 1998 Ordering of the numerosities 1 to 9 by monkeys. *Science* **282**,
 241 746–749. (doi:10.1126/science.282.5389.746)
- 242 2. Scarf D, Hayne H, Colombo M. 2011 Pigeons on Par with Primates in Numerical Competence.
 243 *Science* **334**, 1664–1664. (doi:10.1126/science.1213357)
- 244 3. Beran MJ. 2001 Summation and numerosness judgments of sequentially presented sets of
 245 items by chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* **115**, 181–191. (doi:10.1037/0735-
 246 7036.115.2.181)
- 247 4. Cantlon JF, Brannon EM. 2007 Basic Math in Monkeys and College Students. *PLoS Biol.* **5**,
 248 e328. (doi:10.1371/journal.pbio.0050328)
- 249 5. Rugani R, Fontanari L, Simoni E, Regolin L, Vallortigara G. 2009 Arithmetic in newborn
 250 chicks. *Proc. R. Soc. B Biol. Sci.* **276**, 2451–2460. (doi:10.1098/rspb.2009.0044)
- 251 6. Rumbaugh DM, Savage-Rumbaugh S, Hegel MT. 1987 Summation in the chimpanzee (*Pan*
 252 *troglodytes*). *J. Exp. Psychol. Anim. Behav. Process.* **13**, 107–115. (doi:10.1037/0097-
 253 7403.13.2.107)
- 254 7. Drucker CB, Brannon EM. 2014 Rhesus monkeys (*Macaca mulatta*) map number onto space.
 255 *Cognition* **132**, 57–67. (doi:10.1016/j.cognition.2014.03.011)
- 256 8. Potrich D, Rugani R, Sovrano VA, Regolin L, Vallortigara G. 2019 Use of numerical and spatial
 257 information in ordinal counting by zebrafish. *Sci. Rep.* **9**, 18323. (doi:10.1038/s41598-019-
 258 54740-8)
- 259 9. Rugani R, Kelly DM, Szelest I, Regolin L, Vallortigara G. 2010 Is it only humans that count
 260 from left to right? *Biol. Lett.* **6**, 290–292. (doi:10.1098/rsbl.2009.0960)

- 261 10. Rugani R, McCrink K, de Hevia M-D, Vallortigara G, Regolin L. 2016 Ratio abstraction over
 262 discrete magnitudes by newly hatched domestic chicks (*Gallus gallus*). *Sci. Rep.* **6**, 30114.
 263 (doi:10.1038/srep30114)
- 264 11. Cantlon JF. 2012 Math, monkeys, and the developing brain. *Proc. Natl. Acad. Sci.* **109**, 10725–
 265 10732. (doi:10.1073/pnas.1201893109)
- 266 12. Cantlon JF, Brannon EM. 2006 Shared System for Ordering Small and Large Numbers in
 267 Monkeys and Humans. *Psychol. Sci.* **17**, 401–406. (doi:10.1111/j.1467-9280.2006.01719.x)
- 268 13. Meck WH, Church RM. 1983 A mode control model of counting and timing processes. *J. Exp.*
 269 *Psychol. Anim. Behav. Process.* **9**, 320–334. (doi:10.1037/0097-7403.9.3.320)
- 270 14. Rugani R, Platt ML, Chen Z, Brannon EM. 2020 Middle identification for rhesus monkeys is
 271 influenced by number but not extent. *Sci. Rep.* **10**, 17402. (doi:10.1038/s41598-020-74533-8)
- 272 15. Yerkes R.M. 1934 Modes of behavioural adaptation in chimpanzee to mul-tiple choice
 273 problems. *Comp. Psychol. Monogr.* **10**, 268–271.
- 274 16. Spence K. W. 1939 The solution of multiple choice problems by chimpanzees. *Comp. Psychol.*
 275 *Monogr.* , 1–54.
- 276 17. Rohles FH, Devine JV. 1966 Chimpanzee performance on a problem involving the concept of
 277 middleness. *Anim. Behav.* **14**, 159–162. (doi:10.1016/S0003-3472(66)80025-8)
- 278 18. Rohles FH, Devine JV. 1967 Further studies of the middleness concept with the chimpanzee.
 279 *Anim. Behav.* **15**, 107-IN6. (doi:10.1016/S0003-3472(67)80019-8)
- 280 19. Tommasi L, Chiandetti C, Pecchia T, Sovrano VA, Vallortigara G. 2012 From natural geometry
 281 to spatial cognition. *Neurosci. Biobehav. Rev.* **36**, 799–824.
 282 (doi:10.1016/j.neubiorev.2011.12.007)
- 283 20. Fischer MH. 2001 Number processing induces spatial performance biases. *Neurology* **57**, 822–
 284 826. (doi:10.1212/WNL.57.5.822)
- 285 21. de Hevia M-D, Spelke ES. 2009 Spontaneous mapping of number and space in adults and
 286 young children. *Cognition* **110**, 198–207. (doi:10.1016/j.cognition.2008.11.003)
- 287 22. Rugani R, Regolin L, Vallortigara G. 2007 Rudimental numerical competence in 5-day-old
 288 domestic chicks (*Gallus gallus*): Identification of ordinal position. *J. Exp. Psychol. Anim.*
 289 *Behav. Process.* **33**, 21–31. (doi:10.1037/0097-7403.33.1.21)
- 290 23. Dehaene S, Bossini S, Giraux P. 1993 The mental representation of parity and number
 291 magnitude. *J. Exp. Psychol. Gen.* **122**, 371–396. (doi:10.1037/0096-3445.122.3.371)
- 292 24. Adachi I. 2014 Spontaneous Spatial Mapping of Learned Sequence in Chimpanzees: Evidence
 293 for a SNARC-Like Effect. *PLoS ONE* **9**, e90373. (doi:10.1371/journal.pone.0090373)
- 294 25. Drucker CB, Brannon EM. 2014 Rhesus monkeys (*Macaca mulatta*) map number onto space.
 295 *Cognition* **132**, 57–67. (doi:10.1016/j.cognition.2014.03.011)

- 296 26. Rugani R, de Hevia M-D. 2017 Number-space associations without language: Evidence from
 297 preverbal human infants and non-human animal species. *Psychon. Bull. Rev.* **24**, 352–369.
 298 (doi:10.3758/s13423-016-1126-2)
- 299 27. Vallortigara G. 2018 Comparative cognition of number and space: the case of geometry and of
 300 the mental number line. *Philos. Trans. R. Soc. B Biol. Sci.* **373**, 20170120.
 301 (doi:10.1098/rstb.2017.0120)
- 302 28. Gazes RP, Diamond RFL, Hope JM, Caillaud D, Stoinski TS, Hampton RR. 2017 Spatial
 303 representation of magnitude in gorillas and orangutans. *Cognition* **168**, 312–319.
 304 (doi:10.1016/j.cognition.2017.07.010)
- 305 29. Lazareva OF, Gould K, Linert J, Caillaud D, Gazes RP. 2020 Smaller on the left? Flexible
 306 association between space and magnitude in pigeons (*Columba livia*) and blue jays (*Cyanocitta*
 307 *crystata*). *J. Comp. Psychol.* **134**, 71–83. (doi:10.1037/com0000193)

308

309 **Ethics**

310 All procedures reported in this study were approved by the Institutional Animal Care and Use
 311 Committee (IACUC) of the University of Pennsylvania, and performed in accordance with their
 312 relevant guidelines and regulations. The PROTOCOL # 806050 have been also reviewed by the
 313 Institutional Review Board (IRB) using the expedited procedure set forth in 45 CFR 46.110 and
 314 approved on 05-Feb-2019.

315

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320

321 **Author contributions**

322 R.R., E.B. and M.P. developed the study concept and designed the study, R.R. and Z.C. carried out
 323 the experiment and collected all data. R.R. and Z.C. analysed the data. R.R. drafted the manuscript,
 324 and E.B., Z.C. and M.P. provided several critical revisions. All authors approved the final version of
 325 the manuscript and agree to be held accountable for all aspects of the work and ensure that

326 questions related to the accuracy or integrity of any part of the work are appropriately investigated
327 and resolved.

328

329 **Competing interests**

330 The authors declare no competing interests.

331

332 **Data availability**

333 Our datasets Data and codes are stored and backed up on the Research Data Unipd server:

334 URL: <http://researchdata.cab.unipd.it/527/>

335 DOI: 10.25430/researchdata.cab.unipd.it.00000527

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