

2015

From Primates to Ants: Reviewing the Evidence of Numerical Cognition in Non-Human Species

Nellie Kamkar
Western University

Follow this and additional works at: <http://ir.lib.uwo.ca/wupj>



Part of the [Psychology Commons](#)

Recommended Citation

Kamkar, N. (2015). From Primates to Ants: Reviewing the Evidence of Numerical Cognition in Non-Human Species. *Western Undergraduate Psychology Journal*, 3 (1). Retrieved from <http://ir.lib.uwo.ca/wupj/vol3/iss1/1>

This Article is brought to you for free and open access by Scholarship@Western. It has been accepted

From Primates to Ants: Reviewing the Evidence of Numerical Cognition in Non-Human Species

Nellie Kamkar*

The degree to which non-human animals can engage in numerical computations has been an area of considerable interest in the study of animal cognition. The present review summarizes previous literature examining numeracy in animals with a notable emphasis on the specific types of numerical computations animals are likely to engage in. Specifically, the present review summarizes literature examining both the Object File System and the Approximate Number System in a variety of non-human species. Conclusions of the existence of animal arithmetic proficiency in comparative psychology are critically analyzed.

Throughout human history, there has been a yearning to determine what aspect of cognition is uniquely human. Mathematics, with its intricate detail and complexity, is perhaps an element of human cognition distinct from other animals (Merritt, DeWind, & Brannon, 2012). The present paper will address this presumption by reviewing several empirical studies of arithmetic proficiency in non-human animals, hereafter animals. The current paper will abide by the following ordinal sequence: first, an analysis of the potential advantages of numerical cognition will be addressed from an evolutionary perspective. Next, a detailed review of empirical studies investigating numeracy in various primate species will follow. Third, evidence of numerical abilities in a variety of non-primate species will briefly be reviewed. Finally, a critical analysis of the above evidence will be addressed with a focus on the limitations of making definitive conclusions of arithmetic proficiency in animals.

The Evolution of Numeracy

Many scholars have attempted to discover the specific point in human history during which the concept of mathematics was first introduced. Historians have estimated that approximately thirty thousand years ago, humans first carved lines on various surfaces to quantify factors

relevant to their daily life (i.e., the passage of time; Cantlon, 2012). Some twenty five thousand years following this, the first symbolic numerals that represent quantity emerged—specifically, Sumerian cuneiform (Cantlon, 2012). This raises the question: what factors necessitated the creation of symbolic numerals? From an evolutionary perspective, it was likely advantageous to quantify an object or event; presumably, many of these advantages had a direct survival function. At the most basic level, it is beneficial to choose a food patch that is quantitatively more densely packed. It may also be the case that association with a larger pack of conspecifics provided protection from predation. In light of these critical survival advantages of the ability to reason with quantities, comparative analyses of the use of number across species is warranted. To begin, a critical analysis of the empirical evidence examining arithmetic proficiency in various primate species—our genetically closest living non-human species—is essential. Note that many terms relevant to the study of numerical cognition are provided in the attached glossary (see Appendix A).

Non-Symbolic Number Processing in Primates

The Object File System in Primates

*Initially submitted for PSY 4290G at Western University. For inquiries regarding the article, please e-mail the author at kamkarnellie2@gmail.com.

PRIMATES TO ANTS

In an interesting study of rhesus macaques, Hauser and Carey (2003) demonstrated the object file system's upper limit of four units. Precisely, 68 rhesus macaques spontaneously observed a screen behind which a numerical exchange of eggplants took place. The researchers manipulated these conditions by presenting the monkeys with either possible (i.e., $2 + 1 = 3$) or impossible (i.e., $2 + 1 = 2$) events and noted the preferential looking time of the animals. Remarkably, they found that the macaques looked *longer* at the *impossible events*. The authors concluded that longer looking times were indicative of the macaques' shock and confusion at these impossible scenarios. This study also found that when the answer to the simple numerical formula was four or greater than four, the rhesus macaques failed at distinguishing between possible and impossible events. Note that these animals were given no prior training and thus, the results of this study are not reflective of prior learning. This paper is illustrative of the upper limit of approximately four objects in rhesus macaques.

A later study of the primate object file system found similar results with one notable exception: the influence of age-related performance (Anderson, Stoinski, Bloomsmith, & Maple, 2007). After presenting orangutans with two different quantities of grapes, it was found that the accuracy of older orangutans in choosing the larger quantity was considerably lower than that of both young and middle-aged orangutans. It appears that primates may have an innate ability to discern between small quantities but that this ability falls within certain limitations and shows a gradual decline with age. To extend this research, further investigations have examined the degree to which primates can give neutral stimuli numerical meaning in similar ways that humans do with monetary transactions.

This was addressed by Addessi, Crescimbene, and Visalberghi (2007) in a study

of ten capuchin monkeys. The researchers found that after training these monkeys on the value of tokens A and tokens B, worth one and three food rewards respectively, *some* of the monkeys were later able to maximize their profit by choosing one B token over two A tokens. Presumably, these monkeys have transferred the values of each token in working memory and later computed basic arithmetic calculations to determine the most advantageous choice. To expand these findings of what is considered addition in primates, an earlier study found similar results of rhesus monkeys seemingly engaging in computational subtraction (Sulkowski & Hauser, 2001). Researchers in this study presented rhesus monkeys with two stages, each including a small number of plums. Next, an occluder was placed in front of each stage and an experimenter would remove one or more plums from either stage and allow the monkey the opportunity to approach either stage. The rhesus monkeys in this study spontaneously approached the occluder with the greater number of plums, presumably to avoid the one from which more plums were subtracted. It is noteworthy that this behaviour was spontaneous, as it occurred in the absence of any human training. However, the performance of the monkeys was limited to computations involving numbers less than three, in contrast to previous studies demonstrating the primate object file system's upper limit of four objects. Overall, it appears as though primates can spontaneously discriminate between small numbers of objects and that some members of certain primate species can compute basic mathematical computations with very small numbers, such as numbers below three or four.

The Approximate Number System in Primates

In addition to studies of the object file system of primates, many researchers have examined the approximate number system in

various primate species. For example, Cantlon and Brannon (2007) found that two female adult rhesus macaques correctly chose an array of dots that corresponds to the additive sum of two previously shown dot arrays. Moreover, an earlier study found that two chimpanzees were able to remember which of two opaque containers had a larger sum of bananas for a delay of up to twenty minutes (Beran & Beran, 2004). Notably, the sums of bananas in each container were considerably large, ranging from 5 to 10 units; therefore, the elicitation of the object file system was unlikely in this study. A later study by Beran (2010) demonstrated that three chimpanzees correctly chose the larger of two liquid quantities that contain juice. This study highlights the ability of primates to discern between continuous quantities that complement previous studies with discrete quantities. Thus far, it appears as though primate species can discern between large quantities—as well as small quantities—with some accuracy. But many of these studies have been criticized for their lack of experimental control on other elements of quantity aside from number alone; these other elements include the size of food rewards. To remedy this, Beran, Evans, and Harris (2008) varied the number, size, contour length, and visibility of various food items and recorded the food choices of four chimpanzees. In accordance with the criticism that animals may be attending to overall size of rewards, rather than number, this study found that the chimpanzees preferentially chose the larger *amount* of food—rather than the number of items alone. This ability to choose the greater total amount of a reward is logically advantageous and likely provides animals with survival benefits. For example, it would be more advantageous to choose one large loaf of bread in favour of several small crumbs of bread.

In contrast to the Beran et al. (2008) findings with chimpanzees, Brannon and Terrace (1998) found that after controlling for size,

surface area, shape, and colour, two rhesus monkeys were able to learn the ordering of one to four neutral stimuli solely on the basis of number. These monkeys were able to transfer their knowledge of the ordinal sequence of the numbers one to four to the sequence of the numbers five to nine in the absence of training. In sum, some primates demonstrate basic numeracy skills with numbers greater than four and these skills may be unrelated to confounding aspects of the stimuli presented and specific to number alone. Thus far, empirical evidence for numeracy in primates has presented stimuli through one fundamental sensory mode: the visual system.

Cross-Modal Representation of Numbers

However, number processing also encompasses cross-modal representations of number (i.e., the ability to determine that three sounds of a bell are numerically equivalent to three objects). A study of twenty male rhesus macaques addressed this concern by presenting the animals with visual stimuli and audio stimuli of their conspecifics that either matched or did not match in numerical value (Jordan, Brannon, Logothetis, & Ghazanfar, 2005). The researchers found that the macaques looked significantly longer at the visual stimuli when the number of visual stimuli matched the number of auditory stimuli. These results were interpreted as evidence that these monkeys recognize the correspondence between auditory and visual modalities of number and that this finding serves as evidence for cross-modal representations of number in primates. The empirical findings summarized thus far have examined numeracy in primates using non-symbolic stimuli—such as dot arrays, food rewards, or images and sounds of conspecifics. Perhaps a more comparable measure of mathematical abilities in humans is to assess the degree to which non-human animals can learn numerical symbols.

Symbolic Number Processing in Primates

In a series of famous studies by Tetsuro Matsuzawa with a female chimpanzee named Ai (and later her son Ayumu), it was found that chimpanzees can order numerical sequences (of Arabic numerals) with greater accuracy and speed than humans (Matsuzawa, 2009). However, it is important to note that the role of working memory in these paradigms is critical. These chimpanzees were able to remember the ordinal sequence of various arbitrary symbolic shapes and to associate this sequence with the attainment of a food reward. This does not necessarily demonstrate numerical abilities in chimpanzees but rather highlights the remarkable working memory of both Ai and Ayumu. The extent to which Ai and Ayumu understood the semantic meaning behind the Arabic numerals that they were ordering remains unknown. A separate study of symbolic number processing in primates may address this concern. Harris, Gullede, Beran, and Washburn (2010) first trained six male rhesus macaques on the Arabic numbers one to nine. After this initial training procedure, the macaques reliably chose the larger of two Arabic numerals presented to them, in exchange for its corresponding food reward. Importantly, the second phase of the experiment presented the macaques with an Arabic numeral (x) and the macaque was required to move a cursor x number of times. If the macaques understood the meaning behind the symbol—they would perform the required behaviour the correct number of times; that is, in accordance with the value of the symbol presented. This is precisely what Harris and colleagues (2010) found: the majority of the macaques performed the required behaviour a number of times that was dictated by the numeric symbol presented to them. Tentatively, it appears as though these monkeys were transferring their knowledge of symbolic numerals to an abstract concept of number. However, their performance was a result of

extensive training and even still, not all macaques were able to complete the task successfully. Subsequent research examining the mapping of Arabic numerals onto abstract concepts of number is warranted. It is important to note that the study of number processing in animals has certainly *not* been limited to primate species. The following section will briefly summarize some interesting research that examine the numerical abilities of non-primate species.

Number Processing in Non-Primate Species

In a study using a preferential looking paradigm with eleven domesticated dogs, West and Young (2002) found that the dogs looked longer at impossible events (i.e., $1 + 1 = 1$) than possible events (i.e., $1 + 1 = 2$). Similar to the study of rhesus macaques by Hauser and Carey (2003), the researchers of this study concluded that the longer looking times are indicative of the dogs' understanding that the event is atypical. Empirical evidence of numeracy is not limited to domesticated dogs. A more complicated paradigm involving comparably larger animals, such as Asian elephants, was conducted a few years later.

A study of Asian elephants found that these animals reliably chose numerically larger food rewards (Irie-Sugimoto, Kobayashi, Sato, & Hasegawa, 2009). The researchers first presented five captive elephants with two bins each varying in the number of food baits. The first portion of the study determined a general tendency to choose the numerically larger food reward. In the second portion of the study, eight captive elephants could not visibly see the food rewards but rather, they could hear the sound of the rewards being dropped in each bin. Surprisingly, the elephants in the second portion of the study also reliably chose the bin with the numerically larger food reward. Presumably, the elephants were mentally adding the dropped baits in each bin and responding on this basis.

What is exceptional about this empirical study is that in both portions of the study, the elephants were *not* constrained by the upper limit of three to four items—which is typically found in the primate object file system.

Xia, Siemann, and Delius (2000) trained nine pigeons in the semantic meaning of the symbolic numerals one to six. After being shown an Arabic numeral, the pigeons were required to subsequently peck the correct number of times in order to obtain a food reward. In a similar study to the study of Asian elephants (Irie-Sugimoto et al., 2009), the majority of the pigeons were able to complete the task with numerals up to five. Four pigeons were even able to complete the task successfully with the numeral six; this is evidence that primates may have an upper limit beyond that of primates (which is typically four items).

An interesting study of numeracy in newborn chicks found that the chicks seemingly engaged in simple addition computations (Rugani, Fontanari, Simoni, Regolin, & Vallortigara, 2009). After briefly rearing the newborn chicks with five objects, the researchers presented them with two occluded screens behind which two to five objects were placed. Next, a series of exchanges between the two occluders took place and following this, the baby chick was given a free choice to approach either occluder. The researchers found that the chicks reliably chose the occluder behind which the larger number of objects was placed. The researchers concluded that this study is demonstrative of an ability of newborn chicks to engage in simple addition in the absence of training.

Number processing has been speculated in extremely small animals as well. In a study examining the navigating tendency of desert ants, Wittlinger, Wehner, and Wolf (2006) found that when stilts were placed on the ants' legs that elongate their strides, they overestimated their travel distance. Likewise, when stumps were

placed on the ants' legs that shortened their strides, they underestimated their travel distance. Presumably, these ants were using a mental *step counter* to determine the distance required to travel.

A study of numerical cognition in 56 horses placed two containers, each holding a different number of artificial apples, in front of the horses (Uller & Lewis, 2009). Each horse selected one of the presented containers by touching its snout on the container. The researchers found that the majority of horses were able to reliably select the container with the numerically larger amount of apples. This study is exceptional because it determined numerical discrimination in horses after controlling for the potential influence of olfactory cues by using artificial food rewards. But the horses, like the rhesus macaques studied by Hauser and Carey (2003), could not correctly discriminate between values greater than or equal to four. Although this study depicts basic numerical processing in horses, there is one infamous account of advanced numerical cognition in a horse named Hans.

Numeracy in a Famous Horse

Clever Hans was a horse in the early twentieth century who could respond correctly to various arithmetic questions by tapping his hoof. It was later found, however, that Clever Hans was not necessarily clever in mathematics but rather, he had a remarkable ability to read subtle behavioural cues of individuals posing the question (Shettleworth, 2013; see Appendix B for a modern day case of what may be the Clever Hans effect). When examining numeracy in animals, a critical analysis of the evidence must be employed to avoid making conclusions such as those made in the past with Clever Hans.

Limitations of Previous Research

Methodological Issues

The first limitation of the literature in animal numeracy concerns the availability of research that does *not* find evidence of numerical abilities in animals. It is likely that because many journals favour significant results, a considerable amount of empirical findings with a null effect are not published. This potential publication bias may subsequently inflate the notion that animals engage in number processing. The second limitation of the above literature concerns the issue of statistical power. Indeed, many of the reviewed findings above have considerably small sample sizes (Cantlon & Brannon, 2007; Matsuzawa, 2009). Within these small sampled groups, many of the above researchers only found a limited number of subjects who *could* perform successfully. For example, in the study of capuchin monkeys choosing between tokens, Addessi et al. (2007) found that less than half of the capuchin monkeys optimized their rewards; it is equally important to note the fact that the majority of the animals could *not* make such mental computations. In addition to the methodological limitations of previous research, there are also critical interpretative issues in the literature.

Interpretive Issues

One chief interpretive issue with the reviewed literature is specifically in regards to studies employing preferential looking paradigms. In some studies, longer looking times are interpreted as an animal noticing an *impossible* event (West & Young, 2002; Hauser & Carey, 2003) and in other studies, longer looking times are interpreted as resultant of an animal noticing *cohesive, possible* outcomes (Jordan et al., 2005). Moreover, many empirical findings of what is presumably numerical ordering are likely a result of advanced reward based pairings. For example, Ai and Ayumu's remarkable ability to order Arabic numerals is likely a result of the chimpanzees' ability to pair the selection of various stimuli with a reward in

a specific ordinal sequence (Matsuzawa, 2009). As noted previously, the role of working memory in both Ai and Ayumu's performance must not be dismissed; recall that they were able to correctly remember the ordinal positions of various arbitrary symbols. Finally, it is possible that the performance of many of the animals in the studies reviewed in this paper were relying on the subtle cues of experimenters who were aware of the correct responses themselves (the Hans effect). However, it is paramount that researchers attend to these remarkable abilities (i.e., working memory, associative learning, identifying subtle behavioural cues). This is simply because these alternative explanations to arithmetic proficiency in animals may prove fruitful in identifying advanced animal skills in a multitude of other cognitive domains.

Concluding Remarks

Overall, empirical studies of animal numeracy are illustrative of the possibility that number processing is *not* a unique cognitive ability in humans. Considering the vast myriad of animals that demonstrate numeracy-like abilities, it is likely that animals have a *rudimentary* number system capable of basic number processing. There are several flaws in extending this conclusion to mean that animals have a number sense similar to human computation of mathematics—particularly on the basis of the above empirical literature. This is simply because many of the empirical findings of numeracy in animals have considerable limitations that warrant the attention of future research in the field.

First Received: 12/06/2014

Final Revision Received: 03/03/2015

References

- Addressi, E., Crescimbene, L., & Visalberghi, E. (2007). Do capuchin monkeys (*cebus apella*) use tokens as symbols? *Proceedings of the Royal Society*, *282*, 2579-2585.
- Anderson, U. S., Stoinski, T. S., Bloomsmith, M. A., & Maple, T. L. (2007). Relative numerosness judgement and summation in young, middle-aged, and older adult orangutans (*pongo pygmaeus abelii* and *pongo pygmaeus pygmaeus*). *Journal of Comparative Psychology*, *121*, 1-11.
- Beran, M. J., & Beran, M. M. (2004). Chimpanzees remember the results of one-by-one addition of food items to sets over extended time periods. *Psychological Science*, *15*, 94-99.
- Beran, M. J., Evans, T. A., & Harris, E. H. (2008). Perception of food amounts by chimpanzees based on the number, size, contour length, and visibility of items. *Animal Behaviour*, *75*, 1793-1802.
- Beran, M. J. (2010). Chimpanzees (*pan troglodytes*) accurately compare poured liquid quantities. *Animal Cognition*, *13*, 641-649.
- Brannon, E., & Terrace, H. S. (1998). Ordering of the numerosities 1 to 9 by monkeys. *Science*, *282*, 746-749.
- Cantlon, J. F., & Brannon, E. M. (2007). Basic math in monkeys and college students. *PLoS Biology*, *5*, 2912-2919.
- Cantlon, J. F. (2012). Math, monkeys, and the developing brain. *Proceedings of the National Academy of Sciences*, *109*, 10725-10732.
- Harris, E. H., Gulledege, J. P., Beran, M. J., & Washburn, D. A. (2010). What do Arabic numerals mean to macaques (*macaca mulatta*)? *Journal of Experimental Psychology*, *36*, 66-76.
- Hauser, M. D., & Carey, S. (2003). Spontaneous representations of small numbers of objects by rhesus macaques: Examinations of context and format. *Cognitive Psychology*, *47*, 367-401.
- Ho, E. [EricHo]. (2007, July, 3). *Maggie-math-dog* [video file]. Retrieved from https://www.youtube.com/watch?v=_DeoUax2da8
- Irie-Sugimoto, N., Kobayashi, T., Sato, T., & Hasegawa, T. (2009). Relative quantity judgement by Asian elephants (*elephas maximus*). *Animal Cognition*, *12*, 193-199.
- Jordan, K. E., Brannon, E. M., Logothetis, N. K., & Ghazanfar, A. A. (2005). Monkeys match the number of voices they hear to the number of faces they see. *Current Biology*, *15*, 1034-1038.
- Matsuzawa, T. (2009). Symbolic representation of number in chimpanzees. *Current Opinion in Neurobiology*, *19*, 92-98.
- Merritt, D. J., DeWind, N. K., & Brannon, E. M. (2012). Chapter 24. In *Comparative Cognition of Number Representation* (pp. 452-476).
- Rugani, R., Fontanari, L., Simoni, E., Regolin, L., & Vallortigara, G. (2009). Arithmetic in newborn chicks. *Proceedings of the Royal Society*, *282*, 2451-2460.
- Shettleworth, S. J. (2013). *Fundamentals of comparative cognition*. Bloom, P., & Nadel, L. (Eds.). New York, NY: Oxford University Press, Inc.
- Sulkowski, G. M., & Hauser, M. D. (2001). Can rhesus monkeys spontaneously

PRIMATES TO ANTS

- subtract? *Cognition*, 79, 239-262.
- Uller, C., & Lewis, J. (2009). Horses (equus coballus) select the greater of two quantities in small numerical contrasts. *Animal Cognition*, 12, 733-738.
- West, R. E., & Young, R. J. (2002). Do domestic dogs show any evidence of being able to count? *Animal Cognition*, 5, 183-186.
- Wittlinger, M., Wehner, R., & Wolf, H. (2006). The ant odometer: Stepping on stilts and stumps. *Science*, 312, 1965-1967.
- Xia, L., Siemann, M., & Delius, J. D. (2000). Matching of numerical symbols with number of responses by pigeons. *Animal Cognition*, 3, 35-43.

PRIMATES TO ANTS

Appendix A

Glossary of Key Terms

Approximate Number System: a system of numerical cognition that can determine *approximations* of numerical quantity of large stimuli. The approximate number system, however, is not without constraints: it is limited by Weber's Law. Weber's Law asserts that the objective ratio of difference between two quantities is predictive of quantity discrimination (Cantlon, 2012). In simpler terms, it is considerably easier to discriminate between 10 stimuli and 11 stimuli than it is to discriminate between 99 and 100 stimuli. Notice that in both of the above examples the difference between the two values is equivalent (a difference of 1 value), but it is the ratio of this difference that determines one's discriminative ability. With increasingly large quantities, discriminative abilities of numerical stimuli are progressively less precise and response accuracy is in accordance with Weber's law.

Object File System: numerical cognition that can *precisely* determine quantity but importantly, this system is limited to processing a maximum of three to four objects (Merritt et al., 2012). Responses to non-symbolic numerical tasks—such as asking an individual to discriminate between two screens with varying numbers of dots on each screen—are precise insofar as the values are small (below four).

The Hans Effect: the tendency of animals to respond to subtle behavioural cues (including facial and bodily cues) of individuals who are aware of the correct response. Thus, responses to arithmetic questions cannot be attributed to arithmetic proficiency but rather, high sensitivity to human behavioural cues (Shettleworth, 2013).

Two Types of Number Processing: In the study of numerical cognition, the processing of quantities is subdivided into two distinct categories: *the object file system* and *the approximate number system* (Merritt et al., 2012).

PRIMATES TO ANTS

Appendix B

A Modern Day Clever Hans

In popular media, a domesticated dog by the name of Maggie has appeared on various talent shows for her ability to make simple arithmetic computations. Similar to Clever Hans, after being asked a simple arithmetic problem, Maggie taps her foot the correct number of times in virtually all trials. Notably, her owner is present in all instances during which she is tested and it is apparent that Maggie looks at her owner when formulating her answers. It is rather comical to see the shock and amazement of audience members and popular celebrity judges at what appears to be mathematical calculations in a domesticated dog. A video depicting this scenario can be accessed by visiting the following source: Ho, E. [EricHo]. (2007, July, 3). *Maggie-math-dog* [video file]. Retrieved from https://www.youtube.com/watch?v=_DeoUax2da8 or by typing the words “dog math” in the browser of www.youtube.com.