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Spatial representation of magnitude in gorillas and orangutans

Regina Paxton Gazes

Zoo Atlanta, Atlanta GA

Bucknell University, Lewisburg, PA

Rachel F.L. Diamond

Department of Psychology, Emory University, Atlanta GA

Jasmine M. Hope

Neuroscience Graduate Program, Emory University, Atlanta GA

Damien Caillaud

Dian Fossey Gorilla Fund International, Atlanta GA

Department of Anthropology, University of California Davis, Davis CA

Tara S. Stoinski

Zoo Atlanta, Atlanta GA

Dian Fossey Gorilla Fund International, Atlanta GA

Robert R. Hampton

Department of Psychology, Emory University, Atlanta GA

Yerkes National Primate Research Center, Atlanta GA

24

## Abstract

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Humans mentally represent magnitudes spatially; we respond faster to one side of space when processing small quantities and to the other side of space when processing large quantities. We determined whether spatial representation of magnitude is a fundamental feature of primate cognition by testing for such space-magnitude correspondence in gorillas and orangutans. Subjects picked the larger quantity in a pair of dot arrays in one condition, and the smaller in another. Response latencies to the left and right sides of the screen were compared across the magnitude range. Apes showed evidence of spatial representation of magnitude. While all subjects did not adopt the same orientation, apes showed consistent tendencies for spatial representations within individuals and systematically reversed these orientations in response to reversal of the task instruction. Results suggest that spatial representation of magnitude is phylogenetically ancient and that consistency in the orientation of these representations in humans is likely culturally mediated.

Keywords: Space, SNARC, Ape, Pongo

## 40 **1. Introduction**

41 Behavioral and neurobiological evidence indicates that human adults represent magnitude  
42 dimensions spatially (Dehaene, Bossini, & Giraux, 1993; Fischer, Castel, Dodd, & Pratt, 2003;  
43 Rusconi, Buetti, Walsh, & Butterworth, 2011). For example, picture the numbers one through 10.  
44 If you are like most native English speakers, you pictured them in a horizontal line with one on  
45 the left and 10 on the right. Spatial representation is involved in magnitude processing generally;  
46 it is not confined to processing of number specifically (Holmes & Lourenco, 2011; Walsh,  
47 2003). The orientation of this spatial representation of magnitude varies with culture and task  
48 demands (Bachtold, Baumüller, & Brugger, 1998; Fischer, Shaki, & Cruise, 2009; Shaki &  
49 Petrusic, 2005; Shaki, Petrusic, et al., 2012; van Dijck & Fias, 2011). Across these variations, the  
50 spatial representation of magnitude is evident in that viewing or thinking about small magnitudes  
51 biases visual attention to one area of space while large magnitudes bias attention in the opposite  
52 direction. As a result, English speaking western adults are, in general, quicker to detect cues  
53 presented on the left after being primed with small numbers, and cues presented on the right after  
54 being primed with large numbers (Fischer, et al., 2003). Similarly, when making numerical  
55 judgments, English speakers respond faster to small numbers with a leftward response and large  
56 numbers with a rightward response (Dehaene et al., 1993). These space-magnitude congruency  
57 effects have been most extensively studied using judgments of number (Dehaene et al., 1993),  
58 and are also found for comparisons along other dimensions such as size (Shaki, Petrusic, & Leth-  
59 Steensen, 2012), order (Gevers, Reynvoet, & Fias, 2003), and emotional magnitude (Holmes &  
60 Lourenco, 2011).

61           Orientation of the spatial representation of magnitude varies across cultures, between  
62 individuals, and responds flexibly to experience. It is influenced by both reading and counting

63 such that in contrast to English speakers, Palestinians, who read and count from right to left,  
64 respond faster on average to small numbers with a rightward response and large numbers with a  
65 leftward response (Shaki, Fischer, & Petrusic, 2009; Shaki, Petrusic, et al., 2012). These reliable  
66 group-level differences in orientation of the spatial representation of number are likely caused by  
67 long-term memory representations acquired through cultural experience (van Dijck & Fias,  
68 2011). Nonetheless, the orientation of spatial representation of magnitude is apparently not fixed  
69 by culture, as it can vary between individuals even within a cultural group. While English  
70 speaking adults performing a parity task show consistent, robust group-level left-to-right  
71 representations of number (Wood, Willmes, Nuerk, & Fischer, 2008), the few studies that  
72 present individual data indicate that as few as 56-66% of individual participants show this  
73 orientation (Nuerk, Wood, & Willmes, 2005; Wood, Nuerk, & Willmes, 2006). The remaining  
74 participants either show no clear orientation or the opposite right-to-left orientation. The  
75 orientation of spatial representations also changes in response to language priming, numerical  
76 range, real-world referents, and task instructions (Bachtold, Baumüller, & Brugger, 1998;  
77 Fischer, Shaki, & Cruise, 2009; Shaki & Petrusic, 2005; Shaki, Petrusic, et al., 2012; van Dijck  
78 & Fias, 2011). For example, when asked whether a number is higher or lower than 6, English  
79 speakers show latency differences in opposite directions when referencing numbers on a ruler  
80 (left-to-right) than when referencing numbers on a clock face (right-to-left; Bachtold et al.,  
81 1998). Four is represented on the left as a “small” number when presented with a numerical  
82 range from 4-9, but on the right as a “large” number when presented in a range from 1-5  
83 (Dehaene et al., 1993). Bilingual Russian-Hebrew speakers reverse the orientation of their spatial  
84 representation of number depending on the language used to prime the task (Shaki & Fischer,  
85 2008).

86           Variability and flexibility in the orientation of spatial representations of magnitude are  
87 especially great when humans lack long term memories defining prototypical arrangements in a  
88 domain. For example, adults comparing quantities 1-10 (e.g. select the smaller or larger item;  
89 Shaki, Petrusic, et al., 2012) show group level spatial representations in culturally preferred  
90 directions regardless of task instruction. However, if asked to compare animal sizes (e.g. snail vs.  
91 mouse), English speakers organize their representation with small animals on the left when asked  
92 to identify the smaller animal in the pair, but reverse this orientation when instructed to identify  
93 the larger animal in the pair. The spatial orientation of Arabic speakers also reverses in response  
94 to instructions, but in the opposite direction (Shaki, Petrusic, et al., 2012). Likewise, human  
95 adults judging the smaller or larger quantity in a pair of large, less commonly ordered numerals  
96 (6-50; Lee, Chun, & Cho, 2016) or in a pair of shape arrays (Lee et al., 2016, Patro & Shaki,  
97 2016) show this same reversal in orientation when instructions are reversed. Apparently, in the  
98 absence of the strong norms governing specific orientation of representations, participants  
99 flexibly orient their spatial representations with the to-be-detected magnitude on the preferred  
100 point-of-reference side of space (left for English speakers, right for Arabic speakers; Patro &  
101 Shaki, 2016). Importantly, this systematic reversal in orientation is diagnostic of the presence of  
102 spatial representations- it would not occur if representations did not have spatial properties. Non-  
103 human animals do not have experience or cultural norms to dictate a consistent orientation of  
104 magnitude representation. Therefore if spatial representation of magnitude is a general cognitive  
105 process that exists outside of humans, non-human primates would likely show a similar reversal  
106 in orientation based on task instruction.

107           Recent evidence has suggested that animals as distantly related to humans as chickens  
108 (*Gallus domesticus*), may process magnitudes spatially (Rugani, Vallortigara, Priftis, & Regolin,

109 2015). However, it is probably premature to reach conclusions about the phylogeny of spatial  
110 processing of magnitude with evidence from only humans and chickens, which are separated by  
111 over 300 million years of divergent evolution, show major differences in brain laterality, and are  
112 tested using substantially different methods (Drucker & Brannon, 2014; Harshaw, 2015; Kumar  
113 & Hedges, 1998; Larsson, 2013; Mangalam & Karve, 2015; Rogers, Vallortigara, & Andrew,  
114 2013; Shaki & Fischer, 2015). To determine the extent to which spatial representation is a  
115 fundamental basis for magnitude cognition across primates specifically, we tested for spatial-  
116 magnitude correspondence in two groups of apes: gorillas (*Gorilla gorilla gorilla*) and  
117 orangutans (*Pongo pygmaeus* & *Pongo abelli*) using a task similar to those used in humans.  
118 These species shared a common ancestor with humans approximately 8 and 15 million years ago  
119 respectively (Finstermeier et al., 2013). Non-human primates share many components of human  
120 magnitude processing abilities; they accurately judge differences in quantity, order items by  
121 magnitude, and show performance patterns consistent with human numerical estimation, such as  
122 the symbolic distance effect and conformity to Weber's law (Beran, 2008; Brannon & Terrace,  
123 2002; Cantlon & Brannon, 2006). They additionally show interactions between processing of  
124 space and various magnitudes (time: Merritt, Casasanto, & Brannon, 2010; order: Adachi, 2014;  
125 Drucker & Brannon, 2014; Gazes, Lazareva, Bergene, & Hampton, 2014; social dominance:  
126 Dahl & Adachi, 2014). As in humans, there is neural overlap between numerical and spatial  
127 processing in the intraparietal sulcus of monkeys (Hubbard, Piazza, Pinel, & Dehaene, 2005).

128         Based on work with humans, we designed a task for apes that tests for the presence of a  
129 spatial representation of magnitude but does not make assumptions about the orientation of the  
130 representation. Given the individual variability in orientation shown by human adults (Wood et  
131 al., 2006), and the fact that apes do not have cultural norms to dictate a preferred orientation in

132 spatial representation, there is not sufficient evidence to predict a consistent orientation of  
133 magnitude representation in these species. Apes were presented with a task in which they  
134 selected either the larger or smaller of two quantities of dots (Patro & Haman, 2012). Across  
135 pairs from small (2 versus 3) to large (9 versus 10) quantities, response latencies were compared  
136 for trials in which the correct choice required a leftward or a rightward response. If spatial  
137 representation of magnitude is an evolutionarily ancient foundation of magnitude processing,  
138 apes, like humans, should respond faster to one side of space when processing pairs of small  
139 quantities and faster to the other side of space when processing large quantities. Critically, if  
140 apes represent quantities for which they have no cultural norm similarly to how humans  
141 represent uncommon magnitude domains, we should observe that the orientation of the spatial  
142 representation is reversed between conditions in which the animals are required to pick small and  
143 pick large.

## 144 **2. Method**

### 145 2.1. Subjects and procedure.

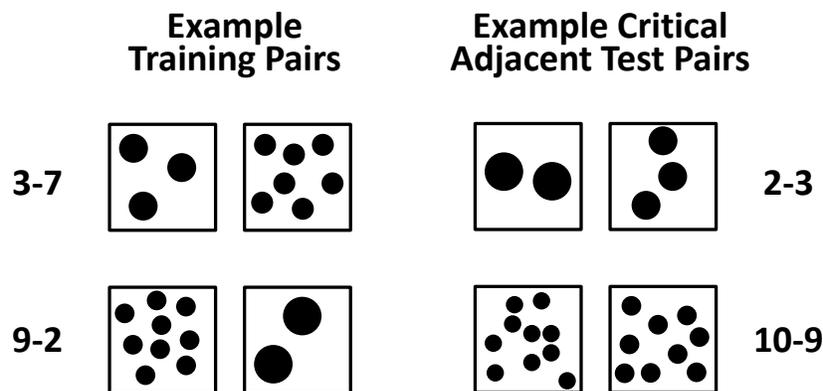
146 Subjects were 9 apes (4 gorillas, 5 orangutans; Table 1) housed at Zoo Atlanta. Subjects were  
147 presented with a quantity comparison task on a touch screen computer affixed to their indoor  
148 housing area. Subjects initiated each trial by touching a green start square in the lower center of  
149 the screen. Two white squares appeared on the left and right sides of the screen, each containing  
150 between two and 10 black dots (Figure 1). Dots were randomly located within the stimulus  
151 borders. The total surface area of the dots presented in each white square was held constant  
152 across stimuli. This resulted in smaller diameter dots and larger overall dot perimeter for the  
153 display the more dots were present in a display. The location of the "small" and "large" stimuli  
154 in a pair was counterbalanced pseudo randomly across trials, such that the lesser quantity of dots

155 appeared on the left and right sides of the screen equally often. Subjects indicated their choice by  
156 touching within the borders of one of the two stimuli. During training, selection of the correct  
157 quantity was reinforced with an auditory reinforcer on 100% of trials, and a food pellet on 80%  
158 of trials. Selection of the incorrect quantity was followed by a negative auditory cue, no food,  
159 and a five-second black-screen time out period.

160 All apes received two conditions presented sequentially— a “pick large” condition, in  
161 which selection of the stimulus with more dots in the pair resulted in reinforcement, and a “pick  
162 small” condition, in which selection of the stimulus with fewer dots resulted in reinforcement.  
163 The order of these two conditions was counterbalanced across subjects (Table 1). Each condition  
164 consisted of a training phase followed by a testing phase. Training sessions contained 102 trials;  
165 6 trials of each of the 17 training pairs. Training pairs consisted of one small magnitude stimulus  
166 (2, 3, or 4) paired with one large magnitude stimulus (5, 6, 7, 8, 9, or 10, excluding pair 4-5;  
167 Figure 1, left; Patro & Haman, 2012). Once subjects performed above 80% correct in 3  
168 consecutive training sessions, they received test sessions containing all remaining possible novel  
169 pairs of quantities two through 10 (Figure 1, right). Test sessions consisted of 104 trials; 5 trials  
170 of each of the 17 training pairs, plus one of each of the 19 novel test pairs. Of these 19 novel test  
171 pairs, the critical pairs for spatial-magnitude congruity analyses were the 8 pairs consisting of  
172 adjacent quantities (2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10). This set of critical test pairs controlled  
173 for the absolute difference between quantities in the pairs, and provided continuous  
174 measurements from low quantity comparisons (pair 2-3) through high quantity (pair 9-10)  
175 comparisons. Training pairs were reinforced as during training, except that 100% of correct trials  
176 were accompanied by a food reinforcer. Consistent with the partial reinforcement experienced  
177 during training, all choices on test pairs were reinforced with an auditory reinforcer only,

178 regardless of whether the response was correct. This non-differential reinforcement prevented  
 179 subjects from learning during the test trials. Subjects received test trials intermixed with training  
 180 trials, until they had made at least one correct response on every numerical test pair in both the  
 181 small on the left and small on the right orientations. After completion of testing in the first  
 182 condition (either pick large or pick small; Table 1), subjects received training and testing in the  
 183 other condition.

184 The number of sessions to reach criterion did not differ between the pick small and pick  
 185 large conditions or between the first and second trained conditions for either training (linear  
 186 mixed model with subject as a random factor: main effect of condition:  $M_{\text{picksmall}} = 8.56 \pm 5.98$   
 187 session,  $M_{\text{picklarge}} = 8.33 \pm 4.24$ ,  $t(7) = 0.17$ ,  $p = .870$ , main effect of training order [first, second]:  
 188  $M_{\text{first}} = 8.56 \pm 4.48$ ,  $M_{\text{second}} = 8.33 \pm 5.81$ ,  $t(7) = -0.17$ ,  $p = .870$ ) or testing (linear mixed model with  
 189 subject as a random factor: main effect of condition:  $M_{\text{picksmall}} = 11.89 \pm 3.76$  session,  $M_{\text{picklarge}} =$   
 190  $13.89 \pm 5.53$ ,  $t(7) = -1.01$ ,  $p = .346$ , main effect of training order:  $M_{\text{first}} = 12.11 \pm 5.04$ ,  $M_{\text{second}} =$   
 191  $13.67 \pm 4.30$ ,  $t(7) = 0.83$ ,  $p = .436$ ).



192  
 193 Fig. 1. Example of stimulus pairs presented during training (left; 3-7 and 9-2) and testing (right;  
 194 2-3 and 10-9). Within a given stimulus quantity all dots were the same size.

195

196 2. 2. Handedness testing.

197 Handedness was measured for each animal using a simple computerized task. Subjects touched a  
198 white dot that appeared randomly in the center and 4 corners of the screen over 150 trials. The  
199 hand used for each touch was recorded, and the proportion of trials in which the subject used the  
200 left hand was calculated (Table 1).

201 2.3. Data analysis.

202 All analyses include only trials from test sessions. Response latencies on novel test trials were  
203 calculated using median latencies on correct trials excluding outliers greater than three standard  
204 deviations above the mean (0.53% of trials excluded). To determine whether apes processed the  
205 magnitude of the stimuli, accuracy and response latencies were analyzed for distance effects and  
206 conformity with Weber's law, both of which are diagnostic of magnitude processing. The  
207 distance effect is indicated by higher accuracy and shorter response latency with increasing  
208 differences between the quantities in the pair. Conformity to Weber's law is indicated by higher  
209 accuracy and shorter response latency with increasing ratios of the larger to the smaller of the  
210 two quantities in the pair. These effects would be expected regardless of whether apes were  
211 relying on dot quantity or dot size to make their choices, as both represent magnitude  
212 dimensions.

213 To test for a spatial representation of magnitude, the difference in response latency  
214 between correct responses made to the right and those made to the left (rightward responses  
215 minus leftward responses) was calculated for each of the eight critical test pairs in which  
216 adjacent quantities were presented (i.e. 2-3, 3-4, 4-5, 5-6, 6-7, 7-8, 8-9, 9-10). For each of the  
217 nine subjects in each of the two conditions simple regression models were fit to estimate  
218 intercepts and slopes of the relationship between the quantity and the latency difference scores

219 (Table 1). Spatial representation of magnitude would be indicated if animals responded faster to  
220 one side of space when processing small quantity test pairs (e.g. 2 vs 3; 3 vs 4) and faster to the  
221 other side of space when processing large quantity test pairs (e.g. 8 vs 9; 9 vs 10), and reverse  
222 this pattern between the pick small and pick large conditions. Unlike humans, apes lack cultural  
223 norms for representing magnitudes in a particular orientation. This lack of culture may lead  
224 individual apes to show different orientations, resulting in an average slope close to 0. However,  
225 if apes reverse the orientation of their representation of magnitude in response to task  
226 instructions, we expect a systematic reversal of individual slopes between the pick small and  
227 pick large conditions. Such a reversal would be evident as a negative correlation between slopes  
228 in the pick small and pick large conditions. We tested for this correlation using Spearman's rank  
229 correlation test.

230         Although apes do not have human-like experience with reading or counting direction,  
231 factors such as species, condition order, or individual hand preferences (Fischer & Brugger,  
232 2011) may determine the orientation of spatial representations. To determine the impact of these  
233 factors on slope orientation we fitted two Linear Mixed Models (LMMs; one for pick small and  
234 one for pick large) to the latency difference scores. These models included the lower quantity in  
235 each adjacent test pair as the independent variable. Species, condition order, and handedness  
236 were added to the models as fixed effect control variables interacting with the lower quantity in  
237 the pair. In addition, the intercept and the slope of the regression lines were allowed to vary  
238 randomly among subjects following normal distributions centered at zero.

239         LMMs were fitted using software R v.3.1.2 (Team, 2014) and R package lme4 (R  
240 package lme4; Bates, Machler, Bolker, & Walker, 2015). The normality of the random effects  
241 and residuals was carefully inspected using normal-quantile plots and Shapiro tests and no

242 deviation to the assumptions of the LMMs was detected. Whether the overall slopes of both  
243 LMM differed significantly from zero was tested with t-tests using the Satterthwaite  
244 approximation of the degrees of freedom (R package lmerTest; Kuznetsova, Brockhoff, &  
245 Christensen, 2015). The 0.05 significance threshold was used in all statistical tests.

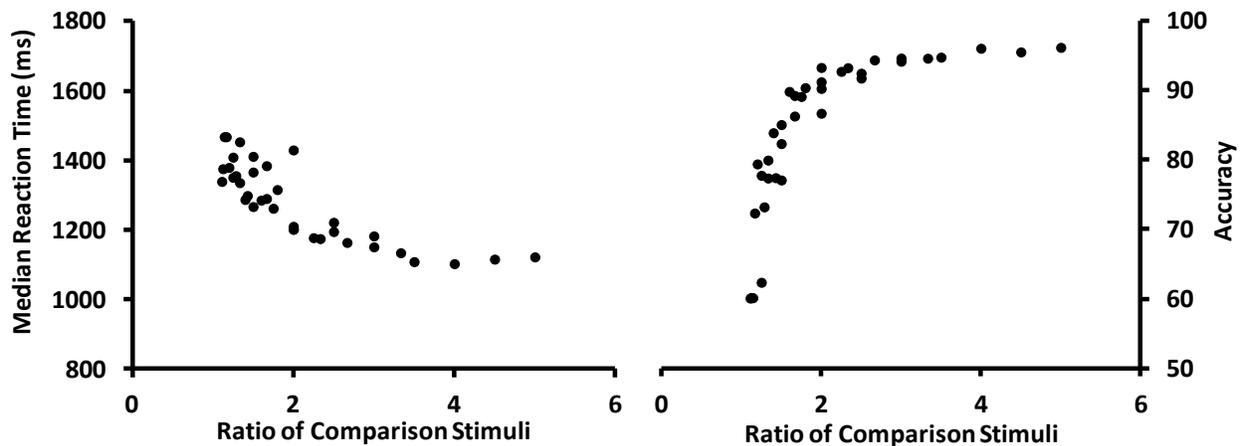
246 The sample size used in this study (9 apes) was planned a priori and corresponded to the  
247 total number of apes available. No subjects were dropped from the study or from the analyses.

### 248 **3. Results**

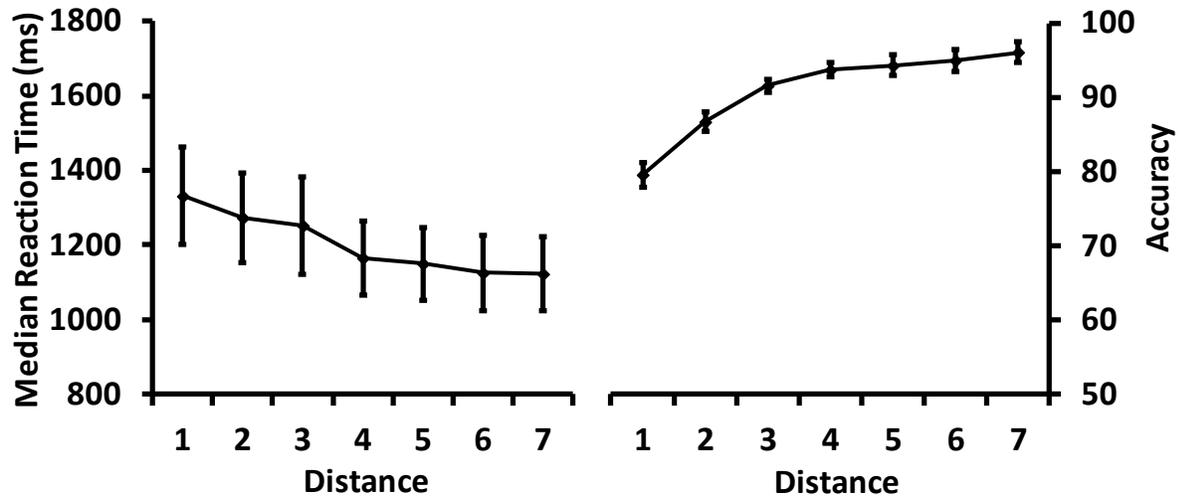
249 **3. 1. Apes engaged in magnitude processing.** Apes performed above chance on novel test trials  
250 (mean for all test pairs combined:  $M = 77.50 \pm 4.30\%$  correct; one sample t-test:  $t(8) = 19.18$ ,  
251  $p < .001$ ), and on the critical subset of test trials with adjacent quantity pairs that were used for the  
252 spatial-magnitude analyses (2 vs 3; 3 vs 4, 9 vs 10, etc.;  $M = 71.01 \pm 4.73\%$  correct; one sample  
253 t-test:  $t(8) = 13.95$ ,  $p < .001$ ).

254 Across all training and test pairs, apes showed performance patterns consistent with  
255 magnitude processing (Cantlon & Brannon, 2006), a prerequisite for spatial-magnitude  
256 correspondence. Performance conformed to Weber's law, with faster response latencies and  
257 higher accuracy associated with larger ratios between comparison quantities (Figure 2;  
258 Spearman's rank correlation: response latency:  $r(34) = -0.86$ ,  $p < .001$ ; accuracy:  $r(34) = 0.97$ ,  
259  $p < .001$ ). The ratios used for these analyses and shown on the x-axis in Figure 2 were calculated  
260 using the number of dots in each stimulus. As expected, the pattern of significance holds when  
261 the ratios are determined using dot diameter as well (Spearman's rank correlation: response  
262 latency:  $r(34) = 0.85$ ,  $p < .001$ ; accuracy:  $r(34) = -0.96$ ,  $p < .001$ ). Additionally, performance was  
263 consistent with the distance effect, with shorter response latencies and higher accuracy  
264 associated with larger distances between quantities in a pair (Figure 3; response latency:

265  $F(7)=27.71, p<.001$ , linear contrasts  $F(1,8)=45.79, p<.001$ ; accuracy:  $F(7)=41.50, p<.001$ , linear  
 266 contrasts  $F(1,8)= 62.82, p<.001$ ). Because low quantities 2, 3, and 4 were either always (pick  
 267 small) or never (pick large) reinforced, a distance effect could result from differences in  
 268 associative strength accrued during training. To determine if this was the case, follow up  
 269 analyses were conducted on pairs from the pick small condition in which the low quantity  
 270 stimulus was 4 (i.e. pairs 4-5, 4-6, 4-7, 4-8, 4-9, 4-10). Quantity 4 was always reinforced in  
 271 training and quantities 5, 6, 7, 8, 9, and 10 were never reinforced in training. The relative  
 272 associative strength of the stimuli was therefore constant across all distances in this subset of test  
 273 pairs. The distance effect held across these pairs (response latency:  $F(5) = 3.84, p=.006$ , linear  
 274 contrasts  $F(1,8) = 4.95, p=.057$ ; accuracy:  $F(5)=8.17, p<.001$ , linear contrasts  $F(1,8) = 11.82,$   
 275  $p=.009$ ), indicating that the distance effect resulted from the ratios of the comparison stimuli, not  
 276 from differences in the reinforcement history of the stimuli.

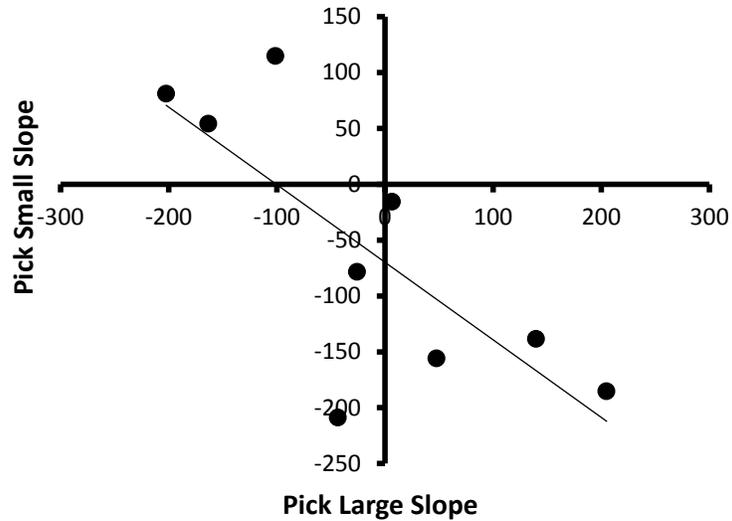


277  
 278 Fig. 2. Median reaction time (*left*) and average accuracy (*right*) by the ratio of the quantity of the  
 279 comparison stimuli in the pair, across all training pairs during test sessions collapsed across pick  
 280 large and pick small conditions.



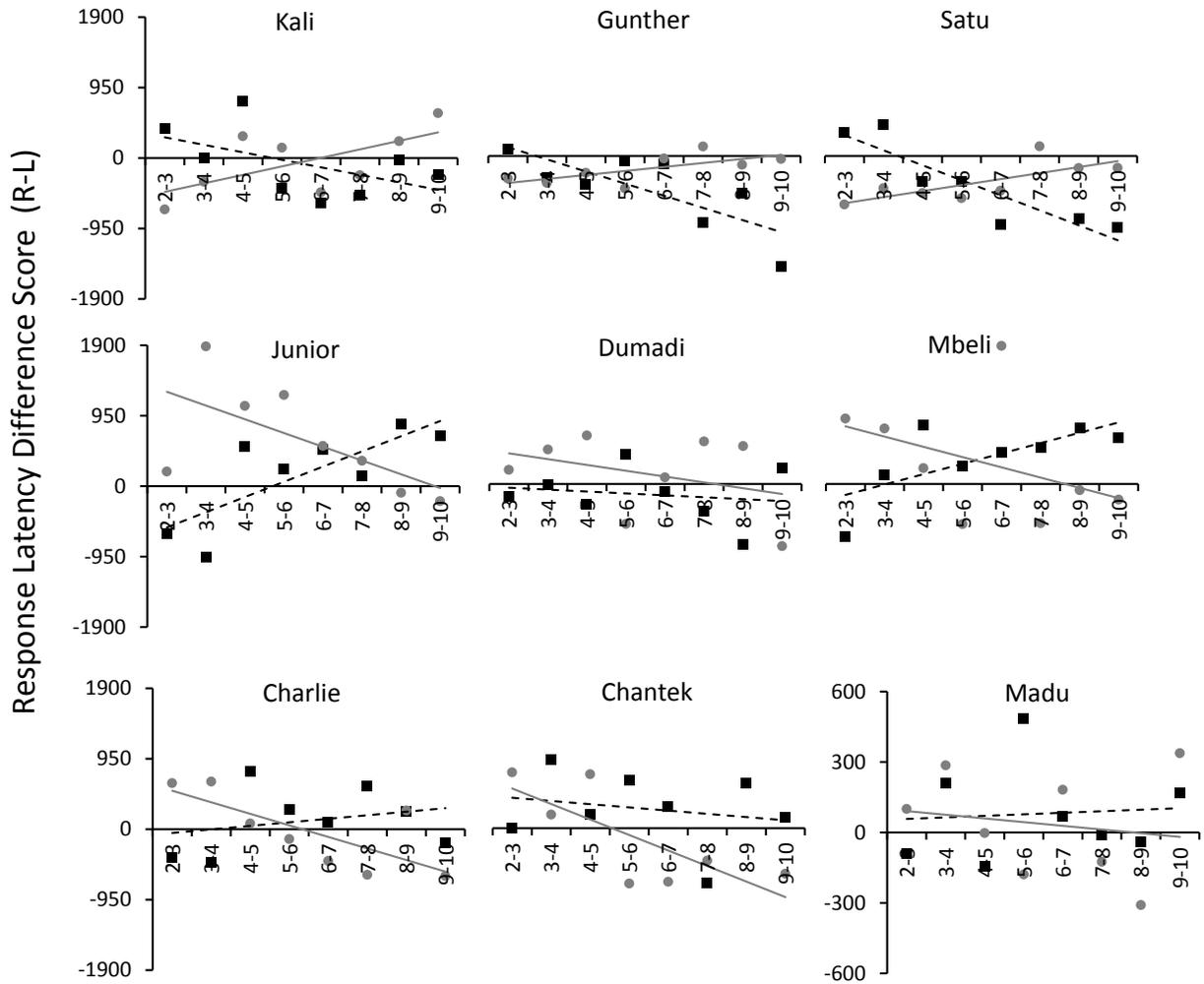
281  
 282 Fig. 3. Median reaction time (*left*) and average accuracy (*right*) in relation to quantity difference  
 283 distance across all training and test pairs collapsed across the pick small and pick large  
 284 conditions.

285  
 286 **3. 2. Task instruction controlled the orientation of spatial representation.** Like humans  
 287 comparing animal sizes and large quantities, apes showed systematic reversal of the orientation  
 288 of their spatial magnitude representation between the pick large and pick small instruction  
 289 conditions. There was a significant negative correlation between individual slopes of the  
 290 response latency regression lines between the pick small and pick large conditions (Figure 4;  
 291 Spearman rank correlation:  $r(7) = -.76, p = .018$ ) such that subjects who showed a right-to-left  
 292 orientation in the pick small condition (Figure 5; positive slope;  $n=5$ ) tended to show a left-to-  
 293 right orientation in the pick large condition (negative slope), and vice versa. The negative  
 294 correlation also indicates stable individual tendencies for spatial representation across conditions;  
 295 animals that showed the strongest spatial representation in one condition also showed the  
 296 strongest spatial representation in the other condition.



297

298 Fig. 4. Negative correlation between spatial-magnitude slopes in the pick small and pick large  
299 condition for the 9 subjects. Animals with strong negative slopes in the pick small condition  
300 tended to show strong positive slopes in the pick large condition (lower right quadrant), while  
301 animals with strong positive slopes in the pick small condition tended to show strong negative  
302 slopes in the pick large condition (upper left quadrant).



303

304

305 Fig. 5. Individual data for the pick small (grey circles) and pick large (black squares) conditions  
 306 across the 8 adjacent test pairs. Response latency difference scores are in milliseconds. Lines  
 307 indicate best fit regression line (pick small: solid grey; pick large: dashed black). Positive slopes  
 308 indicate right-to-left spatial-magnitude orientation, negative slopes indicate left-to-right spatial-  
 309 magnitude orientation. Note: data for Satu pick large 7 vs. 8 and Chantek pick small 8 vs. 9, are  
 310 not shown and were not included in analysis because these data points were outliers ( $> 3$   
 311 standard deviations above the mean).

312

Subject Name	Species	Sex	Age in Years	Proportion Left Handed Responses	First Condition Trained	Pick Large Regression Slope ( <i>p</i> value)	Pick Small Regression Slope ( <i>p</i> value)
Chantek	<i>P.hybrid</i>	M	35	1.0	Pick Large	-43.52 (.616)	-208.95 (.050)*
Charlie	<i>G. gorilla gorilla</i>	M	17	1.0	Pick Small	47.82 (.523)	-155.92 (.034)*
Dumadi	<i>P.abelii</i>	M	6	.28	Pick Large	-25.74 (.689)	-78.38 (.397)
Gunther	<i>G. gorilla gorilla</i>	M	6	.18	Pick Large	-163.26 (.025)*	54.08 (.057)
Junior	<i>P.abelii</i>	M	10	.63	Pick Small	204.96 (.021)*	-185.30 (.094)
Kali	<i>G. gorilla gorilla</i>	M	7	.09	Pick Small	-101.17 (.177)	114.79 (.094)
Madu	<i>P.abelii</i>	F	29	.55	Pick Large	6.55 (.853)	-15.71 (.693)
Mbeli	<i>G. gorilla gorilla</i>	M	10	.97	Pick Large	139.71 (.050)*	-138.49 (.313)
Satu	<i>P.pygmaeus</i>	M	9	.54	Pick Small	-202.32 (.005)*	81.05 (.031)*

313 Table 1. Subject demographics, percent left handed responses on the handedness test, first  
314 condition received, and regression slopes calculated on response latency difference scores  
315 (rightward responses minus leftward responses) across the 8 adjacent test pairs in the pick large  
316 and pick small conditions. \* indicates a slope that differs significantly from 0 ( $p < .05$ ) using an  
317 individual linear regression (7 of 18 possible cases).

318

319 **3. 3. Individual orientations did not differ systematically by species, handedness, or**  
320 **training order.** LMM analysis indicated that apes showed individual variability in orientations  
321 of spatial magnitude congruity (likelihood ratio test of significance of random effects of subject  
322 identity on slopes: pick small:  $X^2(2, N=9) = 6.64, p = 0.022$ ; pick large:  $X^2(2, N=9) = 14.51,$   
323  $p < .001$ ). Therefore, the mean slope across all tested apes was not significantly different from 0  
324 (pick small:  $t(7.94) = -1.40, p = 0.20$ ; pick large:  $t(8.06) = -0.33, p = 0.75$ ). Individual slopes did not  
325 vary systematically by species, handedness, or training order (LMM, t-tests with Satterthwaite  
326 approximation: all  $p > 0.1$ ).

#### 327 **4. Discussion**

328 We found evidence for spatial representation of magnitude in nonhuman apes, suggesting  
329 that use of space to represent other dimensions is phylogenetically ancient. Like humans  
330 processing magnitudes in less familiar domains, apes reversed their orientation of spatial  
331 representation based on instruction, such that they accessed this representation from their  
332 preferred point of reference location in both conditions. Additionally, animals were consistent in  
333 the strength of their representations across conditions, with individual animals tending to show  
334 either strong or weak effects under both pick large and pick small instructions. While apes did  
335 not adopt a single orientation as a group, these results indicate stable tendencies for spatial  
336 representation within individuals.

337 Given the extensive experience most adult humans have with number lines and reading  
338 directions, it is not surprising that group level orientations for small number comparisons tend to  
339 be consistent across task instructions within human cultures (Ginsburg & Gevers, 2015; Lee et  
340 al. 2016; Shaki, Petrusic, et al., 2012). Individual differences in orientation and reversals in  
341 orientation in response to instructions similar to those shown by apes are only seen in humans

342 when participants have no preexisting long term representation organizing the content of the  
343 domain being tested. Like apes, pre-school aged children, who also have limited cultural  
344 experience relative to adults, show variability in spatial orientation across individuals. For  
345 example, while 89% of British preschool children (3-6 years) presented with a line of objects  
346 counted them in a linear order, only 60% of those counted in the culturally typical left-to-right  
347 direction, while 40% counted in the right-to-left direction (Shaki, Fischer, & Gobel, 2012).  
348 Human adults performing a non-numerical quantity discrimination task similar to the one in the  
349 current experiment show instruction based reversal of spatial orientations consistent with that  
350 shown by apes (Patro & Shaki, 2016). This variability indicates that the tendency to organize  
351 information spatially may be a fundamental organizing feature of cognition, but that the  
352 orientation of those representations is impacted by culture and experience.

353         A limitation of our study is that we only tested ape species, and so cannot confidently  
354 draw conclusions outside of great apes. However, evidence from experiments with much more  
355 distantly related chicks (*Gallus domesticus*) may suggest that spatial representation of magnitude  
356 may be more widespread among vertebrates. Three day old chicks have been reported to show a  
357 leftward bias for small numbers and a rightward bias for large numbers (Rugani, et al. 2015).  
358 Chicks trained to find food behind a target displaying 5 dots spontaneously chose the display on  
359 the left when presented with two identical choice stimuli smaller than the target (2 dots) and the  
360 display on the right when presented with choice stimuli larger than the target (8 dots). This may  
361 suggest a phylogenetically ancient predisposition to represent quantity in a left-to-right  
362 orientation. However, concluding that the behavior of chicks in this test is controlled by the same  
363 cognitive processes that result in many humans showing a left to right organization in magnitude  
364 processing may be premature for several reasons. First, the behavioral evidence from chicks

365 indicates considerable inter-individual differences, with more than half the chicks failing to show  
366 the left-to-right orientation (Mangalam & Karve, 2015). Second, avian brains are highly  
367 lateralized compared with primates (Harshaw, 2015; Larsson, 2013; Rogers, Vallortigara, &  
368 Andrew, 2013), and indeed evidence for laterality in nonhuman primates is mixed (Oleksiak,  
369 Postma, van der Ham, Klink, & van Wezel, 2011). Finally, avians and mammals diverged over  
370 300 million years ago (Kumar & Hedges, 1998), so data from more species across this  
371 phylogenetic range are needed before conclusions can be drawn about common origins of  
372 cognitive processes. While Rugani et al. have addressed many of these points (Rugani,  
373 Vallortigara, Priftis, & Regolin, 2015, 2016a, 2016b), it remains possible that the left-to-right  
374 bias seen in humans and chicks may be the result of a convergence in behavior based on distinct  
375 cognitive processes- brain laterality in the chicks and cultural convention in English-speaking  
376 humans. In the present study four of the apes showed orientations of spatial representation in one  
377 direction while three showed orientations in the opposite direction. The remaining two apes show  
378 no clear orientation. These differences in orientation were not explained by species, training  
379 order, or handedness, although it remains possible that these differences could be explained by  
380 other idiosyncratic characteristics including experience with caregivers- these findings,  
381 combined with evidence of flexibility in the spatial orientation of magnitude representation in  
382 humans based on task instruction (Bachtold, Baumuller, & Brugger, 1998; Shaki, Petrusic, &  
383 Leth-Steensen, 2012), culture (Shaki et al., 2012; Zohar-Shai, Tzelgov, Karni, & Rubinsten,  
384 2017), language priming (Shaki & Fischer, 2008), and across individuals (Nuerk et al., 2005;  
385 Wood et al., 2006) suggest that physiological determinants may be of limited importance in  
386 determining the orientation of spatial representation in primates.

387           Because total surface area of the dots was controlled in the present task, total dot  
388 perimeter co-varied positively and dot size co-varied negatively with dot quantity. Previous  
389 findings suggest that non-human primates preferentially rely on quantity information over size or  
390 surface area (Brannon & Terrace, 2000), but it is not possible to determine from our results  
391 whether choices in this task were controlled by quantity, perimeter, or individual dot size.  
392 However, discrimination of quantity, size, and perimeter are all magnitude judgments, and  
393 gorillas and orangutans showed patterns of distance effects consistent with Weber's law and  
394 typical of human performance on magnitude comparison tasks. These performance patterns  
395 indicate that apes were attending to a magnitude dimension of the stimuli, either size, perimeter,  
396 or quantity, and provide additional support for common magnitude representation processes in  
397 human and non-human primates (Beran, 2008; Brannon & Terrace, 2002).

398           The spatial organization of cognition shown by the apes may be a basic organizing  
399 feature of cognition (de Hevia, Girelli, & Cassia, 2012; McCrink & Opfer, 2014; Shaki, Fischer,  
400 et al., 2012; Walsh, 2003). Behavioral congruity between magnitude and space is present from  
401 early in development in humans. Pre-verbal pre-counting infants show interactions between  
402 number and space (de Hevia, Addabbo, Girelli, & Macchi-Cassia, 2014; de Hevia & Spelke,  
403 2010; Lourenco & Longo, 2010), and pre-counting children as young as 4 years of age show  
404 congruity between space and magnitude (Patro & Haman, 2012). Quantities may be represented  
405 topographically in parietal cortex, mimicking representations of space (Harvey, Klein, Petridou,  
406 & Dumoulin, 2013). Additionally, there is overlap in brain areas activated during the processing  
407 of magnitude and space in humans and non-human primates (Cutini, Scarpa, Scatturin,  
408 Dell'Acqua, & Zorzi, 2014; Hubbard et al., 2005), with the horizontal intraparietal sulcus  
409 implicated in both magnitude comparison and spatial attention (Hubbard et al., 2005; Rusconi et

410 al., 2011). The results with apes in the present study combined with evidence from humans  
411 therefore add to a growing literature that suggests that spatial representation of magnitude is a  
412 fundamental characteristic of at least primate minds, and may be much more widespread among  
413 vertebrates.

414

415 Author Contributions.

416 R.P. Gazes developed the study concept and design. R.P. Gazes, J. M. Hope, and R.F.L.  
417 Diamond conducted the experiments and R.P. Gazes and J.M. Hope designed and analyzed the  
418 handedness task. D. Caillaud and R.P.Gazes conducted the statistical analyses. R.P. Gazes  
419 drafted the manuscript. R.P. Gazes, R.F.L. Diamond, R.R. Hampton, and T.S.Stoinski provided  
420 critical revisions of the manuscript and interpretation of findings. All authors approved the final  
421 version of the manuscript for submission.

422

423 Author Note.

424 R.P. Gazes, Zoo Atlanta, now at Bucknell University; R. R. Hampton and R.F.L.  
425 Diamond, Department of Psychology, Emory University and Yerkes National Primate Research  
426 Center; J. Hope, Neuroscience Graduate Program, Emory University; D. Caillaud, Dian Fossey  
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438 Correspondence concerning this article should be addressed to Regina Paxton Gazes,  
439 Bucknell University, Department of Psychology, 1 Dent Drive, Lewisburg PA, 17837. E-mail:  
440 reggie.gazes@bucknell.edu

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