



Published in final edited form as:

Curr Opin Neurobiol. 2006 April ; 16(2): 222–229.

The representation of numerical magnitude

Elizabeth M Brannon

Box 90999, LSRC, Duke University, Durham, NC 27708, USA

Abstract

The combined efforts of many fields are advancing our understanding of how number is represented. Researchers studying numerical reasoning in adult humans, developing humans and non-human animals are using a suite of behavioral and neurobiological methods to uncover similarities and differences in how each population enumerates and compares quantities to identify the neural substrates of numerical cognition. An important picture emerging from this research is that adult humans share with non-human animals a system for representing number as language-independent mental magnitudes and that this system emerges early in development.

Introduction

Adult humans use numbers to label, rank order, quantify and measure almost every aspect of the world. Modern number systems enable us to calculate the velocity of an airplane, solve a differential equation or calculate a 20% tip on a restaurant bill. Although our cultural conventions enable us to use numbers to measure and symbolically represent continuous dimensions such as weight or length, humans also possess a universal system for using continuous mental magnitudes to represent number [1,2]. The goal of this paper is to describe the behavioral and neurobiological evidence that humans possess a system for representing number that does not rely on language and to demonstrate that this system is evolutionarily ancient and in place early in development.

The format of nonverbal numerical representations

Number is a property of sets of discrete entities; we cannot refer to the number of water or dirt. Nevertheless, when number is represented without number words the format of the representation is continuous, not discrete. The main evidence for this idea is that Weber's law applies to nonverbal number discriminations in a similar way to which it characterizes the discrimination of line length, brightness, or any other continuous dimension [3,4]. Weber's law states that the change in stimulus intensity needed for an organism to detect a change is a constant proportion of the original stimulus intensity rather than a constant amount. For example, if an increment of 2 pounds is needed to detect a change in a 10 pound weight, then an increment of 4 pounds would be needed to detect a change in a 20 pound weight. The same holds true for nonverbal number discrimination. For example, Moyer and Landauer [5] first showed that when adults are required to compare the relative magnitudes represented by two Arabic numerals, their reaction time (RT) is systematically influenced by both the linear distance and the absolute magnitude of the values compared. In other words, RT decreases with increasing numerical distance between two values (e.g., people are faster at 2 versus 9 than 2 versus 5), and if distance is held constant, RT increases with numerical magnitude (e.g., people are faster at 2 versus 3 than 4 versus 5). Thus, although number can be represented with

Corresponding author: Brannon, Elizabeth M (brannon@duke.edu).

This review comes from a themed issue on Cognitive neuroscience

Edited by Paul W Glimcher and Nancy Kanwisher

arbitrary symbols (e.g. '2' or 'two'), a nonverbal representation with an analog format underlies these symbols [6–10].

These numerical distance and magnitude effects have been replicated in many different languages and numerical notations [6–10]. Additional evidence that analog magnitude representations of number are language independent and, in fact, universal comes from recent studies of two indigenous Brazilian cultures with languages that contain few number words. The Piraha have words for 'one' and 'two' but refer to all larger quantities with a single term for 'many'. When asked to construct sets of nuts or batteries that matched an example set in number, Piraha participants were flawlessly able to construct sets of one or two objects but their precision decreased with set size [11]. Similarly, the Mundurucu language contains only number words for the values 1–5 and no verbal algorithm for counting. Yet when Mundurucu participants compared the relative magnitude of large numbers of dots (20–80) that were carefully controlled for surface area, perimeter and density, their performance was quite similar to that of French-speaking control participants [2•]. In both groups, accuracy increased as the ratio between the two values (larger: smaller number) increased (Figure 1). Thus, without language for number, adult humans possess magnitude representations of number that obey Weber's Law.

Animal–human parallels

No non-human animal can project the national debt in the year 2021 or balance a checkbook; however, research over the past 100 years has demonstrated that animals can represent the purely numerical attributes of the world around them. Early views on animal numerical ability focused on the idea that number is an unnatural artificial dimension that can be represented by animals only under conditions of extensive training [12]. However, more recent research suggests that many animals attend to the numerical attributes of their world spontaneously and automatically (e.g. [13–16,17•]). This is nicely illustrated by demonstrations that ratio-dependent number discrimination can be found in tamarin monkeys without training in numerical tasks [16] and that experimentally naïve rhesus macaques show a ratio-dependent ability to compute addition operations over large sets [17•]. For example, Hauser and colleagues [17•] adapted a paradigm that was originally developed by Wynn [18] to study addition and subtraction in human infants, to test experimentally naïve monkeys free-ranging on an island in Puerto Rico. Monkeys saw 4 lemons on a stage and then watched as an experimenter raised an occluder that blocked the lemons from view. The monkeys then saw the experimenter deposit 4 additional lemons onto the occluded stage. The occluder was then removed to reveal a possible outcome of 8 lemons or an impossible outcome of 4 lemons. Monkeys looked significantly longer at the 4 lemon outcome, suggesting that their expectation was violated. No difference in looking time was found when the monkeys were shown a 2 plus 2 operation and tested with an outcome of 4 or 6. This suggests that monkeys track addition operations with large sets but only detect violations in the outcome of addition operations when the ratio between the observed and the expected outcome is favorable.

When animals as diverse as monkeys and rats are tested in the same nonverbal number tasks as adult humans, striking parallels are revealed that suggest humans and nonhuman animals share a common format for representing number that is ratio dependent and obeys Weber's Law. In one study, monkeys and adult humans were tested in the identical numerosity ordering task; on each trial two dot arrays appeared and the monkey or college student was required to choose the smaller numerical value and ignore nonnumerical stimulus features, such as the size of the dots or the density of the arrays. The behavior of monkeys and college students was strikingly similar in this task; for both species accuracy and RT were modulated by the ratio of the two values compared [19] (Figure 2). In another set of studies, rats and humans were required to make a specified number of responses (on a keyboard or lever) on each trial [20,

21]. For both species the mean number of responses increased systematically with the magnitude of the required number and the variability in the number of responses increased linearly with the mean number of responses. These studies demonstrate that although no one would dispute the vast mathematical capacity of the human mind, under the right conditions we can observe an imprecise ratio dependent number system in adult humans that is also present in many nonhuman animal species.

The semantic congruity effect is another signature of analog magnitude comparisons that extends to the numerical domain. Semantic congruity systematically affects RT when humans make any type of ordinal comparison (e.g. which is smaller?). The semantic congruity effect refers to the finding that small values on a continuum, such as number, are more rapidly compared when participants are asked ‘which is smaller?’, whereas large values are more rapidly compared when asked ‘which is larger?’. In other words, adults are faster to compare two numerical values when their overall magnitude is congruent with the verbal phrasing of the question. Although it was originally thought that the semantic congruity effect was specific to comparisons that take place on discrete and symbolic representations [22], a recent study illustrates that rhesus macaques also show a numerical semantic congruity effect [23]. In that study a color cue served in lieu of the verbal questions ‘‘which is smaller?’’ and ‘‘which is larger?’’ Monkeys were trained to choose the smaller of two dot arrays (e.g., Figure 2a) when the screen background was red and the larger of two dot arrays when the screen background was blue. The monkeys, similar to humans, were much faster at choosing the smaller of two small values (red cue) compared with choosing the larger of two small values (blue cue). Conversely, they were much faster at choosing the larger of two large values compared with the smaller of two large values. Thus, the semantic congruity effect cannot be a byproduct of a language-specific comparative process but is instead, more generally, a hallmark of the psychological process for comparing analog representations of magnitude [24,25].

Developmental foundations

More than 25 years of research has revealed that human infants in the first year of life represent number [26,27•]. More recently, Xu and Spelke [28] have demonstrated that infants show the same signature property of ratio-dependent discrimination common to adult humans and animals. The investigators used a visual habituation paradigm, wherein 6-month-old infants were repeatedly shown a series of images with a common number of elements until the infants’ looking time substantially decreased. The babies were then tested with new images with either the same number or a new number of elements. When the displays were composed of eight or 16 dots, the infants spent more time looking at the test images with the new number of elements ([28], see also [29•]). By contrast, when habituated to eight or 12 dots, infants did not notice the 2:3 ratio change. A similar method has shown ratio dependence when babies discriminate sequences of sounds on the basis of number [30,31]. Collectively, these studies suggest that at 6 months of age babies require a 1:2 ratio, but that precision increases with age, such that by 9 months of age infants can discriminate a 2:3 ratio in number [28,30,31].

Infants are also able to perform arithmetic operations on their nonverbal analog representations of number. Wynn’s [18] original study on infants’ arithmetic abilities used the stage and screen experimental design described earlier to investigate whether infants would look longer at an impossible mathematical outcome. Infants as young as 5 months looked longer when they viewed an experimenter act out a $2 - 1 = 2$ event compared with a $2 - 1 = 1$ event. In a recent study, McCrink and Wynn [32•] showed 9-month-old infants $10 - 5 = 5$ or 10, and $5 + 5 = 10$ or 5 events, and found that infants looked longer at the mathematically impossible outcome. These results suggest that infants make computations over analog magnitude representations of number (see also [33•]).

Adult humans, human infants and nonhuman animals also share the ability to appreciate the numerical equivalence between sets from different sensory modalities. Barth, Kanwisher and Spelke [34] demonstrated that the nonverbal representations of number held by adults are independent of the sensory modality in which they are originally perceived. In their study, adults were just as accurate at making relative numerosity judgments for two sequences presented in different sensory modalities as compared with those for two sequences presented in a single modality (see also [33•]). Two recent studies by Jordan and co-workers [15,35] suggest that the number representations held by rhesus monkeys and human babies are also unfettered by sensory modality. A wealth of literature documents that infants preferentially look at a visual stimulus that matches a stimulus perceived in a second sensory modality. Jordan and co-workers showed that rhesus monkeys and 7-month-old infants looked preferentially at videos that contained the number of conspecifics that numerically matched the number of vocalizations that they heard (Figure 3; see also [36,37•]). From this research it appears that nonverbal number representations are not tied to the sensory modality in which they were perceived.

How does the brain represent number as analog magnitudes?

The intraparietal sulcus (IPS) has been implicated as a crucial substrate in adult humans for representing the meaning of number on the basis of cases of brain injury, of developmental abnormalities, and of positron emission tomography (PET), functional magnetic resonance imaging (fMRI) and event-related potential (ERP) studies of normal adult brain function [38].

Patient studies have revealed that damage to the parietal cortex typically results in a form of acalculia that disrupts understanding of the meaning of numbers [39,40,41•]). By contrast, damage to other brain areas can disrupt memorized arithmetic facts but leaves an understanding of number intact [8,38,42]. Functional imaging of the normal brain demonstrates that the IPS is activated by numerical stimuli, regardless of their notation (written word versus Arabic numeral) and irrespective of whether stimuli are presented in the visual or auditory modality [43]. Research by Piazza *et al.* [44•] suggests that the IPS also responds to nonsymbolic numerical stimuli. Using an event-related adaptation paradigm, they found that the blood oxygenation level-dependent (BOLD) signal decreased to repeated presentations of a standard numerosity but that recovery of the BOLD signal was systematically related to the degree to which a deviant value differed from the standard value (Figure 4) (but also see the study by Shuman and Kanwisher [45•]). The same paradigm has recently shown that 4-year-old children and adults show overlapping activations in the IPS in response to number and not shape changes [46•]. A crucial unresolved question is whether the IPS supports all analog magnitude judgments (e.g. size, weight, density, brightness) or whether there is a portion of the IPS that is specifically selective for number [45•,47•,48].

Convergent evidence for the role of the parietal cortex in number representations comes from recent demonstrations that homologous brain regions underlie numerical abilities in humans and macaques. In a series of studies, Nieder and Miller [49,50•] found cells in the prefrontal cortex and the fundus of the IPS of rhesus monkeys that are selective for a given numerosity (Figure 5). Monkeys viewed arrays that contained between one and five elements, and were required to indicate whether a second nonidentical array matched the sample numerosity. Individual neurons showed a maximal firing rate to one numerosity and decreased firing rate as a function of distance from the preferred number [51]. These neurons responded to specific numerical values, regardless of nonnumerical stimulus attributes such as circumference, surface area or density. The tuning curves for number-selective neurons increased in their bandwidth, with increasing number leading to increasing representational overlap with

magnitude. This amazing discovery of number cells in the monkey brain provides a compelling physiological basis for the behavioral magnitude and distance effects.

Conclusions

Collectively, research of brain and behavior is revealing a profound similarity in the way in which non-human animals, human infants and adult humans represent the numerical attributes of the world around them. Infants and animals will never achieve the level of abstract mathematical thinking seen in adult humans; however, the foundations of these mathematical abilities were probably present early in our evolutionary history and can be seen early in human development. Similarly, although adult humans use language to exceed the precision of the analog magnitude system, they nevertheless simultaneously possess a phylogenetically and developmentally conservative system for representing number without language.

The challenges for future research are many: How is number converted into an analog magnitude format? Do single neurons represent both cardinal and ordinal number? Is there a portion of the IPS that is exclusively selective for number? What is the relationship between number representation and the myriad of other functions for which parietal cortex is implicated [52]? Are the brain regions recruited for number representation in adult humans already selective for number in infancy and early childhood? How is language mapped onto preverbal representations of number? In answering these questions, we are sure to uncover the foundations of the human capacity for mathematics and better understand one of the most complex and awe-inspiring aspects of the mature human mind.

Acknowledgements

The author thanks J Cantlon, S Cordes, K Jordan, S Mitroff, and the section editors for helpful comments on earlier drafts of this paper. The author is supported by National Institute for Mental Health (NIMH) RO1 MH066154, National Institute for Child Health and Development (NICHD) RO1 HD49912, National Science Foundation (NSF) ROLE/DLS, NSF CAREER award and a Merck Scholars award.

References

Papers of particular interest, published within the annual period of review, have been highlighted as:

- of special interest
 - of outstanding interest
1. Gelman R, Gallistel CR. Language and the origin of numerical concepts. *Science* 2004;306:441–443. [PubMed: 15486289]
 - 2•. Pica P, Lemer C, Izard V, Dehaene S. Exact and approximate arithmetic in an Amazonian indigene group. *Science* 2004;306:499–503. [PubMed: 15486303]The authors demonstrated that the Mundurucu people of Brazil lack number words for sets over five and yet show ratio-dependent number discrimination for large sets.
 3. Welford AT. The measurement of sensory-motor performance: survey and reappraisal of twelve years' progress. *Ergonomics* 1960;3:189–230.
 4. Stevens SS. Neural events and the psychophysical law. *Science* 1970;170:1043–1050. [PubMed: 5475633]
 5. Moyer RS, Landauer TK. Time required for judgements of numerical inequality. *Nature* 1967;215:1519–1520. [PubMed: 6052760]
 6. Buckley PB, Gillman CB. Comparisons of digit and dot patterns. *J Exp Psychol* 1974;103:1131–1136. [PubMed: 4457588]
 7. Dehaene S. The organization of brain activations in number comparison: event-related potentials and the additive-factors methods. *J Cogn Neurosci* 1996;8:47–68.

8. Dehaene, S. Oxford University Press; 1997. The number sense: how the mind creates mathematics.
9. Hinrichs JV, Yurko DS, Hu J-M. Two-digit number comparison: use of place information. *J Exp Psychol* 1981;7:890–901.
10. Tzeng OJ, Wang WS. The first two R's. The way different languages reduce speech to script affects how visual information is processed in the brain. *Am Sci* 1983;71:238–243. [PubMed: 6881679]
11. Gordon P. Numerical cognition without words: evidence from Amazonia. *Science* 2004;306:496–499. [PubMed: 15319490]
12. Davis H, Pérusse R. Numerical competence in animals –definitional issues, current evidence and a new research agenda. *Behav Brain Sci* 1988;11:561–579.
13. Hauser MD, MacNeilage P, Ware M. Numerical representations in primates. *Proc Natl Acad Sci USA* 1996;93:1514–1517. [PubMed: 8643663]
14. Meck WH, Church RM. A mode control model of counting and timing processes. *J Exp Psychol Anim Behav Process* 1983;9 :320–334. [PubMed: 6886634]
15. Jordan KE, Brannon EM, Logothetis NK, Ghazanfar AA. Monkeys match the number of voices they hear to the number of faces they see. *Curr Biol* 2005;15:1–5. [PubMed: 15649357]
16. Hauser MD, Tsao F, Garcia P, Spelke ES. Evolutionary foundations of number: spontaneous representation of numerical magnitudes by cotton-top tamarins. *Proc R Soc Lond B Biol Sci* 2003;270:1441–1446.
17. Flombaum JI, Junge JA, Hauser MD. Rhesus monkeys spontaneously compute addition operations over large numbers. *Cognition* 2005;97:315–325. [PubMed: 16260264]The authors used the Wynn addition paradigm and demonstrated that experimentally naïve rhesus macaques look longer at impossible compared with possible outcomes of addition operations when the impossible and possible values are large and differ by a ratio of 1: 2 but not when they differ by a ratio of 2: 3
18. Wynn K. Addition and subtraction by human infants. *Nature* 1992;358:749–750. [PubMed: 1508269]
19. Cantlon JF, Brannon EM. Shared system for ordering small and large numbers in monkeys and humans. *Psychol Sci.* (in press)
20. Platt JR, Johnson DM. Localization of position within a homogeneous behavior chain: effects of error contingencies. *Learn Motiv* 1971;2:386–414.
21. Whalen J, Gallistel CR, Gelman R. Non-verbal counting in humans: the psychophysics of number representation. *Psychol Sci* 1999;10:130–137.
22. Banks WP, Flora J. Semantic and perceptual processes in symbolic comparisons. *J Exp Psychol Hum Percept Perform* 1977;3:278–290. [PubMed: 864399]
23. Cantlon JF, Brannon EM. Semantic congruity affects numerical judgments similarly in monkeys and humans. *Proc Natl Acad Sci U S A* 2005;102:16507–16511. [PubMed: 16260752]
24. Holyoak KJ, Mah WA. Cognitive reference points in judgments of symbolic magnitude. *Cognit Psychol* 1982;14:328–352.
25. Petrusic WM, Baranski JV, Kennedy R. Similarity comparisons with remembered and perceived magnitudes: memory psychophysics and fundamental measurement. *Mem Cognit* 1998;26:1041–1055.
26. Wynn K. Psychological foundations of number: numerical competence in human infants. *Trends Cogn Sci* 1998;2 :296–303.
27. Feigenson L, Dehaene S, Spelke E. Core systems of number. *Trends Cogn Sci* 2004;8:307–314. [PubMed: 15242690]This study put forth the evidence that there are two distinct systems for representing number in infancy: an analog magnitude system and an object-file system. The object-file system represents each individual object symbolically, rather than representing the set symbolically. There is a limit on the number of object files available so that this system can only represent up to three or four individuals. In support of this theory, infants and non-human animals have been shown to fail to detect numerical disparities in some circumstances, even when ratios are favorable.
28. Xu F, Spelke ES. Large number discrimination in 6-month-old infants. *Cognition* 2000;74:B1–B11. [PubMed: 10594312]
29. Brannon EM, Abbott S, Lutz D. Number bias for the discrimination of large visual sets in infancy. *Cognition* 2004;93:B59–B68. [PubMed: 15147939]The authors experimentally compared the ability of infants to detect changes in number versus changes in continuous extent. Results

challenged the notion that continuous stimulus variables are more salient than number to preverbal infants.

30. Lipton JS, Spelke ES. Origins of number sense: large-number discrimination in human infants. *Psychol Sci* 2003;14:396–401. [PubMed: 12930467]
31. Lipton J, Spelke ES. Discrimination of large and small numerosities by human infants. *Infancy* 2004;5:271–290.
32. McCrink K, Wynn K. Large-number addition and subtraction by 9-month-old infants. *Psychol Sci* 2004;15:776–781. [PubMed: 15482450] Infants looked longer at impossible compared with possible outcomes of addition and subtraction operations with computer-animated displays of large sets of elements that varied dynamically in size.
33. Barth H, La Mont K, Lipton J, Spelke ES. Abstract number and arithmetic in preschool children. *Proc Natl Acad Sci USA* 2005;102:14116–14121. [PubMed: 16172388] In three experiments, the authors tested the ability of preschool children to compare and add numerosity displays. Children were above chance on problems which they were unable to solve symbolically, and accuracy was ratio dependent. In addition, there was no cost in accuracy for comparing sets presented in different sensory modalities.
34. Barth H, Kanwisher N, Spelke E. The construction of large number representations in adults. *Cognition* 2003;86:201–221. [PubMed: 12485738]
35. Church, RM.; Meck, WH. The numerical attribute of stimuli. In: Roitblat, HL., et al., editors. 4984. *Animal cognition*; Erlbaum: p. 445-464.
36. Jordan KE, Brannon EM. The multisensory representation of number in infancy. *Proc Natl Acad Sci USA*. in press
37. Kobayashi T, Hiraki K, Hasegawa T. Auditory-visual intermodal matching of small numerosities in 6-month-old infants. *Dev Sci* 2005;8:409–419. [PubMed: 16048513] The authors tested infants in a violation of expectancy paradigm, where addition events were followed by numerically impossible or possible outcomes. Infants looked longer at impossible outcomes, even when this required summing across sensory modalities (sounds and sights).
38. Dehaene S, Molko N, Cohen L, Wilson AJ. Arithmetic and the brain. *Curr Opin Neurobiol* 2004;14:218–224. [PubMed: 15082328]
39. Lemer C, Dehaene S, Spelke E, Cohen L. Approximate quantities and exact number words: dissociable systems. *Neuropsychologia* 2003;41:1942–1958. [PubMed: 14572527]
40. Cipolotti L, Butterworth B, Denes G. A specific deficit for numbers in a case of dense acalculia. *Brain* 1991;114:2619–2637. [PubMed: 1782535]
41. Varley RA, Klessinger NJ, Romanowski CA, Siegal M. Agrammatic but numerate. *Proc Natl Acad Sci USA* 2005;102:3519–3524. [PubMed: 15713804] The authors demonstrated a dramatic dissociation between grammatical and mathematical syntax in three aphasic patients with diffuse brain damage to the left perisylvian language area. All three individuals were proficient in mathematical syntax, despite being unable to comprehend analogous syntax in the spoken or written language. For example, although the patients understood the referents of ‘John’, ‘Mary’ and ‘hit’, they were unable to differentiate between the statements ‘Mary hit John’ and ‘John hit Mary’. However, they were unimpaired at solving mathematical operations that were structurally dependent in this same general way – for instance, the difference between 52 – 11 and 11 – 52.
42. Cappelletti M, Butterworth B, Kopelman M. Spared numerical abilities in a case of semantic dementia. *Neuropsychologia* 2001;39:1224–1239. [PubMed: 11527560]
43. Eger E, Sterzer P, Russ MO, Giraud AL, Kleinschmidt A. A supramodal number representation in human intraparietal cortex. *Neuron* 2003;37:719–725. [PubMed: 12597867]
44. Piazza M, Izard V, Pinel P, Le Bihan D, Dehaene S. Tuning curves for approximate numerosity in the human intraparietal sulcus. *Neuron* 2004;44:547–555. [PubMed: 15504333] The authors used an event-related adaptation design and found that after repeated presentation of arrays that had a common number of elements, recovery of the BOLD signal in the IPS was dependent on the degree to which new numerosities differed from the habituated value. The IPS did not respond to deviations in the local shape of the array elements.
45. Shuman M, Kanwisher N. Numerical magnitude in the human parietal lobe; tests of representational generality and domain specificity. *Neuron* 2004;44:557–569. [PubMed: 15504334] In direct conflict

with Piazza *et al.* [46^{*}], this paper challenged the claim that the IPS is selective for numerosities, as well as for symbolic number. The authors found that activity levels in the IPS were no greater during blocks in which number varied compared with when number was held constant.

- 46^{*}. Cantlon J, Brannon EM, Carter EJ, Pelphrey K. Notation-independent number processing in the intraparietal sulcus in adults and young children. *PLOS Biology*. In press. The authors used an event-related fMRI adaptation paradigm similar to that used by Piazza *et al.* [44^{*}] and found that brain regions in and around the left and right IPS responded to non-symbolic numerical stimuli similarly in adults and four-year-old children.
- 47^{*}. Pinel P, Piazza M, Le Bihan D, Dehaene S. Distributed and overlapping cerebral representations of number, size, and luminance during comparative judgments. *Neuron* 2004;41:1–20. [PubMed: 14715127]The authors conducted an fMRI study in which adults were required to compare the numerical size, physical size or luminance of two Arabic numerals or letters. The three conditions yielded activation in partially overlapping regions of the IPS. Numerical distance modulated activation in the bilateral anterior IPS, whereas size distance modulated activation in a more posterior region of the IPS, and luminance distance modulated activation in a very posterior sector of the IPS.
48. Kaufmann L, Koppelstaetter F, Delazer M, Siedentopf C, Rhomberg P, Golaszewski S, Felber S, Ischebeck A. Neural correlates of distance and congruity effects in a numerical Stroop task: an event-related fMRI study. *NeuroImage* 2005;25:888–898. [PubMed: 15808989]The authors conducted an fMRI study with number–size interference tasks. Participants chose the numerically or physically larger of two Arabic numerals on different trials. This study did not find regions of the IPS that responded selectively for numerical judgments as opposed to size-based judgments. The results suggest a more general magnitude processing role for the IPS.
49. Nieder A, Freedman DJ, Miller EK. Representation of the quantity of visual items in the primate prefrontal cortex. *Science* 2002;297:1708–1711. [PubMed: 12215649]
- 50^{*}. Nieder A, Miller EK. A parieto-frontal network for visual numerical information in the monkey. *Proc Natl Acad Sci USA* 2004;101:7457–7462. [PubMed: 15123797]The authors reported number-selective cells in the fundus of the IPS, adding to their earlier seminal findings of number-selective cells in the prefrontal cortex.
51. Sawamura H, Shima K, Tanji J. Numerical representation for action in the parietal cortex of the monkey. *Nature* 2002;415:918–922. [PubMed: 11859371]
52. Culham JC, Valyear KF. Human parietal cortex in action. *Curr Opin Neurobiol* 2006;16this issue

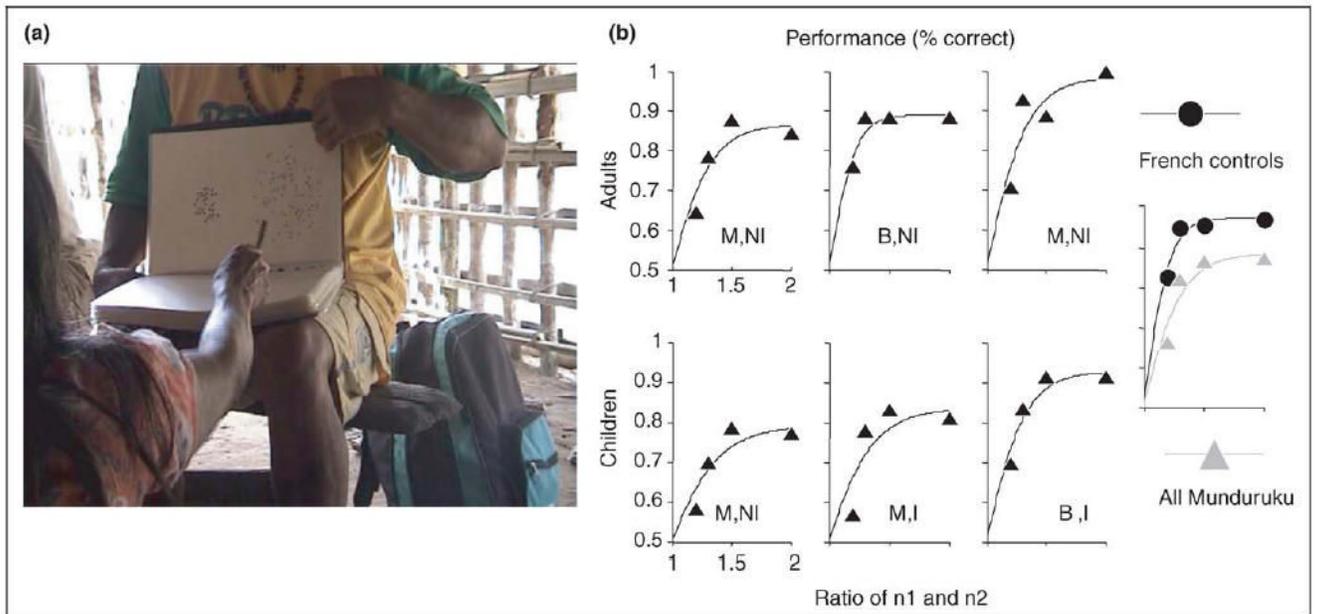


Figure 1. Number representation in societies without language for number. **(a)** A Mundurucu participant being tested in a numerical comparison task. **(b)** The fraction of correct choices as a function of the ratio of the two numerical values being compared (larger: smaller) for children and adults. Reproduced, with permission, from [2].

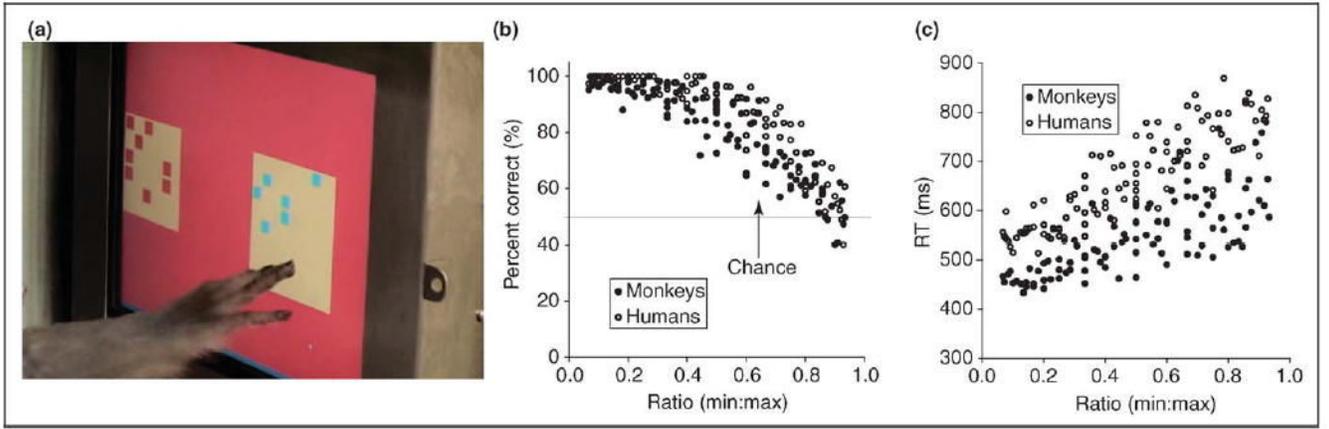


Figure 2. Monkeys and humans share a ratio dependent system for ordering numerosities. **(a)** A monkey choosing the numerically smaller of two visual arrays. Accuracy **(b)** and RT **(c)** in a numerical comparison task as a function of the ratio between the two numerical values (smaller: larger) for monkeys (black circles) and college students (white circles). Reproduced, with permission, from [15].

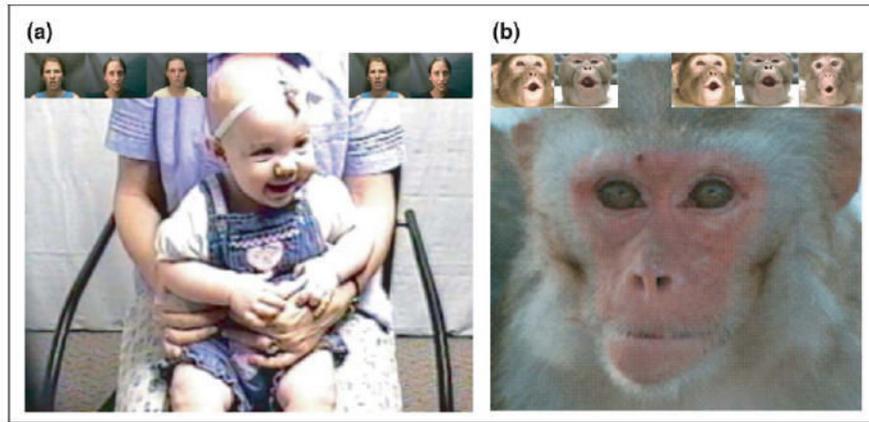


Figure 3. Monkeys and human infants match number across sensory modalities. (a) Image of a 7-month-old infant. Frames from the video images that infants were tested with are shown in the upper corners. (b) Image of a rhesus macaque. Frames from the video images that monkeys were tested with are shown in the upper corners. In both experiments individual human infants and monkeys heard a chorus of two or three conspecifics vocalizing. (Stimuli from Jordan et al. and Jordan and Brannon [15,36]).

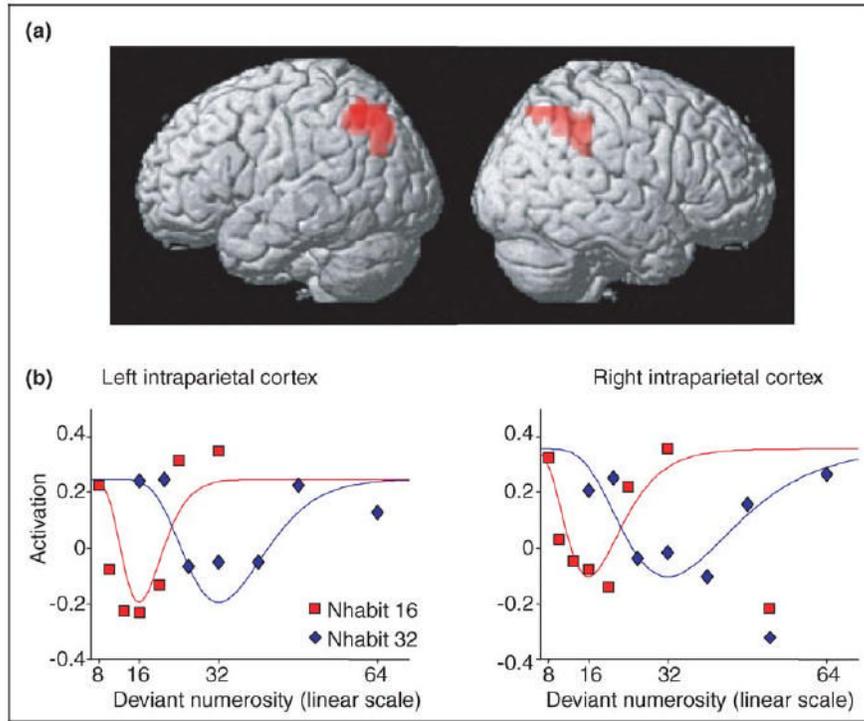


Figure 4. The IPS in adult humans shows ratio dependent response to changes in numerosity. **(a)** Brain regions in human adults that responded to a number change in a passive viewing event-related adaptation study. **(b)** Brain activation (percent change in BOLD signal relative to habituation stimuli) elicited to numerical values is systematically related to the degree to which novel value deviates from habituation value. Reproduced, with permission, from [46•].

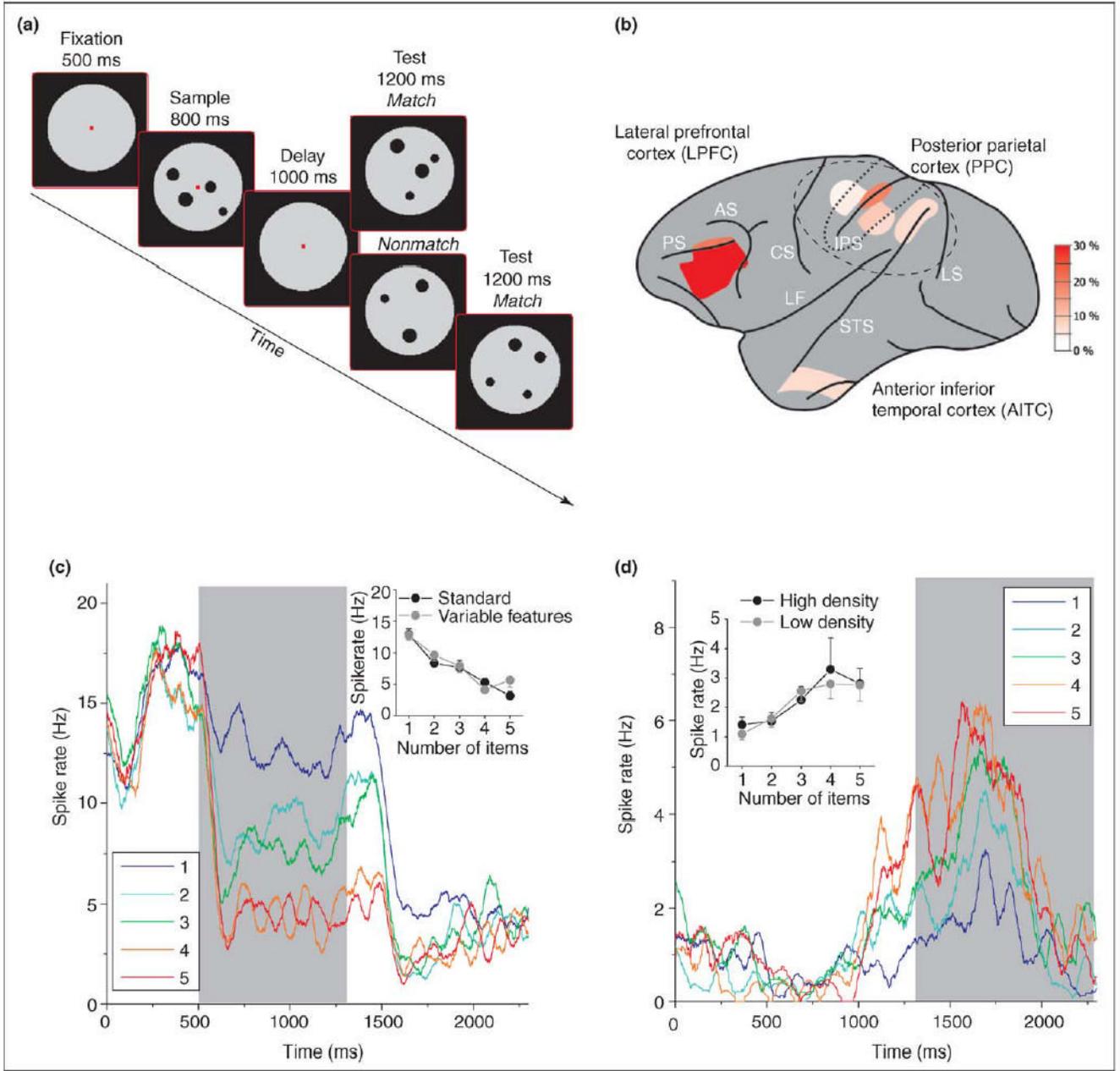


Figure 5. Number selective parietal cells in the monkey. **(a)** Task structure for monkeys tested in an electrophysiology study. Monkeys viewed sample array briefly, and after a short delay were required to indicate whether a second array matched or did not match the numerosity of the sample. **(b)** Lateral view of a monkey brain that illustrates recording sites and is color coded to reflect the relative proportion of number selective cells. **(c,d)** Firing rate as a function of sample numerosity during sample or delay interval for two distinct neurons selective for the numerosity 1 and 4 respectively. Reproduced, with permission, from [50]. Abbreviations: AS, arcuate sulcus; CS, central sulcus; LF, lateral fissure; LS, lunate sulcus; PS, principal sulcus; STS, superior temporal sulcus.