Pigeons on Par with Primates in Numerical Competence

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Counting is a cognitive ability that is unique to humans and is inextricably tied to both language and culture (*1*). However, it has long been thought that our advanced numerical abilities are built on a phylogenetically primitive approximate number system (*2*). Comparative research supports this hypothesis with evidence that taxa from honeybees (*3*) to chimpanzees (*4*) can discriminate stimuli differing in numerosity, that is, the number of elements they contain.

In a landmark study, Brannon and Terrace (*5*) showed that rhesus monkeys could not only discriminate stimuli differing in numerosity but that they could also acquire abstract numerical rules. The monkeys were trained to order stimuli containing one, two, three, or four elements in ascending order. To assess whether the monkeys had learned simple nominal categories or an abstract rule, Brannon and Terrace tested the monkeys with pairs of novel values outside of the training range. The monkeys were able to order the novel pairs, suggesting that they had learned an abstract numerical rule that was not tied to the training numerosities (Fig. 1B). In addition, the monkeys displayed distance effects, with accuracy increasing (Fig. 1C) and response latency decreasing (Fig. 1D) as the numerical distance between the paired items increased. The monkeys' performance was also constrained by Weber's law (*6*); that is, their discrimination performance was dependent on the ratio of the paired items (Fig. 1E). As Brannon and Terrace (*5*) noted, their data suggest that "monkeys represent numerosities 1 to 9 on an ordinal scale."

To identify whether the ability to acquire abstract numerical rules is unique to primates, we trained pigeons with stimuli and procedures comparable to those used by Brannon and Terrace (*5*) with monkeys. Pigeons were trained to order 35 three-item numerical lists (*7*) (Fig. 1A). Each list contained stimuli consisting of one, two, or three elements, and subjects were trained to respond to them in ascending order. Subjects were then tested on pairs of numerosities drawn from the range of one to nine. The pairs were one of three types: familiar-familiar (F-F) pairs contained two numerosities drawn from the training range, familiar-novel (F-N) pairs contained one trained numerosity and one novel numerosity drawn from the values four to nine, and novel-novel (N-N) pairs contained two novel numerosities.

Pigeons performed above chance on the F-F [$t_{(2)} = 7.63$, $P = 0.02$], F-N [$t_{(2)} = 90.33$, $P < 0.0001$], and N-N [$t_{(2)} = 9.19$, $P = 0.01$] pairs (Fig. 1B). Pigeons also displayed a distance effect with accuracy increasing ($r^2 = 0.84$, $P = 0.001$) (Fig. 1C) and response latency decreasing ($r^2 = 0.72$, $P = 0.008$) (Fig. 1D) as the distance between the numerosities of a pair increased. Lastly, consistent with Weber's law, accuracy decreased ($r^2 = 0.79$, $P < 0.001$) (Fig. 1E) as the ratio between the numerosities of a pair approached 1.

Our results demonstrate a correspondence in the way monkeys and pigeons represent numbers and in their ability to acquire an abstract ordinal rule. Although previous studies have compared the representation of number in monkeys and pigeons (*8*), the present study compares their ability to acquire an abstract ordinal rule and apply it to novel numerosities from outside of the training range.

There are two potential explanations for the correspondence between the performance of our pigeons and that of Brannon and Terrace's (*5*) monkeys. One explanation posits that the correspondence is an example of convergent evolution, wherein primates and birds evolved their numerical competence independent of one another. The alternative explanation posits that numerical competence is a homologous trait derived from a common ancestor. Irrespective of its origin, the results of the present experiment add to a growing body of work demonstrating that birds possess a number of abilities that were, at one point in time, considered primate unique, such as episodic memory (*9*) and the use and manufacture of tools (*10*). Indeed, over the past two decades the intellectual status of birds has risen markedly (*11*). Our results suggest that, at least with respect to numerical competence, pigeons are on par with primates and are well perched to inform us about the selection pressures and neural structures required for abstract numerical cognition.

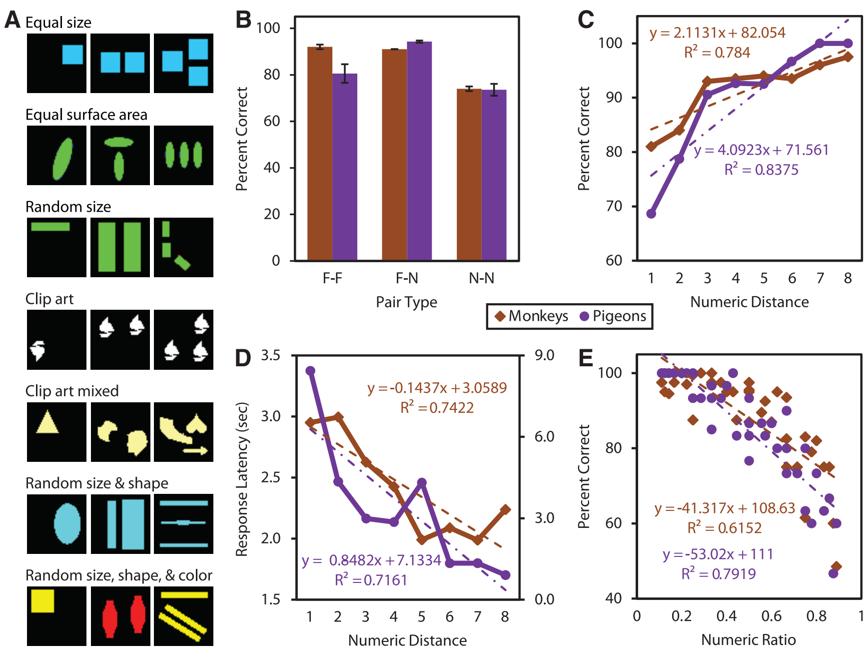

Fig. 1. (**A**) Stimulus sets used in training. (**B**) Performance on the test pairs. Error bars indicate SEM. (**C**) Accuracy as a function of distance. (**D**) Response latency as a function of distance. (**E**) Accuracy as a function of ratio. The dashed lines represent the best-fit linear models. Pigeons (*N* = 3) completed 10 test sessions. The monkey data were redrawn from Brannon and Terrace (*5*).

References and Notes

1. A. Nieder, *Nat. Rev. Neurosci.* **6**, 177 (2005).
2. S. Dehaene, *The Number Sense* (Oxford Univ. Press, New York, 2011).
3. M. Dacke, M. V. Srinivasan, *Anim. Cogn.* **11**, 683 (2008).
4. S. T. Boysen, G. G. Berntson, *J. Comp. Psychol.* **103**, 23 (1989).
5. E. M. Brannon, H. S. Terrace, *Science* **282**, 746 (1998).
6. E. H. Weber, *De Tactu* (Koehler, Leipzig, Germany, 1834).
7. For materials and methods, see supporting material available on *Science* Online.
8. W. A. Roberts, *Learn. Motiv.* **41**, 241 (2010).
9. N. S. Clayton, A. Dickinson, *Nature* **395**, 272 (1998).
10. C. Rutz *et al.*, *Science* **329**, 1523 (2010).
11. N. Clayton, N. Emery, *Curr. Biol.* **15**, R80 (2005).

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Supporting Online Material

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Materials and Methods
References

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